AQUATIC BOTANICAL STUDIES WITH SPECIAL REFERENCE TO THE RED ALGAL FAMILIES CORALLINACEAE AND ACROCHAETIACEAE

by

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This certifies that the material contained herein is the work of the author except where otherwise acknowledged.

TABLE OF CONTENTS

ABSTRACT

This thesis, which constitutes the submission of Dr. Wm. J. Woelkerling for the Degree of Doctor of Science in the University of Adelaide, includes an introductory statement and copies of 43 publications. In the introductory statement, the nature of the research covered in the thesis is outlined, especially with reference to two families of Rhodophyta (Corallinaceae & Acrochaetiaceae) on which extensive work has been published. Summaries of studies in three other areas (mangrove algal communities and seagrasses, other marine studies, freshwater studies) are followed by an annotated list of publications in which the role of the author in joint works is indicated and the two papers containing data submitted previously for a Ph.D. are noted. The enclosed publications are numbered sequentially in accordance with entries in the publications list.

INTRODUCTION

The publications upon which this thesis is based embrace several areas of aquatic botanical research, each of which is summarized in turn. The role of the author in joint papers is indicated after each relevant entry in the publications list which follows this introductory section.

Studies on the Corallinaceae

Since 1976, research interests of the author have centered on the nongeniculate Corallinaceae (Rhodophyta), and a long term research programme has been developed to help resolve a number of general problems related primarily to coralline systematics, and to produce a series of broad-based generic monographs of taxa occurring in southern Australia. Nongeniculate Corallinaceae are among the most distinctive and ecologically significant red algae, and although they are common and often dominant components of many marine benthic communities, most phycologists consider them to be among the most difficult and troublesome groups of Rhodophyta from the taxonomic standpoint.

To date, this programme of research has resulted in a number of publications which may be placed into seven categories. Bibliographic details are provided in the publications list, and copies of the published papers follow the list. The seven categories are:

1. Metamastophora and Mastophoropsis (Woelkerling 1978, 1980a, 1980b). These studies include a world revision of Metamastophora, the establishment of Mastophoropsis, the first use of numerical taxonomic techniques in monographic work on coralline algae, the first use of x-ray microanalysis to demonstrate variability of $CaCO_3$ deposition on the thallus surface, the first use of dark field microscopy to study sexual reproduction in corallines and one of the first uses of scanning electron microscopy to obtain

morphological and taxonomic data on nongeniculate corallines. In addition, detailed accounts of thallus ontogeny were presented, a new interpretation of tissue organization based on meristems was outlined and new data relating to the sexual cycle were presented.

2. Mastophora and Lithoporella (Turner & Woelkerling 1982a, 1982b). These studies, partly completed during the tenure of Honours Degree work of J. Turner, led to three significant discoveries: (a) thallus growth in these genera occurs from three distinct meristems and involves a unique type of vertical branching; (b) after fertilization, the transfer of diploid nuclei from the carpogonium to the auxiliary cell occurs through cells of the carpogonial branch; and (c) in each genus a distinct type of tetrasporangial development occurs which hitherto was unknown in the Corallinaceae. The actual transfer of zygotic nuclei was documented photographically for the first time in a taxon of nongeniculate Corallinaceae. In addition it was shown by means of x-ray microanalysis that Mastophora and Lithoporella could not be delineated on differences in the degree of thallus calcification, whereas attributes associated with the sexual cycle could be used for generic separation. The first detailed accounts of gametic reproduction in the type species of both genera were provided, and the naming and characterization of meristems in the Corallinaceae were considered in relation to data obtained during these studies.

3. Schmitziella (Woelkerling & Irvine 1982). This investigation led to the exclusion of the genus and the subfamily Schmitzielloideae from the Corallinaceae and the

incertae sedis placement of the genus near the Acrochaetiaceae. Important evidence obtained by scanning electron microscope studies of generitype specimens showed that conceptacles do not occur in the type species. A second species placed in the genus was found to be based on misidentified plants of *Melobesia*.

4. *Culture studies* (Woelkerling, Spencer & West 1983; Jones & Woelkerling 1983, 1984).

Joint work with K. Spencer and J. West led to the development of a new marine culture medium (MCM) which is chemically defined and which will support normal growth of coralline algae. During the course of these studies, it was found that 5 mM Ca^{2+}, 1 mM SO_2^{-2}, and 1 µM BO_3^{-3} were optimal concentrations for growth; these are far lower than the concentrations in natural seawater. Subsequent studies by Jones & Woelkerling, partly completed during the tenure of Honours Degree work of P.L. Jones, have been carried out on taxa of the *Pneophyllum* - *Fosliella* complex employing a modified enriched seawater culture medium. Based on factorial experiments involving a cross-gradient growth table, quantitative, statistically analysed data were provided on the effects of various combinations of light and temperature on thallus growth and conceptacle development. Similar types of experiments, combined with quantitative analyses of field populations have provided strong evidence that the presence or absence of trichocytes cannot be used to delineate genera within the complex but that trichocyte position in filaments and spore segmentation patterns (produced by germinating spores and usually evident in older plants) can, thus supporting the taxonomic proposals of Chamberlain (*Bull. Br. Mus. Nat. Hist., Bot.* 11, 1983).

5. Studies on generic concepts (Woelkerling 1983b, 1983c, 1985a, 1985b; Woelkerling, Chamberlain & Silva 1985).

These studies involve taxonomic reassessments of the type collections of taxa originally included in the genera Lithothamnium Philippi & Lithothamnion Heydrich (Woelkerling 1983b, 1985b), Lithophyllum Philippi (Woelkerling 1983c), Spongites Kützing & Neogoniolithon Setchell & Mason (Woelkerling 1985a), and Tenarea Bory, Titanoderma Nägeli & Dermatolithon Foslie (Woelkerling, Chamberlain & Silva 1985). Lithothamnium and Lithophyllum contain over half the described species of nongeniculate Corallinaceae. Evidence was provided during these studies that none of the species originally included in Lithothamnium Philippi conformed to any modern concept of the genus and led ultimately to proposing the conservation of Lithothamnion Heydrich against Lithothamnium Philippi. The concepts of all eight genera have been clarified and placed on a firm nomenclatural foundation as a result of the rediscovery and critical study of each of the generitype specimens. These studies emphasize the need to re-examine the relationships between modern concepts of all nongeniculate taxa (both genera and species) and the relevant type collections so that taxonomic concepts can be clarified properly. Work on a number of other genera is now in progress.

6. The works of M.H. Foslie (Woelkerling 1984).

M.H. Foslie described over 30% (474) of the known species of nongeniculate Corallinaceae, but his publications are fraught with inconsistencies, frequent changes of mind, and labyrinthic discussions of taxonomic relationships. The 1984 book contains

a detailed analysis of Foslie's publications and of his approach to species concepts. It also includes a complete index to all taxa mentioned in all Foslie coralline papers, and as such will facilitate a much needed re-evaluation of all the taxa described by Foslie.

7. Studies of coralline epiphytes (Bramwell & Woelkerling 1984; Harlin, Woelkerling & Walker 1985).

These represent the first quantitative studies of coralline epiphyte distribution on the leaves of a seagrass. The baseline study of Bramwell & Woelkerling found that significant differences occurred in epiphyte cover, density and relative fertility between hosts found in sublittoral and eulittoral environments and that distinct distribution patterns occur on the leaves. This study was extended in Harlin, Woelkerling & Walker to examine the effects of a natural hypersalinity gradient on these patterns, to determine the pattern of coralline community development on the leaves over time, and to assess whether characters used to separate species of these epiphytic corallines remain stable over a hypersalinity gradient. Both the community development work and the character assessment work were the first studies of their type involving epiphytic corallines.

My present research programme is directed almost entirely towards the nongeniculate Corallinaceae; it involves further studies of generic concepts, the production of a world monograph of nongeniculate genera, work on the role of coralline algae in sublittoral communities, and studies aimed at the production of a series of monographs of the southern Australian representatives of each genus. All of these studies

will break new ground in the sense that no studies of a similar sort have been published previously.

Studies on the Acrochaetiaceae

Monographs of the family have been published for southern Australia (Woelkerling 1971), the northeastern USA (Woelkerling 1973b) and the western Sargasso Sea (Woelkerling 1973a). Several studies of species complexes within the family also have emerged (Woelkerling 1970, 1972a). The acrochaetioid algae, like the coralline algae, are considered by many phycologists to be a taxonomically difficult group of Rhodophyta, and the classification proposals set forth in the southern Australian monograph (Woelkerling 1971) have stimulated research by a number of other investigators. Work during the period 1971-1981 provided the basis for an invited review paper (Woelkerling 1983a) in which a comprehensive analysis of the systematics of acrochaetioid algae was presented.

Mangrove Algal Community and Seagrass Studies

Four mangrove community studies (Beanland & Woelkerling 1982, 1983; Davey & Woelkerling 1980, 1985) have been carried out jointly with Honours students and provide the first detailed data on the composition and structure of mangrove algal communities in southern Australia. These communities include the most poleward occurrences of mangroves known, and the quantitative analyses of mangrove algal community structure represent the first studies of their type on mangrove algae anywhere.

The three seagrass studies (Bulthuis & Woelkerling 1981, 1983a, 1983b) are based on Ph.D. investigations carried out by Dr. Bulthuis; they represent three of the eight papers published as a result of these investigations. Dr. Bulthuis invited me to co-author these papers since

he felt that I had played a significant role in conceptualizing the work. My personal policy always has been to let post-graduate students publish their own work without supervisory co-authorship. In this case, however, Dr. Bulthuis specifically invited me to participate and provided compelling arguments in favour of joint authorship. The data presented in these papers are the first detailed studies of their type on Heterozostera and include an entirely new technique for accurately estimating epiphyte biomass on seagrass leaves.

Other Marine Studies

Of the six publications comprising this group, three (Woelkerling 1972b, 1973a, 1975a) deal with the macroscopic algal flora of the western Sargasso Sea. Together, these papers provide the first detailed account of the pelagic and epibiotic Chlorophyceae, Phaeophyceae and Rhodophyceae of the Sargasso Sea. Earlier records had been few and fragmentary, and 75% of the 62 species found have not been reported previously from the region. The remaining three publications include two manuals (Woelkerling 1975c, 1976a) and one book chapter (Kraft & Woelkerling 1981). The index (Woelkerling 1975c) to the papers of F.S. Collins was prepared to facilitate retrieval of data on the hundreds of species Collins dealt with and thus to facilitate systematic studies, particularly on the marine flora of the northeastern USA where Collins did much of his work. The field manual of Florida marine algae (Woelkerling 1976a) was published originally for use as a field guide in conjunction with a course on tropical marine algae. The manual includes the first comprehensive generic keys to the Chlorophyceae, Phaeophyceae and Rhodophyceae found in tropical North American waters. The book chapter (Kraft & Woelkerling 1981) deals with the Rhodophyta of the

Australian and New Zealand region and was prepared for a textbook on Australasian marine botany. This chapter is now being revised for the second edition of the book.

Freshwater Studies

Of the eight papers included in this category, six (Gough, Garvin & Woelkerling 1976; Gough & Woelkerling 1976a, 1976b; Woelkerling 1976b; Woelkerling & Gough 1976; Woelkerling, Kowal & Gough 1976) deal with desmid (Chlorphyceae) community structure in a range of bog and lake environments in relation to habitat and water chemistry. During these studies, the reliability of Sedgwick-Rafter cells for use in obtaining cell density data was critically reviewed and methods for quantifying epiphytic desmids and for observing field populations of desmids in the scanning electron microscope were developed. The remaining two studies (Woelkerling 1975b, Woelkerling & Baxter 1968) deal respectively with the ecology of the freshwater red alga Batrachospermum and with the ecology and distribution of certain aquatic hyphomycetes (fungi) in Wisconsin.

PUBLICATIONS LIST

Major papers are indicated with an asterisk (*); enclosed copies of publications are numbered in accordance with this list.

1968

1. Woelkerling, W.J. & Baxter, J.W. 1968. Aquatic hyphomycetes of Wisconsin: Distribution and ecology. Mycopath. Mycol. appl. 35: 33-36.

   WJW planned the study, collected the data, and helped to analyse the data and write the paper.

1970

2.* Woelkerling, W.J. 1970. Acrochaetium botryocarpum (Harv.)J.Ag. (Rhodophyta) in southern Australia. Br. phycol. J. 5:159-171.

Data in this paper formed part of a Ph.D. thesis completed at the University of Adelaide.

1971

3.* Woelkerling, W.J. 1971. Morphology and taxonomy of the Audouinella complex (Rhodophyta) in southern Australia. Aust. J. Bot., Suppl. Ser. 1:1-91.

Data in this paper formed part of a Ph.D. thesis completed at the University of Adelaide.

1972

4.* Woelkerling, W.J. 1972a. Studies on the Audouinella microscopica (Naeg.)Woelk. complex (Rhodophyta). Rhodora 74:85-96.

5. Woelkerling, W.J. 1972b. Some algal invaders of the northwestern fringes of the Sargasso Sea. Rhodora 74:295-298.

1973

6.* Woelkerling, W.J. 1973a. The Audouinella complex (Rhodophyta) in the western Sargasso Sea. Rhodora 75:78-101.

7.* Woelkerling, W.J. 1973b. The morphology and systematics of the Audouinella complex (Acrochaetiaceae, Rhodophyta) in northeastern United States. Rhodora 75:529-621.

1974

8.* Woelkerling, W.J. 1975a. On the epibiotic and pelagic Chlorophyceae, Phaeophyceae and Rhodophyceae of the western Sargasso Sea. Rhodora 77:1-40.

9. Woelkerling, W.J. 1975b. Observations on Batrachospermum (Rhodophyta) in southeastern Wisconsin streams. Rhodora 77:467-477.

10.* Woelkerling, W.J. 1975c. A Species Index (Including Subspecific

Taxa) to the Algal Publications of Frank Shipley Collins. 92pp. Madison, Wisconsin (Privately published).

1976

11. Gough, S.B., Garvin, T. & Woelkerling, W.J. 1976. Processing field and culture samples of desmids (Desmidiales, Chlorophyta) for scanning electron microscopy. Br. phycol. J. 11: 245-250.

WJW participated equally with other authors in planning the study & in data collection and wrote the paper.

12.* Gough, S.B. & Woelkerling, W.J. 1976a. Wisconsin desmids. II. Aufwuchs and plankton communities of selected hard water lakes, soft water lakes and calcareous spring ponds. Hydrobiologia 49:3-25.

WJW helped plan the study, collected and analysed some of the data and wrote the paper.

13. Gough, S.B. & Woelkerling, W.J. 1976b. On the removal and quantification of algal aufwuchs from macrophyte hosts. Hydrobiologia 48:203-207.

WJW helped plan the study, collected and analysed some of the data and wrote the paper.

14.* Woelkerling, W.J. 1976a. South Florida Benthic Marine Algae: Keys and Comments. Sedimenta V:1-148. (Published by the Comparative Sedimentology Laboratory, Rosenstiel School of Marine and Atmospheric Science, University of Miami).

15.* Woelkerling, W.J. 1976b. Wisconsin desmids. I. Aufwuchs and plankton communities of selected acid bogs, alkaline bogs and closed bogs. Hydrobiologia 49: 209-232.

16.* Woelkerling, W.J. & Gough, S.B. 1976. Wisconsin desmids. III. Desmid community composition and distribution in relation to lake type and water chemistry. Hydrobiologia 51: 3-32.

WJW planned the study, collected most of the data, did all of the analyses and wrote the paper.

17.* Woelkerling, W.J., Kowal, R.R. & Gough, S.B. 1976. Sedgwick-Rafter cell counts: A procedural analysis. Hydrobiologia 48: 95-107.

WJW planned the study, collected and analysed some of the data and wrote most of the paper.

1978

18.* Woelkerling, W.J. 1978. Mastophoropsis canaliculata (Harvey in Hooker)gen. et comb.nov. (Corallinaceae, Rhodophyta) in southern Australia. Br. phycol. J. 13:209-225.

1980

19.* Davey, A. & Woelkerling, W.J. 1980. Studies on Australian mangrove algae. I. Victorian communities: composition and geographic distribution. Proc. R. Soc. Vict. 91: 53-66.

WJW helped plan the study, assisted with data collection and analysis and wrote the final paper.

20.* Woelkerling, W.J. 1980a. Studies on Metamastophora (Corallinaceae, Rhodophyta). M. flabellata (Sonder)Setchell: Morphology and anatomy. Br. phycol. J. 15:201-225.

21.* Woelkerling, W.J. 1980b. Studies on Metamastophora (Corallinaceae, Rhodophyta). II. Systematics and distribution. Br. phycol. J. 15: 227-245.

1981

22.* Bulthuis, D.A. & Woelkerling, W.J. 1981. Effects of in situ nitrogen and phosphorous enrichment of the sediments on the seagrass Heterozostera tasmanica (Martens ex Aschers.)den Hartog in Western Port, Victoria, Australia. J. exp. mar. Biol. Ecol. 53:193-207.

WJW helped plan the study and helped write the final paper.

23.* Kraft, G.T. & Woelkerling, W.J. 1981. Rhodophyta - systematics and biology. In: Marine Botany: An Australasian Perspective, ed. by M.N. Clayton & R.J. King, pp. 61-103. Longman Cheshire, Melbourne.

Equal participation of both authors occurred in the preparation of this book chapter.

1982

24.* Beanland, W.R. & Woelkerling, W.J. 1982. Studies on Australian mangrove algae II. Composition and geographic distribution of communities in Spencer Gulf, South Australia. Proc. R. Soc. Vict. 94: 89-106.

WJW helped plan the study and analyse the data and wrote the final paper.

25.* Turner, J.A. & Woelkerling, W.J. 1982a. Studies on the Mastophora-Lithoporella complex (Corallinaceae, Rhodophyta). I. Meristems and thallus structure and development. Phycologia 21:201-217.

WJW helped plan the study, collected some data, assisted in data analysis and wrote the final paper.

26.* Turner, J.A. & Woelkerling, W.J. 1982b. Studies on the Mastophora-Lithoporella complex (Corallinaceae, Rhodophyta). II. Reproduction and generic concepts. Phycologia 21: 218-235.

WJW helped plan the study, collected some data, assisted in data analysis and wrote the final paper.

27.* Woelkerling, W.J. & Irvine, L.M. 1982. The genus Schmitziella Bornet & Batters (Rhodophyta): Corallinaceae or Acrochaetiaceae? Br. phycol. J. 17:275-295.

WJW planned the study, collected and analysed most of the data and wrote the paper.

1983

28. Beanland, W.R. & Woelkerling, W.J. 1983. Avicennia canopy effects on mangrove algal communities in Spencer Gulf, South Australia. Aquatic Bot. 17: 309-313.

WJW helped plan the study and analyse the data and wrote the paper.

29.* Bulthuis, D.A. & Woelkerling, W.J. 1983a. Seasonal variation in standing crop, density, and leaf growth rate of the seagrass Heterozostera tasmanica in Western Port and Port Phillip Bay, Victoria, Australia. Aquatic Bot. 16: 111-136.

WJW helped plan the study and helped write the final paper.

30.* Bulthuis, D.A. & Woelkerling, W.J. 1983b. Biomass accumulation and shading effects of epiphytes on leaves of the seagrass Heterozostera tasmanica in Victoria, Australia. Aquatic Bot. 16: 137-148.

WJW helped plan the study and helped write the final paper.

31. Jones, P.L. & Woelkerling, W.J. 1983. Some effects of light and temperature on growth and conceptacle production in Fosliella cruciata Bressan (Corallinaceae, Rhodophyta). Phycologia 22: 449-452.

WJW helped plan the study and analyse the data, and wrote the final paper.

32.* Woelkerling, W.J. 1983a. The Audouinella (Acrochaetium - Rhodochorton) complex (Rhodophyta): Present perspectives. Phycologia 22: 59-92. (Phycological Reviews 8).

33.* Woelkerling, W.J. 1983b. A taxonomic reassessment of Lithothamnium (Corallinaceae, Rhodophyta) based on studies of R.A. Philippi's original collections. Br. phycol. J. 18: 165-197.

34.* Woelkerling, W.J. 1983c. A taxonomic reassessment of Lithophyllum (Corallinaceae, Rhodophyta) based on studies of R.A. Philippi's original collections. Br. phycol. J. 18: 299-327.

35.* Woelkerling, W.J., Spencer, K.G. & West, J.A. 1983. Studies on selected Corallinaceae (Rhodophyta) and other algae in a defined marine culture medium. J. exp. mar. Biol. Ecol. 67: 61-77.

WJW planned the study, collected and analysed most of the data and wrote the paper.

1984

36. Bramwell, M.D. & Woelkerling, W.J. 1984. Studies on the distribution of Pneophyllum - Fosliella plants (Corallinaceae, Rhodophyta) on leaves of the seagrass Amphibolis antarctica (Cymodoceaceae). Aust. J. Bot. 32: 131-137.

WJW helped plan the paper and analyse the data, and wrote the final paper.

37.* Jones, P.L. & Woelkerling, W.J. 1984. An analysis of trichocyte and spore germination attributes as taxonomic characters in the Pneophyllum - Fosliella complex (Corallinaceae, Rhodophyta). Phycologia 23: 183-194.

WJW helped plan the study and analyse the data, and wrote the final paper.

38.* Woelkerling, W.J. 1984. M.H. Foslie and the Corallinaceae: An Analysis and Indexes. J. Cramer, Vaduz. 142 pp. (Bibliotheca Phycologica Vol. 69).

1985

39.* Davey, A. & Woelkerling, W.J. 1985. Studies on Australian mangrove algae. III. Victorian communities: Structure and recolonization in Western Port bay. J. exp. mar. Biol. Ecol. 85: 177-190.

WJW helped plan the study, assisted with data collection and helped write early drafts of the paper; the final draft was written by the senior author.

40.* Harlin, M.M., Woelkerling, W.J. & Walker, D.I. 1985. Effects of a hypersalinity gradient on epiphytic Corallinaceae (Rhodophyta) in Shark Bay, Western Australia. Phycologia 24: 389-402.

WJW and MMH participated equally in planning the study, in data analysis and in writing the final paper.

41.* Woelkerling, W.J. 1985a. A taxonomic reassessment of Spongites (Corallinaceae, Rhodophyta) based on studies of Kützing's original collections. Br. phycol. J. 20: 123-153.

42. Woelkerling, W.J. 1985b. Proposal to conserve Lithothamnion against Lithothamnium (Rhodophyta: Corallinaceae). Taxon 34: 302-303.

43.* Woelkerling, W.J., Chamberlain, Y.M. & Silva, P.C. 1985. A taxonomic and nomenclatural reassessment of Tenarea, Titanoderma and Dermatolithon (Corallinaceae, Rhodophyta) based on studies of type and other critical specimens. Phycologia 24: 317-337.

WJW planned the study, collected and analysed most of the data and helped write the paper.

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MYCOPATHOLOGIA

ET

MYCOLOGIA APPLICATA

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AQUATIC HYPHOMYCETES OF WISCONSIN: DISTRIBUTION AND ECOLOGY

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AQUATIC HYPHOMYCETES OF WISCONSIN: DISTRIBUTION AND ECOLOGY

by

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(29.IV.1966)

INTRODUCTION

This paper summarizes the results of a preliminary study of the distribution and ecology of the aquatic hyphomycetes of Wisconsin. Previous distribution surveys of this group in the United States have been made in California by RANZONI (1953), in Wyoming, Indiana and Oregon by BAXTER (1960, 1962, 1964); and in the northeastern and southeastern United States by PETERSEN (1962, 1963) and UMPHLETT (1957). No extensive ecological study of the aquatic hyphomycetes has been made in the United States. Our knowledge of the ecology of this group is based primarily on recent studies conducted in Europe and Japan. DUDKA (1964) found a correlation between the amount of dissolved oxygen and the abundance of these fungi. SUZUKI & NIMURA (1960) investigated the effect of pH on the aquatic hyphomycete population in Japanese lakes. MARVANOVA & MARVAN (1963) studied the occurrence and relative abundance of certain species in different types of streams.

METHODS

Samples of decaying angiosperm leaves were collected from 62 streams and lakes in all parts of the state and brought into the laboratory for examination. The material was placed in covered petri dishes partially filled with demineralized water and allowed to stand for 5 to 7 days. Sporulation had usually occurred by the end of this period and the species present were then identified.

At selected stations the water was analyzed chemically for alkalinity, carbon dioxide, hardness, nitrates, nitrites, dissolved oxygen and pH. The direct reading engineer's laboratory, model DREL (Hach Chemical Co.), was used for these determinations. Field notes on the rate of stream flow, water temperature and nature of the bottom were also taken at most stations.

Results

Eighteen species in fourteen genera were encountered during the course of this study (Table I). No clear pattern of geographic distribution was discernible. In tabulating the distribution data the collection records were divided into two groups-northern and southern-roughly corresponding to the distribution of the boreal and deci-

Table I

List of aquatic hyphomycetes collected in Wisconsin

Species	No. of collections	Remarks
Alatospora acuminata Ing.	5	
Anguillospora crassa Ing.	2	
A. longissima (Sacc. & Syd.) Ing.	16	Occurred in 26 % of the collections.
A. pseudolongissima Ranzoni.	2	
Articulospora tetracladia Ing.	2	
Clavariopsis aquatica DeWild.	5	
Culicidospora gravida Petersen.	1	
Dendospora erecta Ing.	1	
Flagellospora penicillioides Ing.	1	
Lemonniera aquatica DeWild.	27	Occurred in 45 % of the collections.
Lunulospora curvula Ing.	3	
Tetrachaetum elegans Ing.	15	Occurred in 25 % of the collections
Tetracladium marchalianum DeWild.	21	Occurred in 36 % of the collections.
T. setigerum (Grove) Ing.	4	
Tricelophores monosporus Ing.	4	
Tricladium angulatum Ing.	2	
T. gracile Ing.	11	Occurred in 18 % of the collections.
Varicosporium elodeae Kegel.	1	

duous forest elements in the state. *Lemonniera aquatica, Tetrachaetum elegans* and *Tricladium gracile* appeared in a significantly greater number of samples taken from northern Wisconsin than in samples taken from the southern half of the state. The distribution of *Anguillospora longissima* and *Tetracladium marchalianum* was roughly equal in both areas.

Collection sites varied greatly in their physical and chemical characteristics. Samples were obtained from stagnant waters as well as from swiftly flowing streams. The habitats had bottoms that ranged from extremely silty to rocky. Cold, cool, and fairly warm waters were encountered. Oxygen values from 1.7 ppm to 12.1 ppm were recorded. Carbon dioxide levels ranged from 12 to 124 ppm, while the nitrogen content ranged from .05 ppm to 2.3 ppm. Total hardness varied almost 150 % (160 ppm to 385 ppm) and alkalinity

showed over 300 % variation (120 ppm to 370 ppm). Hydrogen ion concentration varied from 8.25 to 8.7.

Generally speaking, a greater variety of species and more luxuriant growth were found in moderately swift to swift waters than in slow-moving or stagnant waters. This was in agreement with the findings of other investigators. *Tetracladium marchalianum* and *Tricladium gracile* preferred swift currents. All of the most frequently found species occurred in all of the habitat types. As many as four species were recorded from a single stagnant water station and in one case a location with a moderately swift current yielded no aquatic hyphomycetes.

No correlation between abundance of aquatic hyphomycetes and type of stream bottom could be detected; species were equally abundant in silty, sandy and rocky locations. Furthermore, species occurred with equal frequency in cold, cool and fairly warm waters. Only *Anguillospora longissima,* among the common species, was not found in warmer waters; DUDKA (1964) reports, however, that it is one of the few species present throughout the summer in Ukrainian streams.

No clear relation of dissolved oxygen level to the abundance of aquatic hyphomycetes was noted in the present study, in contrast to the results reported by DUDKA. Among the commonly encountered species, only *Tetrachaetum elegans* seemed to prefer well oxygenated waters. *Anguillospora longissima, Lemonniera aquatica, Tetracladium marchalianum* and *Tricladium gracile* all proved indifferent to the oxygen regime; this generally agreed with DUDKA'S findings. *Lunulospora curvula* and *Tricelophorus monosporus* were present in water containing less than 4 ppm of dissolved oxygen.

The greatest variety of species and most abundant growth of individual species occurred on leaves collected from waters with low carbon dioxide levels (less than 50 ppm). Differences in carbon dioxide level appeared to have no effect on the frequency and abundance of *Lemonniera aquatica. Lunulospora curvula* was found at stations with carbon dioxide readings as high as 110 ppm.

The range in pH was comparatively narrow (8.25 to 8.7), and no definite preferences were discernible. It is interesting to note, however, that 18 species were found growing in this pH range whereas SUZUKI & NIMURA (1960) found only nine species at pH 6.2—6.5 and only five species at pH 3.8—5.8.

Nitrogen levels (nitrates plus nitrites) did not seem to have any marked effect on the occurrence and abundance of the aquatic hyphomycetes collected during the course of this study. *Lemonniera aquatica* tended to be found more often in waters comparatively rich in nitrogen.

Total hardness appeared to have a limiting effect on development of these fungi at levels in excess of 250 ppm. Only three species – *Lemonniera aquatica, Lunulospora curvula* and *Tetrachaetum elegans* – were found in waters with total hardness values higher

than this level. High alkalinity levels also showed a limiting effect. Only *Lemonniera aquatica* and *Lunulospora curvula* were present in waters registering alkalinity readings over 250 ppm.

Summary

1. Eighteen species in fourteen genera of aquatic hyphomycetes were found in a survey of Wisconsin streams and lakes. No clear pattern of geographic distribution was evident but several species were more frequently encountered in northern areas.

2. Moderate to swift currents were found to support the most abundant growth and greatest variety of species. Type of bottom and relative water temperature showed no detectable effect.

3. Most of the commonly-occurring species were indifferent to the oxygen regime. Nitrogen levels did not appear to affect the abundance of these fungi and no pH preference was discernible throughout the relatively narrow range that was recorded.

4. Carbon dioxide level and abundance of aquatic hyphomycetes varied inversely. Total hardness and total alkalinity appeared to have a limiting effect at concentrations in excess of 250 ppm.

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ACROCHAETIUM BOTRYOCARPUM (HARV.) J. AG. (RHODOPHYTA) IN SOUTHERN AUSTRALIA

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The morphology, ecology, cytology and systematics of *Acrochaetium botryocarpum* (Harv.) J. Ag. have been studied. This species occurs throughout the year in southern Australia and grows on a variety of hosts. The variable appearance of the prostrate system results from the effect of the substratum upon its morphology. Plants reach a height of 6 mm; cells of the erect filaments contain a single chromoplast with a variable number of pyrenoids. Tetrasporangial plants occur mainly in winter and sexual plants occur mainly in spring and early summer; the two generations are isomorphic. Stages of fertilisation have been observed and photographed. *Acrochaetium polyrhizum* (Harv.) J. Ag. is referred to the synonomy of *A. botryocarpum*, and *A. codicolum* Brg., *A. grande* (Levr.) De Toni fil. and *A. rhizoideum* (Drew) Sm. are regarded as probable synonyms. This study of *A. botryocarpum* indicates that host specificity, substrate relations, form of spermatangia and immediate post-fertilisation activity may not be as reliable as formerly thought for making taxonomic distinctions within the *Acrochaetium-Rhodochorton* complex.

The *Acrochaetium-Rhodochorton* complex (Rhodophyta) contains over 280 described taxa of which fewer than 15% are known to reproduce sexually. The lack of detailed ecological and morphological information for nearly all species and the frequent establishment of new taxa based on inadequate material are in part responsible for the widespread uncertainty and disagreement concerning which criteria are the most reliable indicators of taxonomic limits within the complex (e.g. compare the systematic proposals of Drew, 1928; Papenfuss, 1945, 1947; Kylin, 1956; and Feldmann, 1962). Furthermore, the complete life history is definitely known for only a few species of Acrochaetiaceae (Rosenvinge, 1909; Drew, 1935; Swale and Belcher, 1963; West, 1968, 1969). These taxa appear to be diplobiontic and exhibit either an isomorphic or heteromorphic alternation of haploid sexual and diploid tetrasporophyte generations. The long assumed occurrence of haplobionty (Svedelius, 1915, p. 49; Fritsch, 1945, p. 625; Kylin, 1956, p. 86) within the complex, however, has not been ruled out. Cytologically, acrochaetioid algae remain very poorly known except for the reports of Knaggs (1964), Magne (1964) and West (1969).

During the course of studies on the southern Australian members of this complex, large populations of *Acrochaetium botryocarpum* (Harv.) J. Ag. were encountered frequently, thus presenting an opportunity to help clarify some of the problems surrounding this species in particular and the *Acrochaetium-Rhodochorton* complex in general. Harvey (1854) recorded both sexual and tetrasporic plants, thus suggesting that *A. botryocarpum* was diplobiontic. Subsequent publications (Bornet, 1904; Hamel, 1927; May, 1947), however, reported an absence of tetrasporic plants in Harvey's material. These investigators concluded that Harvey was mistaken and that *A. botryocarpum* was, in reality, a haplobiontic organism. Levring (1953) recently provided a brief morphological account of this species but left a number of points to be clarified.

The aims of the present investigation on *A. botryocarpum* have been (1) to determine within this species the extent of variation which can occur in various morphological criteria employed in making taxonomic distinctions in the *Acrochaetium-Rhodochorton* complex, (2) to study details of its life history, (3) to investigate several aspects of its cytology, and (4) to clarify its taxonomic limits.

MATERIALS AND METHODS

Morphological investigations have been carried out as far as possible on living material or on liquid collections originally preserved in approximately 1:10 formalin in seawater and in most cases subsequently transferred to 19:1 70% ethanol and glycerin. Preserved material was stained in 2% aqueous fast green FCF for 10 min to 15 h, destained where necessary in distilled water, and mounted on slides in 20% aqueous Karo (Johansen, 1940, p. 24) with 2% phenol added to prevent fungal growth. Dried herbarium specimens, even over a century old, responded very well to soaking in 10% aqueous sodium carbonate for 30–60 min and were then stained in the same manner as liquid preserved material. Specimens from all collections made by the author have been deposited in the University of Adelaide Herbarium (ADU) along with a representative set of slides. Line drawings have been made with the aid of a Leitz drawing head microscope attachment.

Material for cytological investigation was fixed for 12–24 h in a modified Karpechenko solution (Papenfuss, 1946) made up with distilled water, rinsed in tap water for 30–60 min and, in cases where storage was necessary, taken up a graded ethanol series for storage in 70% ethanol at 0–4° C until used. Material was stained by a modified schedule of Smith (1934), as follows:

1. For material stored in 70% ethanol, hydrate for 2 min each in 50% and 30% ethanol and then transfer to distilled water; for material in the fixative, wash for 30–60 min in running tap water and then transfer to distilled water.
2. Place a small amount of material in a drop of distilled water on a slide, separate filaments and add coverslip.
3. Wrap slide in a piece of facial tissue, place in slide press and squash.
4. Remove tissue and place slide, coverslip side up, on a block of dry ice for several minutes.
5. With a scalpel blade, lever off the coverslip. Immediately place slide in absolute ethanol for 2 min.
6. Transfer slide to 90% ethanol for 2 min.
7. Transfer to iodine solution (Smith, 1934) for 15 min.
8. Rinse in 2 changes of distilled water to remove excess iodine mordant.
9. Stain in crystal violet solution (Smith, 1934) for 15 min.
10. Rinse in 2 changes of distilled water to remove excess stain.
11. Again place in iodine solution for 3 min.
12. Rinse in 95% ethanol to remove excess mordant.
13. Dip in picric acid solution (Smith, 1934) for 1 s.
14. Immediately wash in absolute ethanol for a few seconds.
15. Immerse in clove oil until stain ceases to come out of preparation (about 10–30 min).
16. Wash in 2 changes of xylol to remove excess clove oil and then immerse in 2 further changes of xylol for 30 min each.
17. Drain off excess xylol; mount in euparal.

A small press was used to squash preparations to ensure even and intense pressure without moving the material. Freezing the squashed preparations with dry ice allows for easy subsequent removal of the coverslip and dehydration without damage to the preparation. Because of very resistant cell walls, it has been very difficult to squash preparations flat enough for photographic purposes. Enzymatic hydrolysis in 10% pectinase at 27–28° C for 3 h prior to squashing helped soften tissues to a limited extent, but acid hydrolysis in 1N HCl or basic hydrolysis in 1N Na_2CO_3 (Magne, 1964) for various times (1–20 min) and at various temperatures (20–60° C) yielded inferior or unusable preparations.

Other staining methods have been tried without success. The Feulgen technique, although tried on numerous preparations, gave only one slide in which even faint staining resulted. Dixon (1966, p. 174) and West (1968, p. 92) reported similar results, but Magne (1964) and Westbrook (1935) used the method successfully on Rhodophyta. Additional methods which failed to give usable preparations include staining with acetocarmine (Austin, 1959; Cole, 1963), aceto-orcein, brazilin (Dixon, 1966) and toluidine blue after fixation in a variety of solutions.

MORPHOLOGY AND ECOLOGY

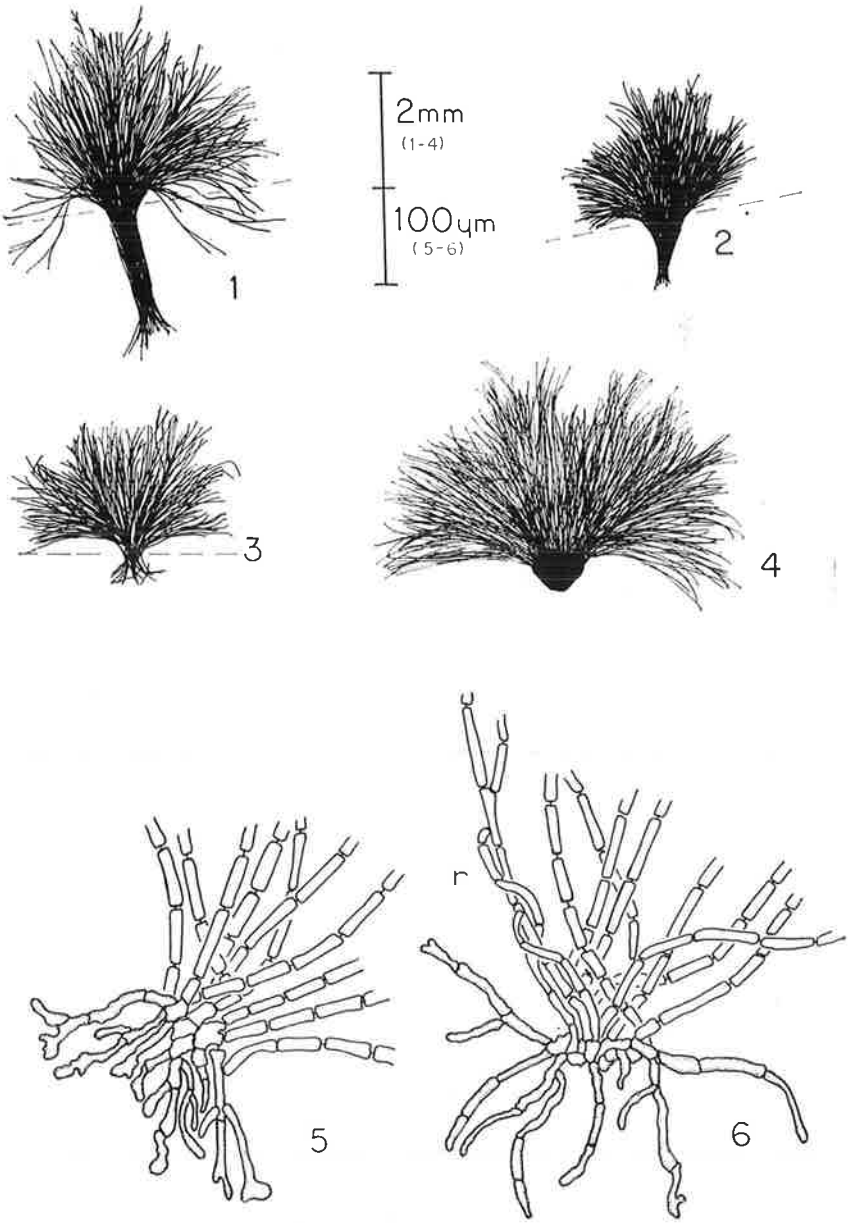
Acrochaetium botryocarpum occurs throughout the year in southern Australia and is found mainly in the lower littoral and upper sublittoral regions. Dense populations of sexual and/or sporangial plants frequently develop, including mixed populations of sexual and tetrasporangial individuals of identical morphology. Plants occur on a variety of Phaeophyta (*Chordaria*, *Cystophora*, *Dictyopteris*, *Ecklonia*, *Petalonia*, *Polycerea*, *Sargassum* and *Scytosiphon*) as well as on *Codium* (Chlorophyta), *Nemalion* (Rhodophyta), *Cymodocea* (Angiospermae) and on rock. Previously (Levring, 1953, pp. 472, 484; Papenfuss, 1945, p. 313), this species was thought to be confined to a single host, *Scytosiphon lomentaria* (Lyngb.) J. Ag., and plants on *Codium* were referred to a distinct species, *Acrochaetium polyrhizum* (Harv.) J. Ag. (As noted below, *A. polyrhizum* is here regarded as a synonym of *A. botryocarpum*; this discussion therefore covers plants hitherto referred to both species.)

Individual plants can reach a height of 6 mm or more, and while they are basically heterotrichous, the prostrate system can vary considerably in appearance and in orientation to the substratum (Figs. 1–4). This variation results from the effect of the substratum upon the form of the prostrate system and is evident in plants collected in one locality on different substrates. On hosts of loose, open construction (e.g. *Codium*, *Nemalion*), the prostrate system usually consists of an extensive, more or less funiform, mass of endophytic filaments (Figs. 1, 2) while on nearby hosts of somewhat firmer construction (e.g. *Chordaria*, *Scytosiphon*) the prostrate system is composed of a few short filaments which barely penetrate the host surface (Fig. 5). Occasionally, the prostrate filaments are supplemented by descending corticating rhizoids (Fig. 6) which assist in anchorage and support. Hosts of very firm construction (e.g. *Cymodocea*) and rock do not permit penetration, and the prostrate system takes the form of a pseudoparenchymatous disc (Fig. 4). The single filament prostrate system illustrated by Hamel (1927, Fig. 42) and the several-celled prostrate system illustrated by Levring (1953, Fig. 19B) were not observed.

Regardless of the construction of the prostrate system, the erect system of all these plants is of similar morphology. Filaments develop monopodially by means of transverse divisions of apical cells and are freely and irregularly branched. Filaments occasionally terminate abruptly in multicellular hair-like prolongations, or they may gradually taper towards the tips. Unicellular hairs are unknown.

Cells of the main axis are (10–) 15–20 (–30) μm in diameter and 30–120 μm long but can taper to 6–15 μm wide in the laterals and are usually 3–6 μm wide in the hair-like prolongations. Cells 1–6 diameters long occur in the lower portions of main axes in all plants, but in some individuals most cells tend to be 1–2 diameters long while in others they are mostly 2–6 diameters long. Cribb (1956) made similar observations. Occasionally, cells of the hair-like prolongations reach a length of over 20 diameters; these frequently break off giving the laterals a stubby appearance.

A single lobate plastid containing (1–) 2–6 (–18) pyrenoids is present in cells of the erect filaments (Fig. 15); shorter cells generally contain fewer pyrenoids. Plastids are often only weakly developed and lack pyrenoids in cells of the hair-



FIGS. 1–4. Habit of single plants of *A. botryocarpum* on different substrates; dotted line indicates level of host surface Fig. 1. On *Codium pomoides* J. Ag. (Guichen Bay, S. Australia, *Womersley*, ADU, A29268). Fig. 2. On *Nemalion helminthoides* (Vell. in With.) Batt. (Pt Elliot, S. Australia, *Woelkerling*, ADU, A32847). Fig. 3. On *Codium fragile* (Sur.) Hariot (Robe, S. Australia, *Woelkerling*, ADU, A32310). Fig. 4. On *Cymodocea antarctica* Endlicher (Pt Elliot, S. Australia, *Woelkerling*, ADU, A32237). FIGS. 5, 6. Prostrate system (shaded portion) of *A. botryocarpum* plants removed from different substrates. Fig. 5. Plant removed from *Chordaria* (Pt Lonsdale, Victoria, *Woelkerling*, ADU, A30886). Fig. 6. Plant removed from *Polycerea*; note descending rhizoidal filaments (r) (Wedge Bay, Tasmania, *Wallaston and Mitchell*, ADU, A27681).

like prolongations and prostrate filaments and occasionally become fragmented into several portions in the latter.

Young plants, similar to the wild plants described above, developed in culture from monospores, carpospores and tetraspores of wild plants, but cultured individuals never became reproductive.

Nuclei were not observed in unstained preparations even under phase contrast, but stained preparations clearly revealed a single nucleus per cell. Nucleoli were not definitely observed.

Both asexual and sexual reproductive organs are borne on the erect system. Monosporangia constitute the main mode of reproduction and are present throughout the year. Formation of a monosporangium begins with a densely cytoplasmic protuberance which arises near the distal end of a cell, enlarges, and is eventually cut off (Figs. 7–9). The new cell either develops directly into a sporangium or becomes a stalk cell which eventually produces one or more monosporangia by further divisions. Sometimes several monosporangia form successively within old sporangial walls by repeated divisions of one stalk cell (Figs. 10, 11). Boney (1967), Levring (1935) and Rosenvinge (1909) have made similar observations in other members of the complex.

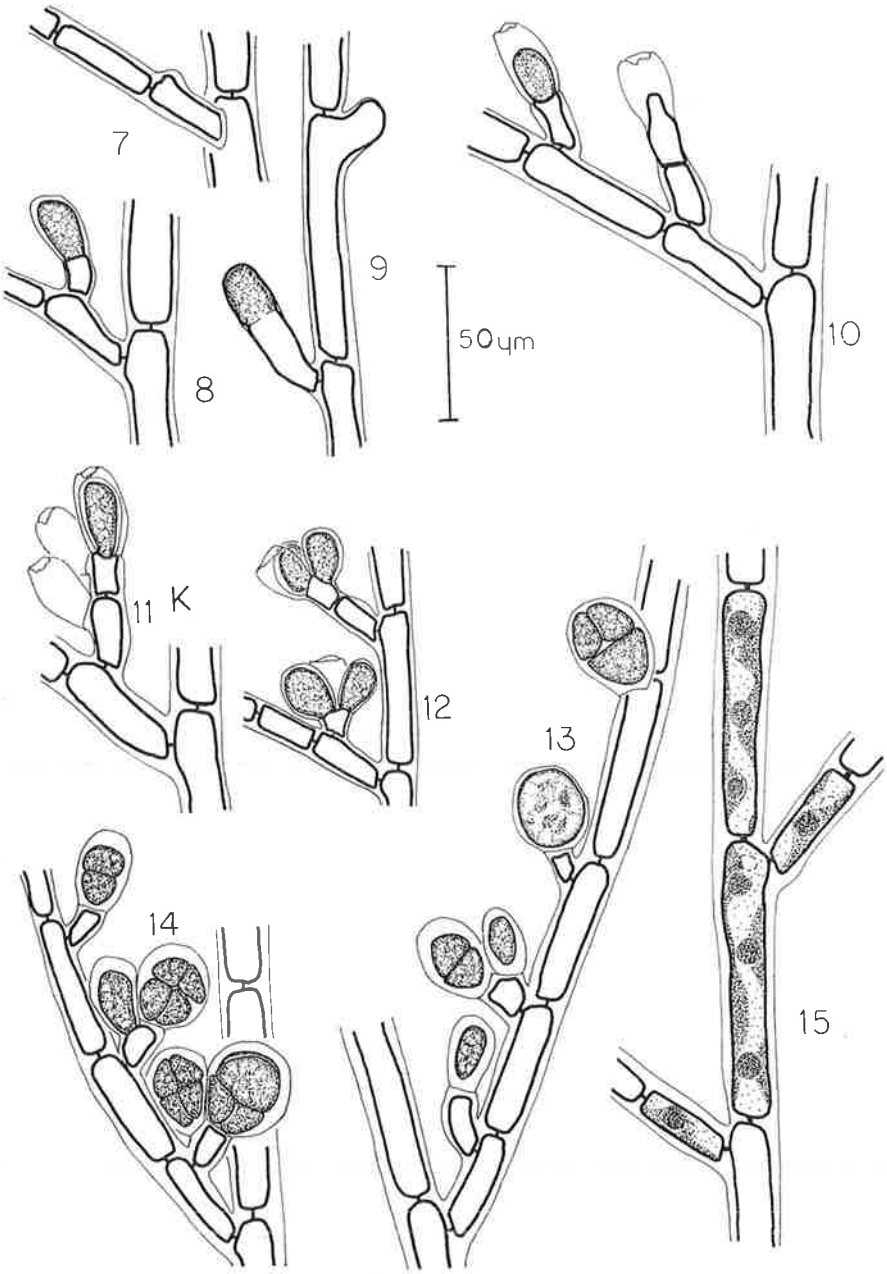
The monosporangia of *A. botryocarpum* are ovoid, 12–18 (–24) μm in diameter and 18–25 (–40) μm long, are sessile or stalked, and are borne singly, in pairs, or rarely in groups of 3–5 adaxially on the lower cells of laterals (Figs. 11, 12).

The existence of a tetraspore-producing generation in this species has been a matter of speculation in the literature for a long time, as noted above. Womersley (personal data in ADU), however, found some tetrasporic plants in a collection of Mitchell (ADU, A19795), and this, together with a number of similar collections made by the author, confirms the original report of tetrasporic plants made by Harvey (1854). Tetrasporangia are borne on plants similar in morphology to sexual and monosporangial plants, and the sporangia develop in the same manner as monosporangia. The sporangia, bearing cruciately divided contents, are mostly 18–24 μm in diameter and 25–40 μm long and are generally borne singly or in pairs on unicellular stalks on the lower cells of laterals (Figs. 13, 14).

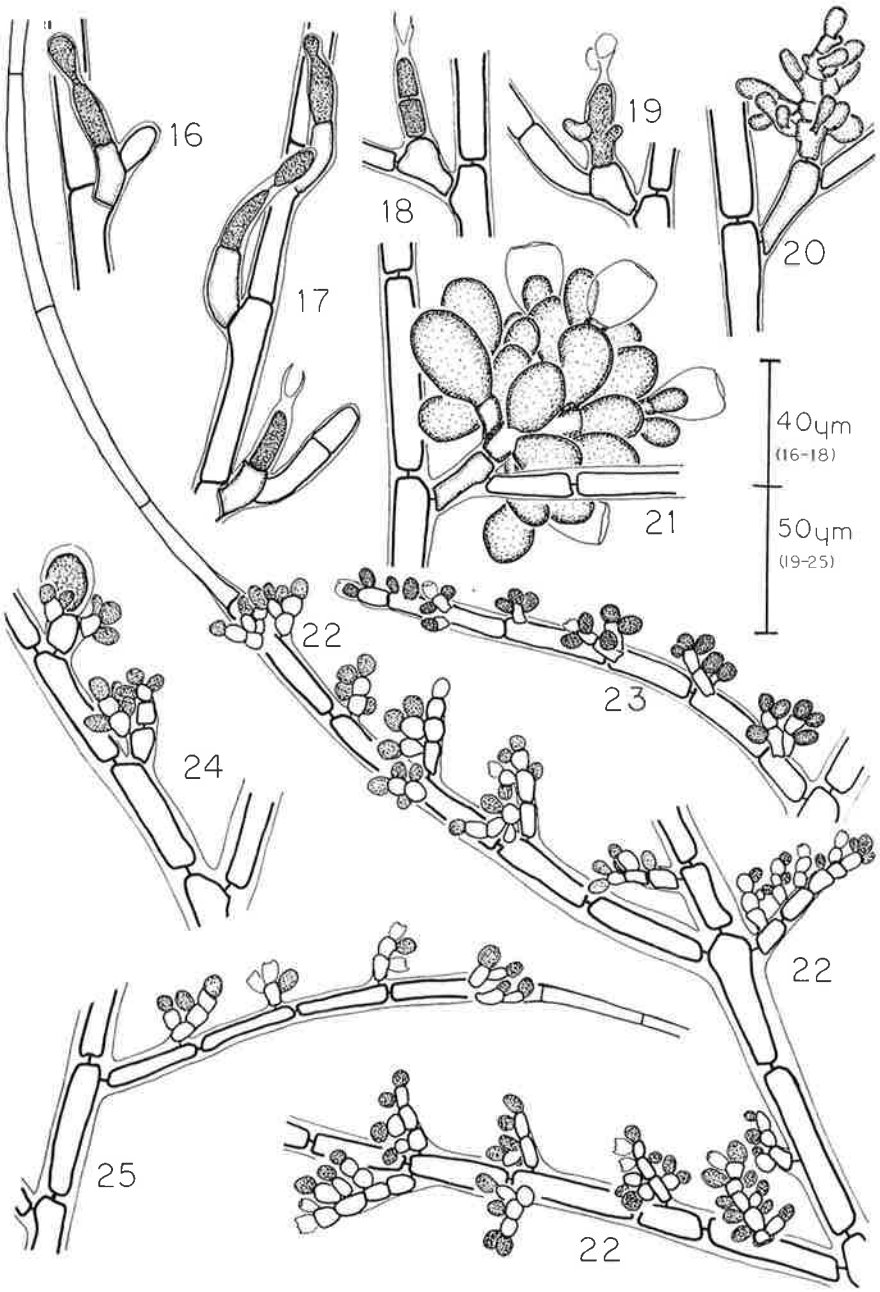
Sexual plants are mainly monoecious but occasional dioecious individuals occur. Spermatangia are ovoid to globose, up to 6 μm in diameter and 6 μm long, and may be sessile or stalked. They develop singly, in pairs, or in unilateral or more or less corymbose clusters (Figs. 22–25).

A carpogonium consists of a more or less bottle-shaped ventral portion supporting a rather slender, bulbous-tipped trichogyne. Carpogonia normally terminate one-celled stalks which are usually situated near the axils of laterals (Figs. 16, 17). Stalk cells occasionally give rise to short, unbranched filaments shortly before or after fertilisation (Figs. 16, 17).

Prior to fertilisation, the carpogonium contains a large, more or less centrally located, nucleus and a much smaller trichogyne nucleus (Fig. 26). The origin and function of the trichogyne nucleus remain uncertain, but it usually disintegrates just before or soon after fertilisation (Figs. 28, 30). The basal portion of the carpogonium remains more or less the same size throughout the pre-fertilisation period, but the trichogyne may continue to enlarge until a spermatium becomes attached.



FIGS. 7–15. *A. botryocarpum*. Figs. 7–9. Development of monosporangia (American River, Kangaroo Is., S. Australia, *Woelkerling*, ADU, A30878). Figs. 10–12. Arrangement of monosporangia (American River, Kangaroo Is., S. Australia, *Woelkerling*, ADU, A30878). Figs. 13,14. Formation and arrangement of tetrasporangia (Campbell's Cove, S. Australia, *Mitchell*, ADU, A19795). Fig. 15. Plastids in cells of erect filaments (America River, Kangaroo Is., S. Australia, *Woelkerling*, ADU, A30878).



FIGS. 16–25. *A botrycarpum*. Figs. 16–21. Carpogonia and carposporophyte development (American River, Kangaroo Is., S. Australia, *Woelkerling*, ADU, A30878). Figs. 16 and 17. Mature carpogonia just before and after fertilisation. Fig. 18. Fertilised carpogonium transversely divided. Fig. 19. Fertilised carpogonium undivided prior to gonimoblast cell formation. Fig. 20. Young carposporophyte. Fig. 21. Mature carposporophyte. Figs. 22–25. Spermatangia. Note spermatangia borne on ordinary vegetative cells (Fig. 23), in pairs on unicellular stalks (Figs. 23 and 25) and in larger clusters on branched stalks (Figs. 22 and 24); also note muticellular hair-like prolongation (Fig. 22); (American River, Kangaroo Is., S. Australia, *Woelkerling*, ADU, A30878).

One or occasionally several spermatia eventually come into contact with the trichogyne (Fig. 27) and, at the point of contact, both spermatium and trichogyne walls subsequently break down to allow entry of the male nucleus. The trichogyne often appears to have split open (Figs. 18, 27). The male nucleus does not divide after contact with the trichogyne, in contrast to the male nuclei of *Batrachospermum* (Kylin, 1917) and *Nemalion* (Wolfe, 1904; Kylin, 1916; Cleland, 1919) in other families of Nemaliales.

Spermatia of *A. botryocarpum* may be capable of amoeboid movements, judging from the shape of one spermatium just after contact with the trichogyne (Fig. 27), but further investigation is needed to confirm this observation. Rosenvinge (1927) previously has reported amoeboid movements in spermatia of *Phyllophora membranifolia* (Good. et Woodw.) J. Ag. (Gigartinales).

After the spermatial nucleus enters the trichogyne, it migrates to the basal region of the carpogonium and comes into apposition with the female nucleus (Fig. 28). Nuclear fusion follows (Fig. 29) and the resulting diploid nucleus can be distinguished from nuclei of vegetative cells only by its somewhat larger size (Fig. 30).

Both male and female nuclei appear to remain in interphase throughout the preceding sequence of events as Kylin (1916, 1917) has reported for several other Nemaliales (*Batrachospermum*, *Nemalion*).

Once fertilisation is effected, the trichogyne becomes separated from the rest of the carpogonium by a progressive thickening of the lower trichogyne wall until a complete closure occurs. Following this, the trichogyne soon disintegrates and disappears.

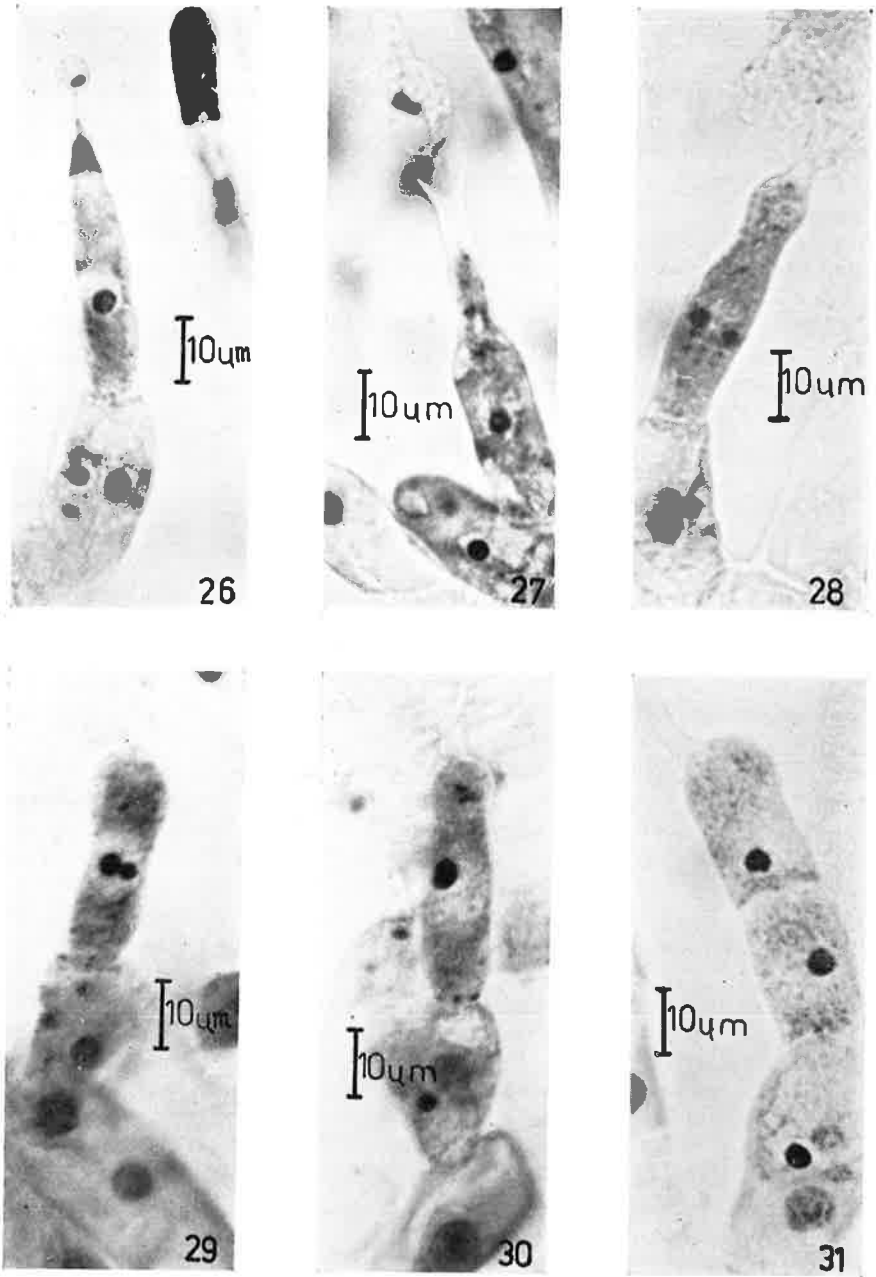
TABLE I. Seasonal occurrence of tetrasporangial, exclusively monosporangial and sexual plants in seven populations of *Acrochaetium botryocarpum*.

Date	ADU Herb. No.	Tetrasp.	Monosp.	Sexual
28. vii. 1967	A32238	48	2	0
14.viii.1967	A31926	4	40	6
8.ix.1967	A31331	0	21	29
6.x.1967	A31367	0	1	49
3.xi.1967	A15103	0	1	49
1.xii.1967	A31983	0	13	37
24.i.1967	A31189	0	45	5

Note: The first six collections come from two localities (Pt Elliot and Victor Harbor, S. Australia) approximately 5 miles apart whilst the last comes from a point (Apollo Bay, Victoria) distant from the others.

Following fertilisation, the carpogonium usually divides transversely before producing gonimoblast filaments (Figs. 18, 31). Rarely, however, no such division precedes gonimoblast formation (Fig. 19). Mature gonimoblasts consist of a few short simple or branched filaments and numerous thin walled, ovoid carposporangia up to 25 μm in diameter and 35 μm long (Fig. 21).

Plants of *A. botryocarpum* appear to have chromosome numbers of n = c. 5 and 2n = c. 10 based on observations of eight haploid and six diploid division figures, the latter being from both carposporophytes and tetrasporophytes. The occurrence of both haploid sexual and diploid tetrasporangial plants in the life history strongly suggests that *A. botryocarpum* is diplobiontic rather than haplobiontic as suggested by some earlier authors (p. 159).



FIGS. 26–31. Stages in fertilisation in *A. botryocarpum*. Fig. 26. Unfertilised carpogonium with nuclei in carpogonium and trichogyne. Fig. 27. Carpogonium with attached spermatium. Fig. 28. Male and female nuclei in apposition just prior to fusion. Fig. 29. Start of nuclear fusion. Fig. 30. Fertilisation just completed. Fig. 31. Two-celled carposporophyte after the initial transverse division of the fertilised carpogonium.

The life cycle of this species appears to be seasonally controlled. An analysis of 50 randomly selected plants in each of seven collections (Table I) made from July to January indicates that mature tetrasporophytes occur mainly in winter and sexual plants occur mainly in spring and early summer. Mixed populations of sexual and tetrasporangial plants occur for a short time in late winter, while monosporangia are present throughout the year. The numerous other collections of this species examined conform to the results of this analysis.

Rosenvinge (1909) and Drew (1935) reported similar seasonal control in other species of the complex, and West (1968) found that tetrasporangia of *A. pectinatum* (Kylin) Hamel developed in culture only when the plants were maintained on a maximum of 10 h light/day. All this evidence indicates that tetrasporangial plants of some acrochaetioid algae, including *A. botryocarpum*, require short days to become reproductive.

SYSTEMATIC IMPLICATIONS

As a result of these studies, several taxa hitherto regarded as distinct species have been or probably will be found to be cospecific with *Acrochaetium botryocarpum*.

A. polyrhizum (for an illustration of isotype material, see Levring 1953, Fig. 14) is here considered to be synonymous with *A. botryocarpum* after comparing isotypes and numerous other collections of the two taxa. *A. polyrhizum* was originally described from Pt Fairy, Victoria by Harvey (1863, synop: lvi) growing on *Codium tomentosum* Stackh. (= *C. pomoides* J. Ag.? ?). Harvey apparently distinguished it from *A. botryocarpum* on differences in habit and in cell length/width ratio in the erect axes. However, all intermediate forms of habit (Figs. 1–4) and cell length/width ratio occur in southern Australian plants collected during this study, thus making specific distinctions between the two unreliable on these bases. Levring (1953) separated the two taxa mainly on differences in host (*A. polyrhizum* confined to *Codium*; *A. botryocarpum* confined to *Scytosiphon*) but, as stated above, plants of this species complex have been found on a variety of hosts, thus making taxonomic distinctions based on host differences unreliable also.

To date, sexual plants on *Codium* referable to *A. polyrhizum* have not been collected, but tetrasporangial plants are known (ADU, A32292). The presence or absence of sexual reproduction on particular hosts does not appear to be a sound criterion of specific distinction in this instance, especially since the two taxa cannot be separated satisfactorily on other morphological grounds. Besides, sexual plants referable to *A. botryocarpum* have been found on all other known hosts and on rock, and it seems likely that they will eventually be collected on *Codium* as well. In view of present evidence, it appears that the two taxa are best regarded as conspecific.

A. codicolum Børg. (Børgesen, 1927, p. 33) from the Canary Islands, *A. grande* (Levr.) DeToni fil. originally described from the Juan Fernandez Islands, and *A. rhizoideum* (Drew) Sm. from California all have morphologies similar to and are probably conspecific with *A. botryocarpum*, but since the type collections and/or adequate type locality material has not been examined, they are left as distinct taxa for the present. Plants agreeing with the descriptions of all these

taxa occur in southern Australia, but since they cannot be separated satisfactorily from each other on morphological grounds, all are referred to *A. botryocarpum*. Cribb (1956, p. 186) reported similar conclusions concerning these taxa.

A. grande is also reported from Australia (Levring, 1953, p. 480) and New Zealand (Levring, 1955, p. 416). Plants collected by Womersley (ADU, A8795), which are probably those referred by Levring (1953, p. 481) to *A. grande*, have been examined and found to be rather depauperate specimens of *A. botryocarpum*. It therefore seems likely that other Australian and New Zealand collections regarded by Levring (1953, 1955) to belong to *A. grande* will be found to be identical with *A. botryocarpum*.

In addition to clarifying some of the problems associated with *A. botryocarpum* in particular, the results of this study suggest that a re-evaluation of several criteria used in making taxonomic distinctions in the *Acrochaetium-Rhodochorton* complex is needed. These criteria include host specificity, substrate relations, form of spermatangial clusters and immediate post-fertilisation activity.

Host specificity has been considered a reliable criterion for specific distinction for so long that Baardseth (1941, p. 46) remarked, '. . . it has become common practice to describe plants of *Acrochaetium* as new as soon as they are found in a new host.' Many authors (e.g. Hoyt, 1920; Hamel, 1927; Drew, 1928; Dawson, 1953; Levring, 1953; Chapman, 1962) have regarded host specificity as an important taxonomic criterion, and Boney and White (1967) have indicated the reliance placed upon it in classifying the endozoic members of the complex. However, as we have seen, *A. botryocarpum* has been found on a variety of hosts as well as rock, and other southern Australian species previously thought to be confined to single hosts are also known to occur on several hosts (unpublished data). Furthermore, Abbott (1962, pp. 107, 114, 115) recently referred collections partly endophytic in *Liagora* to species previously thought to be confined to hosts other than *Liagora* and West (1968, p. 99) in culturing *A. pectinatum* (Kylin) Hamel noted that, 'There is no requirement for an organic substrate as one might expect for an epiphyte or epizoite.' White and Boney (1969) have also successfully isolated and cultured endophytic and endozoic species. This evidence casts doubt upon the value of host specificity in acrochaetioid taxonomy, and upon the validity of numerous taxa published solely on that basis.

Substrate relations (i.e. the form and position of the prostrate system in relation to the host surface) have also played an important role in acrochaetioid taxonomy at the specific level. Many phycologists (e.g. Rosenvinge, 1909; Børgesen, 1915; Hamel, 1927; Drew, 1928; Dawson, 1953) have distinguished species solely on the basis of whether they were epiphytic or partly to entirely endophytic. Both epiphytic and partly endophytic plants of *A. botryocarpum* occur, and whether or not a given plant is epiphytic or partly endophytic appears to depend largely on how penetrable the host surface is. Thus the results of this study support the view of Papenfuss (1947, p. 434) that, 'Basal structure must be suspected of being, at least in part, adaptive to the substratum.' Criteria relating to epiphytism versus endophytism may not, therefore, be systematically reliable for the complex as a whole.

Abbott (1962, pp. 82, 117) recently suggested that the form of the sperma-

tangial clusters may be of taxonomic significance. She distinguished four types: corymbose or nearly corymbose clusters, lateral circinnately formed clusters, paniculate clusters and spermatangia borne on ordinary vegetative cells. However, since spermatangia of *A. botryocarpum* occur in both corymbose clusters and directly on ordinary vegetative cells, further study on other species appears necessary before the systematic value of criteria relating to the form of spermatangial clusters can be fully evaluated.

Differences in immediate post-fertilisation activity (i.e. whether the fertilised carpogonium divides longitudinally, transversely or not at all) have been regarded as systematically significant at the generic level by some phycologists (e.g. Yamanda, 1944; Feldmann, 1962). The occurrence of both divided and undivided fertilised carpogonia in *A. botryocarpum*, however, suggests that other taxa should be carefully examined before relying too heavily on post-fertilisation criteria for making taxonomic distinctions.

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By W. J. WOELKERLING*

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CONTENTS

Abstract

The morphology and taxonomy of the southern Australian representatives of what has been frequently referred to as the "*Acrochaetium–Rhodochorton*" complex of the Rhodophyta have been studied. The type species of both *Acrochaetium* and *Rhodochorton* are placed in the genus *Audouinella* and the group is now referred to as the *Audouinella* complex.

Two genera are recognized in this region: *Audouinella* (syn. *Acrochaetium*, *Balbiania*, *Chromastrum*, *Grania*, *Rhodochorton*), known to reproduce sexually, contains 12 southern Australian species (including *A. blumii* sp. nov.) and is referred to the Audouinellaceae nom. nov. *Colaconema*, treated here as a genus comparable with form genera of the Fungi Imperfecti, contains 14 southern Australian form species, all unknown in the sexual state.

The generic classification proposals of Feldmann (1962), Kylin (1956), and Papenfuss (1945, 1947) are not supported by this study.

Few morphological features of audouinelloid algae are of general systematic value, but pyrenoid numbers, sporangial dimensions, and cell dimensions appear to be the most reliable criteria for systematic purposes. Other features (e.g. form of the prostrate system, chromoplast shape, occurrence and position of hairs, spermatangial morphology, and immediate post-fertilization development) show too much variation to be used reliably in species and/or generic separation.

Information on the tropical Australian species is briefly summarized.

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I. Introduction

The southern Australian (i.e. mainland Australia from south-western Western Australia to eastern Victoria, Tasmania, and other islands) representatives of the *Audouinella* complex (Acrochaetiaceae or *Acrochaetium–Rhodochorton* complex; see later discussion) have been inadequately known, and the only recent account is that of Levring (1953) which left a number of points to be clarified. Harvey (1854, 1860, 1863) first reported their occurrence in this region; subsequent records include those of Abbott (1962), Cribb (1956), Guiler (1952), May (1947), Papenfuss (1945), Wilson (1892), Woelkerling (1970), and Womersley (1950).

Very little is known, although much speculation exists, about the taxonomic significance of various morphological criteria within the *Audouinella* complex. Over 85% of the more than 280 described taxa have been assigned to the complex on vegetative and asexual* grounds alone, and their taxonomic position is therefore uncertain. Furthermore, the *Audouinella* complex recently has been linked to the Helminthocladiaceae (Nemaliales, Rhodophyta) through the discoveries of von Stosch (1965), Fries (1967), Martin (1967, 1969), and Umezaki (1967, 1967*a*) which showed that certain members of this family produce sporophytes of audouinelloid morphology. Similarly, several members of the Chaetangiaceae (Nemaliales; see Boillot 1968 and Ramus 1968) are known to produce stages of audouinelloid morphology. Thus it appears likely that some members of the *Audouinella* complex represent stages in the life history of other Rhodophyta.

This account reviews the systematic history, morphology, and relationships of audouinelloid algae and includes a taxonomic treatment of the southern Australian representatives based on extensive field and herbarium investigations including the examination of many of the type collections. Emphasis has been placed on studies of living and liquid-preserved populations rather than on isolated plants, and the variation noted within populations has served as a basis for determining taxonomic limits. The techniques employed in these studies have been detailed elsewhere (Woelkerling 1970); abbreviations for herbaria follow Lanjouw and Stafleu (1964).

II. Taxonomic History of the Audouinella Complex

Our knowledge of audouinelloid algae dates from 1777 (Lightfoot) and includes a number of important taxonomic accounts (Abbott 1962; Boergesen 1915 *et seq.*; Bornet 1904; Drew 1928, 1935; Feldmann 1962; Hamel 1925, 1927; Israelson 1942; Kylin 1906, 1907, 1944; Murray and Barton 1891; Naegeli 1861; Nakamura 1941, 1944; Papenfuss 1945, 1947). These papers all reflect the uncertainty and disagreement over which criteria are best suited for establishing specific, generic, and higher category limits.

Species Concepts

Species limits of audouinelloid algae are often difficult to determine; as West (1968, p. 98) has stated: "We have relatively few morphological features upon which to base a taxonomic system". Numerous species have been established on minute differences, without regard for possible intraspecific variation, on very scanty material,

* The term asexual as used in this paper is defined in its classical sense, i.e. devoid of male or female organs.

and/or without adequate comparison with existing taxa. Specific concepts have become so confused that some phycologists (e.g. Chihara 1967; Hoyt 1920; Nienhuis 1968; Williams 1948) have become hesitant about assigning collections to any one species.

Prior to 1900 about 70 species had been described, and since that time, when the development and structure of the prostrate system, type of host organism, and chromoplast shape became prominent taxonomic criteria, over 200 taxa have been added. This investigation as well as several recent papers (Abbott 1962; Feldmann 1962; West 1968; Woelkerling 1970) indicate that these criteria are to a greater or lesser extent unreliable for taxonomic purposes. Knaggs (1966, 1967, 1967*a*) has also shown the extent to which environmental factors can influence the morphology of audouinelloid algae growing in the intertidal zone. A more plastic species concept appears to be necessary for audouinelloid algae, and many of the hitherto described taxa are probably best regarded as forms of fewer, more variable species.

Generic Concepts

Eleven of the 20 generic names (*Acrochaetium*, *Audouinella*, *Balbiania*, *Byssus*, *Callithamnion*, *Ceramium*, *Chantransia*, *Chantransiella*, *Chromastrum*, *Colaconema*, *Conferva*, *Grania*, *Kylinia*, *Liagorophila*, *Pseudacrochaetium*, *Pseudochantransia*, *Rhodochorton*, *Rhodothamniella*, *Thamnidium*, *Trentepohlia*) hitherto used for audouinelloid algae can no longer be applied to this complex under various rules of the International Code of Botanical Nomenclature (1966 edition, edited by J. Lanjouw *et al.*, and cited hereafter as the "Botanical Rules"). Early investigators (e.g. Lightfoot 1777; Dillwyn 1809; C. Agardh 1817) variously referred audouinelloid algae to *Byssus*, *Ceramium*, and *Conferva* while some later phycologists (e.g. Lyngbye 1819; Kuetzing 1849; Harvey 1846, 1851, 1854, 1863) placed all marine species in *Callithamnion* Lyngbye. Silva (1950) has discussed the use of the generic name *Trentepohlia* Martius (1817, p. 351) for audouinelloid algae. These five genera are based on species of non-audouinelloid morphology and therefore cannot be used for members of this complex.

The generic name *Chantransia* dates from 1801 and has been applied incorrectly to audouinelloid algae in a number of senses; according to Papenfuss (1947*a*) this name is synonymous with *Oedogonium* (Chlorophyta).

Chantransiella Brebner (see De Toni 1924, p. 63), *Pseudacrochaetium* von Stosch (1965, p. 495), and *Rhodothamniella* Feldmann (1954, Introduction and p. 68; 1962, p. 220) have not been validly published (Article 36) while *Pseudochantransia* Brand (1897, p. 318; 1910, p. 117), *Thamnidium* Thuret in Le Jolis (1863, p. 110), and *Trentepohlia* Pringsheim (1862, p. 29; non Martius 1817) are superfluous. *Thamnidium* and *Trentepohlia* are predated by *Rhodochorton* Naegeli (1861, p. 355) while *Pseudochantransia*, created as a "genus artificale" and recognized by several subsequent authors (e.g. Israelson 1942; Ravanko 1968; Skuja 1938), is based on a taxon which at that time was known to be a stage in the life history of *Batrachospermum* (Batrachospermaceae, Nemaliales).

Nine generic names (discussed below in chronological order) based on type species of audouinelloid morphology have been used in more recent accounts, but investigators have not been able to agree upon either the number of genera involved or the manner in which they are separated (compare, for example, the classification schemes of Drew 1928; Feldmann 1962; Kylin 1956; and Papenfuss 1945).

Audouinella

Audouinella Bory (1823, p. 340), established for taxa with cylindrical filaments without swellings at the crosswalls and with external, naked, ovoid, opaque, and stipitate sporangia, has been restricted by most authors (e.g. Feldmann 1962; Hamel 1925; Kylin 1956) to freshwater audouinelloid algae only. Papenfuss (1945), however, placed within *Audouinella* all marine and freshwater taxa with one or more spiral chromoplasts per cell.

Bory originally included three taxa within *Audouinella*. *A. funiformis* was subsequently removed to *Ectocarpus* Lyngbye (Phaeophyta), and Sirodot (1873) found *A. chalybaea* to be a juvenile stage of a species of *Batrachospermum*. The status of *A. miniata* (= *A. hermanni* (Roth) Duby; see Bory 1823, p. 341) remained in doubt for some time, and De Toni (1897, p. 66) suggested that *Audouinella* be reserved as a "genus artificale" for plants representing stages in the life histories of other freshwater Rhodophyta.

Israelson (1942), however, concluded after a study of over 200 collections that *Audouinella hermanni* (as *Chantransia hermanni*) is an independent species with an isomorphic alternation of generations. He also regarded *Rhodochorton violaceum* (Kuetzing) Drew, a sexual taxon studied intensively by Drew (1935), to be conspecific with *Audouinella hermanni*. A personal examination of some American material of this taxon strongly supports Israelson's conclusions as does the study of Budde (1933). *Audouinella*, with *A. hermanni* as type species, is therefore a valid genus in accordance with the "Botanical Rules" (see Papenfuss 1945, p. 299 for further discussion).

Rhodochorton

Naegeli (1861, p. 355) established *Rhodochorton* for audouinelloid algae reproducing by tetraspores only, but subsequently (see Hamel 1927, p. 50; Feldmann 1962) chromoplast structure became an equally important delimiting criterion, and Papenfuss (1945) based the genus solely on chromoplast shape and number. Drew (1928, 1935), however, concluded after a thorough review that *Rhodochorton* should include virtually all freshwater and marine audouinelloid algae described up to that time since there appeared to be no satisfactory criteria of generic separation.

Rhodochorton purpureum (Lightfoot) Rosenvinge (syn. *R. rothii* (Turton) Naegeli and *R. tenue* Kylin; see Papenfuss 1945, p. 327, and West 1969), the type species of *Rhodochorton*, undergoes sexual reproduction (West 1969); hence *Rhodochorton* sensu Naegeli and sensu Feldmann must be modified since they are restricted to asexual species.

Chromoplast shape and number also appear unreliable as criteria upon which to base *Rhodochorton*. Drew (1928, pp. 156, 177, Fig. 33) has pointed out that cells of *R. purpureum* (as *R. rothii* and *R. tenue*) have a single reticulate-lobed chromoplast which may become dissected into several smaller portions, and Kuckuck (1897, pp. 344, 345, Fig. 5) has shown that the chromoplasts may be irregularly band-shaped rather than distinctly discoid. Thus both the number of chromoplasts per cell and their shape vary in *R. purpureum*, a further indication (see p. 14) that these features appear to be of little or no taxonomic value at the generic level as has been suggested by Papenfuss (1945).

Rhodochorton sensu Drew (1928, 1935) is identical with and predated by *Audouinella* Bory and consequently is here considered congeneric with *Audouinella*.

The retention of *Rhodochorton* based on a modified haplobiontic life cycle of the type species (West 1969) does not appear justified in view of potentially similar situations in other genera of the Nemaliales (von Stosch 1965) and in other Rhodophyta (Magne 1967; Schotter 1968). Besides, details of the sexual cycle in nearly all audouinelloid algae are very incomplete and any generic segregation based on life cycle differences is, therefore, quite premature.

Knaggs (1966*a*, 1967*a*, 1968) has dealt extensively with *R. purpureum* in European waters.

Acrochaetium

Acrochaetium Naegeli (1861, p. 402) originally included audouinelloid algae which reproduce by monospores (Naegeli called them zoospores), but it also has been variously circumscribed to include all asexual audouinelloid algae (Bornet 1904; Collins 1906), all marine audouinelloid taxa (Boergesen 1915 *et seq.*), and all audouinelloid taxa with a single parietal chromoplast per cell (Papenfuss 1945). Feldmann (1962) and Kylin (1956) based *Acrochaetium* on several different combinations of characters, and Abbott (1962, p. 80) stated: "I have chosen to use the name *Acrochaetium* in its widest sense".

Acrochaetium daviesii (Dillwyn) Naegeli, the type species of *Acrochaetium*, shows no morphological features which would justify generic separation from *Audouinella* at present. Criteria hitherto used to separate the two genera (chromoplast shape, type of sporangium, habitat, immediate post-fertilization events) appear unreliable as taxonomic characters as a result of this study (see below), and a comparison of material of the type species of *Audouinella* and *Acrochaetium* by the present investigator has failed to uncover any other features of generic significance. Specimens examined include plants of *Audouinella hermanni* from the United States and Europe (including several collections studied by Israelson 1942) and material of *Acrochaetium daviesii* from the United States, Europe, and Australia. Consequently, *Acrochaetium* is here considered synonymous with *Audouinella*. Drew (1928) and Nakamura (1941, 1944) previously rejected *Acrochaetium* as a distinct genus.

Balbiania

Sirodot (1876, p. 149) founded *Balbiania*, based on *B. investiens* (Lenormand) Sirodot, for freshwater audouinelloid algae which reproduce sexually. Schmitz and Hauptfleisch (1896, p. 332) restricted the genus to monoecious freshwater species, and Hamel (1925) limited it to sexual audouinelloid algae attached to plants of *Batrachospermum*. Feldmann (1962) circumscribed *Balbiania* on chromoplast and reproduction morphology.

Following Kylin (1956, p. 87), *Balbiania* is regarded here as synonymous with *Audouinella* since, as Swale and Belcher (1963, p. 288) stated: "... there is no fundamental difference between *Balbiania* and other members of the *Rhodochorton–Acrochaetium* complex ...". Other investigators not recognizing *Balbiania* include Drew (1935, p. 449), Fritsch (1945, p. 450), and Murray and Barton (1891).

Colaconema

Colaconema Batters (1896, p. 8) was established for endophytic audouinelloid algae with creeping, irregularly branched filaments often anastomosing and sometimes loosely united laterally, and with monosporangia formed from portions of terminal or

intercalary cells, the remaining portions serving as cup-like bases. A report of clustered monosporangia (Kylin 1944, p. 29) was later questioned by Papenfuss (1947, p. 434); such spores did not occur in type collection plants examined during this study.

Since none of the taxa originally included in *Colaconema* (*C. bonnemaisoniae*, *C. chylocladiae*, *C.* (?) *reticulatum*) is known in the sexual state, the systematic position of the genus has been uncertain. Batters (1902), Newton (1931), and Taylor (1957) referred it to the same family as other audouinelloid algae, but Hamel (1930, p. 89) placed it in the Chaetangiaceae as a "genus insertae sedis", and Dawson (1966, p. 326), Fritsch (1945, p. 424), Howe and Hoyt (1916), and Rosenvinge (1909, p. 71) suggested that it was allied to *Erythrotrichia* Rosenvinge (Bangiophycidae). Feldmann (1955) divided Batters's genus into *Colaconema*, based on *C. bonnemaisoniae*, and *Colacodictyon* Feldmann, based on *C. reticulatum* (Batters) Feldmann; the former was placed in the Florideophycidae while the latter was referred to the Bangiophycidae. The use of the generic name *Colaconema* in this study is discussed below (p. 8).

Kylinia

Rosenvinge (1909, p. 141) established *Kylinia* for audouinelloid algae with spermatangia borne on "peculiar, narrow, cylindrical, colourless, or feebly coloured androphore (= stalk) cells". Kylin (1944) restricted *Kylinia* to marine audouinelloid algae with unicellular holdfasts while Papenfuss (1947) limited it to taxa with stellate chromoplasts.

According to Rosenvinge (1909), the fertilized carpogonium divides transversely, but Yamada (1944, p. 18) reported a longitudinal first division, and Feldmann (1958) stated that carposporangia were produced directly from an undivided fertilized carpogonium. Boney and White (1967) did not observe any post-fertilization stages. Pending further study, *Kylinia* is maintained here as a doubtfully distinct genus on the basis of Rosenvinge's original criteria.

Grania

Rosenvinge (1909, p. 134) founded the subgenus *Grania* for audouinelloid algae with ribbon-like chromoplasts, terminal and intercalary carpogonia, and seriate carposporangia, but later (Rosenvinge 1935) included *Grania* within *Rhodochorton* sensu Drew. Kylin (1944, p. 26), however, elevated *Grania* to generic rank with *G. efflorescens* (J. Ag.) Kylin as type species, and Feldmann (1962) maintained the genus.

Following Papenfuss (1945, p. 302), *Grania* is here considered synonymous with *Audouinella* as there appears to be no differences of generic importance between *G. efflorescens* and other species of *Audouinella.*

Liagorophila

Yamada (1944, p. 16) established *Liagorophila* for *L. endophytica*, a marine endophyte of audouinelloid morphology in which the fertilized carpogonium divides longitudinally prior to gonimoblast formation. Abbott (1966), Fan and Li (1964), Feldmann (1962), and Kylin (1956) all have recognized the genus; pending further study it is maintained here as a doubtfully distinct genus.

Chromastrum

Papenfuss (1945, p. 320) proposed the genus *Chromastrum*, based on *C. floridulum* (Dillwyn) Papenfuss, for audouinelloid algae with one or more than one stellate chromoplast per cell. According to Kylin (1944), however, *Kylinia rosulata*, the type species of *Kylinia*, has stellate chromoplasts. Papenfuss (1947) therefore placed *Chromastrum* in synonymy with *Kylinia.* Feldmann (1958) later stated that Kylin had misidentified his plant and that the true *Kylinia rosulata* had parietal chromoplasts. The illustrations of Boney and White (1967) of *K. rosulata* are difficult to interpret as regards chromoplast shape.

The generic name *Chromastrum* appears to have priority at present were a genus of audouinelloid morphology based on stellate chromoplasts to be recognized. However, differences in chromoplast shape appear to be generally unreliable for taxonomic purposes (see below), and since no other significant differences appear to separate *C. floridulum* from *Audouinella*, the genus *Chromastrum* has been referred here to the synonymy of *Audouinella.*

Family and Order Concepts

Most investigators in this century (e.g. Boergesen 1915; Kylin 1956; Scagel 1957; Taylor 1957) have regarded the complex as forming a distinct family, commonly known as the Acrochaetiaceae. Prior to the monograph of Hamel (1925), however, *Rhodochorton* was frequently referred to the Ceramiaceae (see also Papenfuss 1945, p. 302), and most investigators of the last century as well as Arwidsson (1936) and Setchell and Gardner (1930) referred all audouinelloid algae to the Ceramiaceae. Collins and Hervey (1917), Hamel (1925), and Newton (1931) among others placed audouinelloid algae in the Helminthocladiaceae; Howe (1914) and Taylor (1928) referred them to the Nemalionaceae (= Helminthocladiaceae); and Hauck (1885) and Foslie (1890) placed them in the Wrangeliaceae, a family no longer recognized but at that time included in the Nemaliales.

The order Acrochaetiales was proposed independently by Chemin (1937, p. 300) and Feldmann (1953, p. 12). Chemin's diagnosis was inadequate and, according to Dixon (1961*a*, p. 10) was not accepted by subsequent authors. Feldmann characterized the order by the absence of a "true carpogonial branch" (see p. 18), but Dixon (1961*a*), Abbott (1962), and Papenfuss (1966) have opposed this suggestion.

Taxonomic System Adopted in this Paper

This study of southern Australian audouinelloid algae together with a thorough review of the literature has resulted in a division of the *Audouinella* complex into two groups: (1) the Audouinellaceae nom. nov. (p. 22) for taxa known to reproduce sexually, and (2) the form genus *Colaconema* (p. 40) for asexual taxa of uncertain systematic position. The evidence favouring this arrangement is discussed below.

The family names Acrochaetiaceae Fritsch (1944, p. 258), Chantransiaceae Rabenhorst (1868, p. 400), and Rhodochortonaceae Nasr (1947, p. 92), formerly applied to the complex, must be rejected under Article 18 of the "Botanical Rules" since they are derived from generic names (*Acrochaetium*, *Chantransia*, *Rhodochorton*) which either have been illegitimately applied to audouinelloid algae or are considered to be synonymous with *Audouinella*. The family name Audouinellaceae Feldmann

(1962, p. 220) was not validly published under Articles 36 and 37 of the "Botanical Rules" and therefore has no status (Article 12).

Although not at present considered a member of the Audouinellaceae, the form genus *Colaconema*, treated here as being comparable with form genera of the Fungi Imperfecti, is dealt with in association with the Audouinellaceae because of similarities in vegetative morphology. The establishment of form genera for algae has been suggested previously by Brand (1897) who created *Pseudochantransia* for taxa which represented stages in the life histories of other freshwater Rhodophyta and by De Toni (1897, p. 66) who suggested using *Audouinella* for the same group.

The adoption of the above taxonomic proposals necessitates a number of taxonomic name changes which are summarized in Table 1. Taxa not occurring in southern Australia are referred to by previously published names in spite of evidence suggesting they should be placed either in *Audouinella* or *Colaconema*. Many of these taxa are probably conspecific with species described earlier and it seems best, therefore, not to suggest new nomenclatural combinations until the status of each taxon has been re-examined carefully.

Relationships with other Florideophycidae

The occurrence of monosiphonous phases of similar morphology in the life history and the presence of pyrenoids in many species strongly indicate that the Audouinellaceae and the Helminthocladiaceae (Nemaliales) may have had a common origin. Pyrenoids are unknown in other families of Florideophycidae. The Chaetangiaceae (Nemaliales) also contains species known to produce stages of audouinelloid morphology, thus suggesting a link with those Audouinelliaceae lacking pyrenoids. In view of this, the suggestion of Feldmann (1953) that audouinelloid algae be placed in a separate order appears unwarranted. Although extant species of the Audouinellaceae have a simple reproductive morphology in comparison with other members of the Nemaliales, the family definitely appears to be linked to several other families in that order in certain vegetative and cytological features and is, therefore, retained with those families in the Nemaliales.

III. MORPHOTAXONOMIC CHARACTERISTICS

The basic features of audouinelloid algae are well known from the monographic treatments of Boergesen (1915), Drew (1928), Hamel (1927), and Rosenvinge (1909) and the papers of Abbott (1962), Drew (1935), Swale and Belcher (1963), West (1968, 1969), and Woelkerling (1970), but a study of morphological variation in and the consequent taxonomic significance of these features in populations of southern Australian species together with a thorough review of the literature has resulted in a reassessment of a number of taxonomic criteria hitherto associated with the group.

VEGETATIVE FEATURES

Habitat

Audouinelloid algae inhabit all seas and some freshwater and semiterrestrial habitats. Marine species occur from the supralittoral to a depth of at least 40 m (Lund 1959), and dense populations sometimes develop in favourable situations (Fig. 24*A*).

TABLE 1

PROPOSED NOMENCLATURAL CHANGES AND ORIGINAL NAMES OF SOUTHERN AUSTRALIAN AUDOUINELLOID ALGAE

Audouinella australis (Levring) comb. nov. (*Kylinia australis* Levring 1953: 487).

Audouinella barbadense (Vickers) comb. nov. (*Chantransia barbadensis* Vickers 1905: 60).

Audouinella botryocarpa (Harvey) comb. nov. (*Callithamnion botryocarpa* Harvey 1854: 563).

Audouinella daviesii (Dillwyn) comb. nov. (*Conferva daviesii* Dillwyn 1809: 73).

Audouinella dictyotae (Collins) comb. nov. (*Acrochaetium dictyotae* Collins 1906: 193).

Audouinella floridula (Dillwyn) comb. nov. (*Conferva floridula* Dillwyn 1809: 73).

Audouinella liagorae (Boergesen) comb. nov. (*Chantransia liagorae* Boergesen 1915: 57).

Audouinella microscopica (Naegeli) comb. nov. (*Callithamnion microscopicum* Naegeli in Kuetzing 1849: 640).

Audouinella repens (Boergesen) comb. nov. (*Acrochaetium repens* Boergesen 1915: 52).

Audouinella thuretii (Bornet) comb. nov. (*Chantransia efflorescens* var. *thuretii* Bornet 1904: XVI).

Colaconema humilis (Rosenvinge) comb. nov. (*Chantransia humilis* Rosenvinge 1909: 117).

Colaconema macula (Rosenvinge) comb. nov. (*Chantransia macula* Rosenvinge 1909: 114).

Colaconema nakamurai Woelkerling nom. nov. (*Acrochaetium unifilum* Levring 1953: 427).

Colaconema pacifica (Kylin) comb. nov. (*Acrochaetium pacificum* Kylin 1925: 11).

Colaconema phacelorhiza (Boergesen) comb. nov. (*Acrochaetium phacelorhizum* Boergesen 1915: 54).

Colaconema plumosa (Drew) comb. nov. (*Rhodochorton plumosum* Drew 1928: 173).

Colaconema polyidis (Rosenvinge) comb. nov. (*Chantransia polyidis* Rosenvinge 1909: 132).

Colaconema porphyrae (Drew) comb. nov. (*Rhodochorton porphyrae* Drew 1928: 188).

Colaconema spiculiphila (Dawson) comb. nov. (*Acrochaetium spiculiphilum* Dawson 1953: 22).

Colaconema spongiocola (Weber van Bosse) comb. nov. (*Acrochaetium spongiocolum* Weber van Bosse 1921: 195).

Colaconema tenuissima (Collins) comb. nov. (*Chantransia virgatula* f. *tenuissima* Collins P.B.A., No. 741).

Some authors (e.g. Hamel 1925; Kylin 1956) referred freshwater taxa to *Audouinella* and marine taxa to other genera, but others (e.g. Drew 1935; Israelson 1942; Papenfuss 1945; Skuja 1934) felt that such separation reflected only an ecological situation and was not concomitant with morphological characters. Although the latter view is accepted here, habitat (freshwater *v.* marine) has value as a character in keys since no species is known to occur in both environments. (See, however, Knaggs 1966.)

Habit

The heterotrichous habit of audouinelloid algae has long been recognized (e.g. Harvey 1854; Kuckuck 1897; Naegeli 1861). Southern Australian species fall into three groups: (1) prostrate system usually absent and represented by a unicellular holdfast; (2) prostrate system present but less in extent than the erect system; (3) prostrate system present and equal to or greater in extent than the erect system.

Among species in this region, *Audouinella australis* and *A. microscopica* usually possess unicellular holdfasts but on rare occasions several-celled prostrate systems develop (Figs. 4*G–H*, 10*G*). *Acrochaetium affine* (Howe and Hoyt 1916, p. 118), *A. opetigenum* (Boergesen 1915, p. 38), and *Rhodochorton robustum* (Boergesen) Nakamura (Nakamura 1941, p. 284) show similar variation. Sexual plants of *Acrochaetium* (= *Audouinella*) *pectinatum* and *Rhodochorton* (= *Audouinella*) *floridulum* have unicellular holdfasts while tetrasporangial plants possess multicellular prostrate systems (Knaggs and Conway 1964; West 1968).

This variation suggests that the presence or absence of a prostrate system may not be a generally reliable criterion of generic (Kylin 1944) or in most cases of specific (e.g. Boergesen 1915; Drew 1928; Hamel 1927; Hoyt 1920; Levring 1953; Rosenvinge 1909) distinction as was formerly thought. Nevertheless, heterotrichous features are among the most conspicuous characters of audouinelloid algae and can sometimes serve as useful though not foolproof characters in keys.

Mode of Attachment

Within southern Australia, audouinelloid algae occur on or in marine algae, on marine angiosperms, in sponges, and on rock. Hosts with a loose, open construction (e.g. *Codium*, *Helminthocladia*) usually support partly to entirely endophytic plants, while those of more compact construction (e.g. *Lenormandiopsis*, *Scytosiphon*) or of a filamentous nature (e.g. *Chaetomorpha*, *Cladophoropsis*) support largely or entirely epiphytic plants. *Audouinella botryocarpa*, for example, may remain epiphytic or become partly endophytic depending upon the nature of the host (Woelkerling 1970). *A. daviesii* remains completely epiphytic on *Amphibolis* but penetrates the slimy tissues of *Codium* and *Polycerea* (Figs. 7*B*, 22).

Plants grown from spores in laboratory cultures during the present study also adapted to different substrates. No penetration of filaments is possible when spores of *Audouinella botryocarpa* developed on glass slides, but on a porous surface resembling *Codium*, penetration readily occurred.

In cases where several species occur simultaneously on the same host, the prostrate filaments usually penetrate to the same extent. Thus *Audouinella botryocarpa* and *A. daviesii* grow completely epiphytically on *Amphibolis*; *Colaconema humilis* and *Audouinella microscopica* develop completely epiphytically on *A. botryocarpa*; and *A. blumii* and *A. liagorae* grow completely immersed in *Helminthocladia australis* and *H. densa*.

One southern Australian collection of *Porphyra* (ADU, A31808), however, contains endophytic plants of *Colaconema porphyrae* and epiphytic plants of *Audouinella microscopica*. Bornet (1904, p. XVIII) cited several similar instances and concluded that the degree of penetration was not determined by the greater or lesser compactness of the host tissue.

In spite of these apparent exceptions, the accumulated evidence (see also Abbott 1962, p. 113; Boergesen 1915, p. 14; Drew 1928, p. 173; Kylin 1944, p. 21; Levring 1937, p. 88) strongly favors Papenfuss's view (1947, p. 434) that "basal structure must be suspected of being, at least in part, adaptive to the substratum". Consequently criteria related to the mode of attachment do not appear to be generally reliable indicators of taxonomic limits (at least in the species studied) as has been thought by earlier investigators (e.g. Boergesen 1915 *et seq.*; Bornet 1904; Drew 1928; Hamel 1927; Rosenvinge 1909), and many species limits probably require revision.

Host Specificity

Rosenvinge (1909, p. 82) first suggested that some species were confined to certain hosts, but four of the six endophytic species cited as examples by him were known at that time from only one or two collections, and the other two were known from only a small but unspecified number of collections. Nevertheless, Rosenvinge's observations quickly became incorporated into audouinelloid systematics (Boergesen 1915; 1919, p. 322; Weber van Bosse 1921, p. 194), and Baardseth (1941, p. 46) later noted "... it has become common practice to describe plants of *Acrochaetium* as new as soon as they are found in a new host". Many authors (e.g. Chapman 1962; Dawson 1953; Drew 1928; Hamel 1927; Hoyt 1920; Kylin 1944; Levring 1935 *et seq.*) have regarded host specificity as an important taxonomic criterion, and Boney and White (1967*a*) have indicated the reliance placed upon it in classifying the endozoic members of the complex.

It is becoming increasingly clear that most or all species are not confined to single hosts and that taxonomic limits based on host specificity are probably arbitrary and unrealistic. *Audouinella botryocarpa*, for example, was thought to grow only on *Scytosiphon* (Levring 1953, p. 484) but is now known to occur on a wide variety of hosts and on rock (Woelkerling 1970). *Audouinella liagorae* occurs on *Helminthocladia* as well as *Liagora*, and *Audouinella repens*, reported by Boergesen (1915, p. 52; 1920, p. 452) to grow on *Hypnea* and *Griffithsia*, has been found on *Leptosomia* and *Naccaria* in southern Australia. Similar findings for other species have been published by Abbott (1962, pp. 107, 113, 114, 115) and Collins and Hervey (1917, p. 98).

Culture studies also indicate that audouinelloid algae are not bound to particular hosts. *Audouinella botryocarpa*, *A. liagorae*, and *Colaconema polyidis* have been successfully maintained in culture during the present study after isolation from their hosts or when grown from spores. Boney and White (1968), Swale and Belcher (1963), West (1968), and White and Boney (1969) have had similar success.

Most taxa reportedly confined to single hosts are known from one or several collections and have been described as distinct taxa by virtue of growing on a particular host. Many of these taxa probably will be reduced to synonymy when the types can be examined and assessed on more stable morphological criteria.

Spore Germination and Persistence

Spores of audouinelloid algae may be septate (i.e. divide into two or more, usually equal-sized, daughter cells prior to producing filaments) or aseptate (i.e. give rise to filaments directly), and they may be persistent (i.e. the cell representing the original

spore is easily recognized in mature plants) or non-persistent (i.e. the original spore soon loses its identity). These characteristics rapidly increased in systematic importance after Bornet (1904) first commented upon their potential value and have been employed in audouinelloid taxonomy by many phycologists (e.g. Abbott 1962; Boergesen 1915 *et seq.*; Collins 1906; Collins and Hervey 1917; Drew 1928; Feldmann 1942; Hamel 1927; Jao 1936; Levring 1935 *et seq.*; Nakamura 1941, 1944).

Among species in this region, however, both persistent and non-persistent spores occur in *Audouinella repens* (Figs. 11*A*, *B*), and both septate and aseptate spores are found in *Colaconema porphyrae* (Figs. 21*B–G*). *Audouinella liagorae* may have persistent septate spores (Figs. 9*B–E*) or, according to Abbott (1962, p. 100), non-persistent aseptate spores. Abbott (1962) records similar variation in several other species, all of which suggests that criteria associated with spore persistence and germination appear to be unreliable for delimiting species limits in most cases.

Prostrate System

Most epiphytic plants of the species studied have partly or entirely pseudoparenchymatous prostrate systems while endophytic, endozoic, and saxicolous plants generally have non-coherent or entangled filamentous prostrate systems. Harvey-Gibson (1891, p. 204) first attached taxonomic significance to differences in prostrate system structure, and although a number of authors (e.g. Boergesen 1915; Bornet 1904; Levring 1953; Rosenvinge 1909) used these features, few species have been distinguished solely on this basis (see, however, Jao 1936, p. 244).

Considerable intraspecific variation in prostrate system structure occurs in southern Australian taxa. Saxicolous plants of *Audouinella floridula*, for example, produce a filamentous prostrate system while epiphytic plants have a pseudoparenchymatous one (Fig. 8*A*). Most plants of *A. botryocarpa* have pseudoparenchymatous prostrate systems but occasionally (on *Polycera* and *Cladosiphon*) they remain largely filamentous (Woelkerling 1970). *Colaconema spiculiphila* possesses a mainly filamentous prostrate system but pseudoparenchymatous patches occur as well (Figs. 14*G–I*).

Similar variation has been recorded in *Rhodochorton membranaceum* (Kuckuck 1897; Lund 1959; Rosenvinge 1923–4), *Audouinella efflorescens* (Lund 1959), and *Acrochaetium* (= *Audouinella*) *pectinatum* (West 1968). Differences in prostrate system structure, therefore, appear untrustworthy in a number of species as systematic criteria.

Cell length, width, and length/width ratio become important criteria in distinguishing taxa which normally do not form well-developed erect systems (Batters 1896; Jao 1936; Levring 1953), but because most of these taxa are so poorly known, it is difficult to evaluate the taxonomic significance of these criteria until additional populations can be examined.

Erect System

Height

Vegetatively mature plants of southern Australian species range in height from less than 20 μm (*Audouinella australis*) to over 20 mm (*A. floridula*). Maximum height (i.e. the maximum length of erect filaments regardless of reproductive maturity) varies considerably in some species; mature plants of *A. australis* range from 15 to 350 μm tall, those of *A. pectinata* from under 1 to 3 mm tall, and those of *A. liagorae* from under 75 to 400 μm tall. Levring (1935, p. 38), Lund (1959, p. 182), and West (1968, p. 96) have reported similar variation in other species.

Such variation restricts maximum height as a feature in determining taxon limits. It is, however, of some value as a character in keys, since the minimum height of mature plants of some species nearly always exceeds the maximum height of others.

Mode of Development

Erect filaments normally develop in a monopodial manner by means of apical divisions, but in pseudolateral hair production (p. 14), the subterminal cell becomes meristematic after formation of a terminal hair and produces a branch which displaces the originally terminal hair to a lateral position (Figs. 10*F*, 17*D*, 18*C*, 21*L*, 21*P*). This occurs in *Audouinella blumii*, *A. liagorae*, *A. microscopica*, *A. pectinata*, *Colaconema pacifica*, *C. plumosa*, *C. porphyrae*, and *C. tenuissima* in southern Australia.

Kylin (1906, p. 125), who first described this mode of development, interpreted it as sympodial growth, and Boergesen (1915, p. 31), Lund (1942, p. 55; 1959, p. 174), Nakamura (1941, p. 289), and Rosenvinge (1909, p. 83; 1911, p. 211) followed suit. Drew (1928) even distinguished two species by the presence or absence of pseudolateral hairs (formed by "sympodial growth").

Growth associated with pseudolateral hair formation does not, however, appear to be truly sympodial. Sympodial growth as generally understood refers to a mode of development which occurs in a regular, predictable way (Dawson 1966, p. 357), and since branching associated with the formation of pseudolateral hairs in the *Audouinella* complex is neither regular nor predictable in all species examined, the term "sympodial" is best not used to describe it. Further work is required to determine the systematic significance of such growth.

Branching

Although the degree of branching and/or branch arrangement has been used to distinguish taxa (e.g. by Boergesen 1915; Collins 1906; Dawson 1953; Drew 1928; Hamel 1928; Kylin 1944; Levring 1953; Rosenvinge 1909), considerable intraspecific variation occurs in these characters among southern Australian species. *Audouinella microscopica* and *Colaconema tenuissima* often produce nearly simple erect filaments (Figs. 10*E*, 21*A*) but more densely branched individuals also occur (Figs. 10*J*, 21*K*). In more or less regularly branched species (e.g. *Audouinella microscopica*, *Colaconema plumosa*), irregular arrangements frequently occur (Figs. 10, 18*C*), and irregularly branched species may likewise have axes or portions of axes with regular branching. Drew (1928) and West (1968) have made similar observations.

Such variation casts doubt on the value of these features in separating taxa in many cases, but the degree of branching may have limited use as a character in keys if the extremes of branching are involved.

Cells

Most southern Australian species have more or less cylindrical cells, but doliiform, fusiform, or irregularly shaped cells occur in a few taxa. Cell width ranges from 3 to 35 μm and length from 5 to 150 μm in the species examined.

Cell shape is of questionable value as a taxonomic character since non-cylindrical cells do not occur regularly in any species studied, but cell dimensions appear to have definite taxonomic value at least in the species studied. Caution must be exercised, however, that recorded limits are not regarded as absolute. Furthermore, it must be

made clear from what portion of the erect filaments cell measurements are taken, since variation in length, width, and length/width ratio can occur from lower to upper portions of filaments. Unless otherwise indicated, the figures recorded here apply to the whole of the erect system.

Hairs and Hair-like Prolongations

Unicellular hairs and multicellular hair-like prolongations occur in a number of southern Australian species and usually lack pyrenoids and contain no or only feebly developed chromoplasts. Hairs are distinctly narrower and longer (up to 450 μm long in *A. liagorae*) than ordinary vegetative cells and arise terminally, but they may become displaced to a lateral position (Figs. 3*A*, 4*L*, 10*F*). Multicellular hair-like prolongations, termed pseudohairs by Hamel (1927, p. 7), occur terminally on erect filaments in which the final cells gradually or abruptly become narrower, more elongate, and less pigmented than normal vegetative cells.

Abbott (1962, p. 92), Boergesen (1915, pp. 15, 22), Drew (1928, pp. 161, 165, 166, 169, 182), Jao (1936), Kylin (1944), and Taylor (1960) among others have attached systematic importance to the occurrence and/or position of hairs and hair-like prolongations. These features, however, do not occur consistently in any southern Australian species and appear, therefore, to be of little or no taxonomic significance. Baardseth (1941, p. 38), Boergesen (1927, p. 20), Hoyt (1920, p. 474), and Rosenvinge (1909, p. 84) have made similar observations.

Chromoplasts

Chromoplasts of audouinelloid algae may be band-shaped, lobate, stellate, spiral, discoid, or irregular in shape and may be parietal (lining the cell walls) or axial (radiating from a central portion along the cell axis) in position. Plastid position is often difficult to determine, especially in taxa with small and/or narrow cells. Erect filaments of most species examined contain one chromoplast per cell, but in *Audouinella floridula* several to many plastids regularly develop.

Ever since Kylin (1906, p. 122) first attached systematic significance to differences in chromoplast shape and number, phycologists have employed these criteria to separate species and/or genera in the *Audouinella* complex (e.g. Kylin 1944; Papenfuss 1945, 1947; Rosenvinge 1909). Some southern Australian species (e.g. *A. botryocarpa*, *A. daviesii*, *A. floridula*) consistently produce plastids of a particular shape, but in other species marked variation occurs. A single erect filament of *A. pectinata*, for example, can have cells with lobate, irregularly discoid, and spiral chromoplasts (Figs. 3*D–L*; see also West 1968, pp. 92, 95). Cells of erect filaments of *A. blumii* usually contain single, irregularly lobate plastids while cells of prostrate filaments have one to several lobate to irregularly discoid plastids (Figs. 1*E–L*). Cells of the erect filaments of *A. botryocarpa*, *A. blumii*, and *Colaconema phacelorhiza* each contain a single chromoplast, but cells of the prostrate system sometimes possess two or more plastids.

Intraspecific variation in chromoplast shape and number has also been noted by Abbott (1962, p. 100), Boergesen (1937, pp. 39, 41), Drew (1928, pp. 156, 176, 177, 182), Feldmann (1962, p. 220), Levring (1937, p. 94), Rosenvinge (1909, pp. 131, 135), and West (1968, p. 98). These criteria therefore appear unreliable for distinguishing genera and, with rare exceptions (e.g. *Audouinella floridula*), species. They may, however, have limited use in taxonomic keys in cases where plastid number and morphology are distinctive and constant.

Pyrenoids

Audouinelloid algae either lack pyrenoids, have only one pyrenoid per chromoplast, or have one to many pyrenoids per chromoplast. The number of pyrenoids per chromoplast appears to be one of the most stable features of audouinelloid algae; all southern Australian species (and, judging from the literature, all members of the complex) can be placed readily and consistently into one of the above groups. Following a thorough examination of all members of the complex, pyrenoids may be found to have generic significance. Recognition of this feature as a determinant for genera is at present, however, premature since this conclusion would be based on work on a limited number of species in one geographic region.

Pyrenoid position, in contrast, has little apparent value as a systematic criterion at least in the species studied. As Rosenvinge (1909, p. 83) stated "... in some species with very thin filaments it may become difficult to decide if the pyrenoid is axial or parietal, and transitions may perhaps occur".

Previously, pyrenoid characteristics have been used in conjunction with chromoplast morphology to distinguish taxa within the *Audouinella* complex by some investigators (e.g. Boergesen 1915; Drew 1928; Kylin 1944; Levring 1937; Rosenvinge 1909).

REPRODUCTIVE FEATURES

Life History

Information on the life history of most audouinelloid algae remains deplorably incomplete. In a few species (e.g. *Audouinella botryocarpa*, *A. daviesii*, and *A. liagorae* in southern Australia), it almost certainly involves an alternation of haploid sexual and diploid tetrasporophyte generations with a diploid carposporophyte attached to the gametophyte (see also Drew 1928; Rosenvinge 1909; Swale and Belcher 1963). Both the haploid and the diploid tetrasporophyte generations reproduce asexually by means of monospores, a feature known in only a few other taxa of Florideophycidae.

West (1968) and Knaggs and Conway (1964) reported a slightly heteromorphic alternation of generations in several species, and West (1969) found a diphasic alternation in *Rhodochorton purpureum*, but an isomorphic alternation occurs in the majority of species so far as is known. Cytological evidence relating to the occurrence of an alternation of generations has been presented by Knaggs (1964) and Magne (1964).

Sexual stages have been described for some additional species (e.g. *A. blumii*, *A. dictyotae*), but tetrasporophytes of these are unknown. Svedelius (1915) and many subsequent authors assumed that meiosis occurred soon after fertilization, that both sexual and carposporophytic stages were haploid, and that no tetrasporophytic stage existed in these species. It is just as likely, however, that tetrasporophytes exist but either have not been found or have been described as distinct species.

Most taxa are not known to reproduce sexually and have been assigned to the *Audouinella* complex on non-sexual features alone. Sexual reproduction may have been lost or never developed (Papenfuss 1945, p. 304), sexual stages may exist but either have not been found as yet or have been described as distinct species, or these taxa may represent stages in the life histories of other Rhodophyta (p. 2; see also Magne 1967). Additional studies are needed to clarify the full life cycle of such species.

The presence or absence of sexual reproduction has been employed to distinguish both genera and species. Bornet (1904) proposed placing sexual species in one genus (*Chantransia*) and asexual species in another genus (*Acrochaetium*) and was followed by Collins (1906). Feldmann (1962) reserved *Rhodochorton* for asexual taxa with discoid chromoplasts.

Rosenvinge (1909, p. 80) argued that Bornet's system "... would not lead to a natural classification of species ...", and according to Fritsch (1945, p. 450) this opinion was accepted by later authors. Nevertheless, the *type* of classification suggested by Bornet appears to be the most logical way of dealing with this complex at the present time and has been adopted in this paper (p. 7). The use of *Colaconema* Batters as a form genus for asexually reproducing audouinelloid taxa not only helps to clarify relationships within the complex by segregating out taxa of uncertain systematic status, but it also permits a more "natural" classification of those species known to reproduce sexually.

Bornet's choice of generic names cannot be adopted here because *Chantransia*, as previously shown (p. 3), is not available for use for audouinelloid algae and because the type species of *Acrochaetium*, known to reproduce sexually, is considered to belong to *Audouinella* (p. 5).

Several authors (e.g. Boergesen 1915, p. 15; Hamel 1927, p. 11; Rosenvinge 1909, pp. 86, 127) employed the presence or absence of sex organs to distinguish species, but this feature is used here in the definition of genera, and therefore cannot be used to distinguish species.

Monosporangia

Monosporangia develop throughout the year and are the only known method of reproduction for many species. Sporangia may be sessile or on simple or branched stalks, may occur singly, in pairs, or occasionally in clusters, and are distributed over the erect (rarely the prostrate) filaments in an irregular, seriate (secund), alternate, opposite, axillary, and/or fasciculate manner in the species examined. Among species in southern Australia sporangia vary in size from 4 μm wide by 5 μm long in *Audouinella microscopica* and *Colaconema macula* to 24 μm wide by 40 μm long in *Audouinella botryocarpa.* In some species (e.g. *A. botryocarpa*, *Colaconema plumosa;* see also Boney 1967; Levring 1935; Rosenvinge 1909), several monosporangia may form successively either from repeated division products of one stalk cell or from the entire contents of subtending stalk cells.

Batters (1896, p. 8) created *Colaconema* for audouinelloid algae with monosporangia subtended by cup-like stalk cells, and Kylin (1944, p. 29) distinguished *Colaconema* by the presence of intercalary sporangia. These criteria appear to be of dubious taxonomic value, but further study is needed to clarify the situation. As recognized here, *Colaconema* includes all audouinelloid algae unknown in the sexual state.

Both the manner in which monosporangia are borne (sessile, stalked, etc.; see Boergesen 1915; Drew 1928; Rosenvinge 1909) and the manner in which monosporangia are arranged (see Boergesen 1915 *et seq.*; Drew 1928; Levring 1953; Taylor 1957) have been used to distinguish species, but both vary significantly in the species examined and appear to be unreliable in most cases for making specific distinctions. Although monosporangia are largely sessile in some species (e.g. *Audouinella*

blumii, *A. dictyotae*, *Colaconema tenuissima*) and are largely on branched stalks in others (e.g. *Audouinella daviesii*, *A. pectinata*), frequent exceptions occur. Some species may commonly have axillary (e.g. *A. barbadense*, *A. daviesii*), seriate (*A. microscopica*, *A. thuretii*), or opposite (*Colaconema plumosa*) sporangia, but in no species do these arrangements occur exclusively or consistently.

Differences in monosporangium size definitely appear to have systematic significance at the species level and have been used by some authors in the past (Rosenvinge 1909; Taylor 1957, etc.). Measurements recorded here are based on southern Australian material and do not necessarily represent the known size range for these species from elsewhere.

Bisporangia

Bisporangia occur on some sexual plants of *Audouinella dictyotae* (Figs. 13*C*, *E*) in southern Australia and have been recorded for eight other species (*Acrochaetium actinocladium* Abbott 1962, *A. alcyonidae* Jao 1936, *A. canariense* Boergesen 1927, *A. intermedium* Jao 1936, *A. mahumetanum* Hamel 1927, *A. occidentale* Boergesen 1915, *Chantransia bispora* Boergesen 1910, *Rhodochorton bisporiferum* Baardseth 1941). Nothing is known cytologically about these spores, and although presumably haploid in *Audouinella dictyotae*, they may represent abortive or incompletely divided tetraspores in other species. Baardseth (1941) and Jao (1936) attached systematic value to them, but because of infrequent occurrence and cytological uncertainty, their taxonomic significance cannot be assessed at present.

Tetrasporangia

Tetrasporangia are known for 10 southern Australian species and, with rare exceptions, are larger than monosporangia and cruciately divided. Abbott (1962, p. 101) and Boergesen (1927, p. 20) recorded irregularly zonately divided sporangia; one such sporangium has been found in *Audouinella liagorae* (Fig. 9*H*). Knaggs (1966*a*) has provided evidence to indicate that, in one species at least (*Rhodochorton purpureum* (Lightf.) Rosenvinge), light intensity plays an important role in tetrasporangial formation.

The presence or absence of tetrasporangia has been used to distinguish both genera (Naegeli 1861) and species (Boergesen 1937, pp. 32, 43). Drew (1928), however, has concluded that generic distinctions could not be made on this basis, and her conclusions are supported here. It also follows that specific distinctions based on the presence or absence of tetrasporangia probably are also systematically unsound.

Multipartite Sporangia

Multipartite sporangia have not been observed in this study, but are reported in *Acrochaetium polysporum* Howe (1914) and *A. multisporum* Boergesen (1937). Both authors regarded them as the distinguishing features of the species.

According to Drew (1937, 1939), two types of multipartite sporangia occur: polysporangia (formed meiotically) and parasporangia (formed mitotically). Howe and Boergesen used the term polysporangium, but since cytological data are lacking, it seems best to term them multipartite sporangia. Their systematic significance, if any, remains unconfirmed.

Spermatangia

Spermatia develop in spermatangia which may be sessile on a vegetative filament, terminal or lateral in groups of one to three on one- or two-celled stalks, or form a part of a spermatangia cluster on a branched stalk system (Figs. 5*A–C*, 7*G*, 11*H*). Stalk cells are nearly always distinctly smaller than other vegetative cells, may contain only poorly developed chromoplasts, and in most cases form a small branch system. The terms androphore (Rosenvinge 1909, p. 141; Hamel 1927, p. 9, etc.), antheridium (Rosenvinge 1909; Drew 1928; Levring 1935, etc.) and spermatocysta (Feldmann 1962) have been discarded in favor of the more widely accepted terms spermatangium and stalk cell.

Rosenvinge (1909, p. 141) established *Kylinia* for taxa with spermatangia borne on "androphore cells", and Feldmann (1962) characterized both *Kylinia* and *Balbiania* by this type of stalk cell. Papenfuss (1945, p. 304), however, regarded the presence of "androphores" as insignificant generically. Moreover, they have not been found in the type or other collections of *Audouinella australis* examined by the writer, contrary to the report of Levring (1953, p. 489). Unless Levring was mistaken in his observations, these "androphores" appear to occur unpredictably; Levring himself (1953, p. 488, Fig. 21) illustrated both sessile and stalked spermatangia. This suggests that generic segregation based on the presence or absence of "androphores" is unsound.

Similarly, Swale and Belcher (1963), contrary to Feldmann (1962), did not regard the spermatangial morphology of *Rhodochorton* (= *Balbiania*) *investiens*, the type species of *Balbiania*, to be sufficiently distinct to warrant generic segregation.

The number of spermatangia per cluster, spermatangial position, and form of the spermatangial clusters (i.e. corymbose, lateral circinnate, paniculate) have been used to distinguish species (Abbott 1962; Drew 1928; Hamel 1927; Rosenvinge 1909). However, *Audouinella barbadense*, *A. dictyotae*, and *A. repens* produce spermatangia singly, in pairs, and in clusters (Figs. 6*F*, *G*, 11*H*, 13*E–G*) and *A. barbadense*, *A. liagorae*, *A. repens*, and *A. australis* produce both terminal and lateral clusters (Figs. 5*A–C*, 6*F*, *G*, 9*J*, *M*, *N*, 11*H*). *A. dictyotae* may or may not have spermatangia on carpogonial stalk cells (Figs. 13*E–G*), and in *A. botryocarpa* spermatangia may occur as corymbose, unilateral, or paniculate clusters or they may form sessile or stalked groups of one to three (Woelkerling 1970). Hence specific distinctions based on differences in spermatangial morphology appear too variable to be taxonomically reliable at least in the species examined.

Carpogonia

The carpogonium of audouinelloid algae consists of a more or less bottle-shaped ventral portion and a trichogyne and may be sessile on a vegetative filament, terminal on a simple or rarely a branched stalk, or according to Rosenvinge (1909) and West (1969) intercalary in a filament. Stalk cells are generally smaller than other vegetative cells and bear only one carpogonium, but in *A. dictyotae* up to three carpogonia form on a single stalk cell (Fig. 13*I*). Drew (1928) referred to the unfertilized female organ as a procarp, a term no longer used for such a structure.

Feldmann (1953, 1962) proposed the order Acrochaetiales (p. 7) for audouinelloid algae because of their simple vegetative structure and "... par l'absence de rameau carpogonial ...". Dixon (1964) has discussed the concept of a carpogonial branch and

Dawson (1966, p. 350) defined a carpogonial branch as a "reproductive filament or row of cells terminating in a carpogonium". If one accepts this definition, species of *Audouinella* may or may not have a carpogonial branch. For the sake of clarity and consistency, the term carpogonial branch is best discarded (with reference to *Audouinella*) in favor of carpogonium and subtending stalk cell(s), the latter being homologous with stalk cells bearing other reproductive structures.

Post-fertilization Development and the Carposporophyte

The fertilized carpogonium may divide either transversely or longitudinally (Abbott 1966; Yamada 1944), or it may give rise directly to gonimoblast filaments and/or carposporangia (Figs. 13*J–N*). Mature gonimoblasts consist of a few cells or short filaments bearing terminal and/or lateral carposporangia.

A sterile filament sometimes arises from the carpogonial stalk cell shortly before or after fertilization in *A. barbadense*, *A. botryocarpa*, *A. daviesii*, and *A. dictyotae* (Figs. 7*J*, 13*H*, *L*).

Differences in immediate post-fertilization activity (i.e. whether the fertilized carpogonium divides transversely, longitudinally, or not at all) have been used to distinguish genera within the *Audouinella* complex (Feldmann 1962; Yamada 1944). However, the fertilized carpogonium of *Audouinella dictyotae* may either divide transversely or cut off gonimoblast cells and/or carposporangia without dividing (Fig. 13*J*); Woelkerling (1970) reported a similar situation in *A. botryocarpa*. This variation indicates that immediate post-fertilization events may not be reliable taxonomic criteria, but further investigations on other species are needed.

CONCLUSIONS

The presence or absence of sexual reproduction is considered to provide useful separation of the two southern Australian genera recognized (*Audouinella* and *Colaconema*) while the number of pyrenoids per chromoplast, cell dimensions of erect filaments, monosporangial dimensions, and in some taxa, cell dimensions of the prostrate filaments are important taxonomic characters at the specific level. Heterotrichy, the type of prostrate system, and the degree of branching of erect filaments may be of value as characters in keys.

Morphological features of apparently limited systematic value include length of erect filaments, chromoplast shape, number of chromoplasts per cell, sporangial arrangement, and method of sporangial attachment (sessile *v.* stalked).

Characteristics apparently too variable to be of taxonomic value at least among the species studied include mode of attachment to the substrate, host specificity, branch arrangement, type of spore germination, presence or absence of hairs, hair-like prolongations, tetrasporangia, and "carpogonial branches", position of hairs and of pyrenoids, and spermatangial morphology.

It has not been possible to assess fully the systematic value of mode of development of erect filaments, monosporangium shape, carposporangial dimensions, immediate post-fertilization development, and the presence or absence of bisporangia, multipartite sporangia, and "androphores".

Audouinelloid algae have always been difficult to separate taxonomically. As Hoyt (1920, p. 469) wrote: "It is often impossible to decide with certainty to what species a single given plant should be referred". Whenever possible, numerous plants should be examined to build a composite picture of the population before identification is attempted.

IV. Key to Southern Australian Audouinelloid Algae

The *Audouinella* complex is represented in southern Australia by *Audouinella* (12 species) and *Colaconema* (14 species), but since species of *Audouinella* are not often found in the sexual state, the two groups are combined in the analytical key hereunder.

1. Prostrate system present; filamentous or pseudoparenchymatous 2
1. Prostrate system almost always absent; plants attached to substrate by a single cell which may rarely divide to form several cells 24
2. Erect filaments present, 75 μm to 25 mm long and almost always consisting of more than 5 cells 3
2. Erect filaments absent or less than 50 μm long and almost always consisting of 5 or fewer cells 27
3. Erect filaments generally over 1 mm long and in most plants (except in some individuals of *Audouinella botryocarpa*) far exceeding the prostrate filaments in length 4
3. Erect filaments generally less than 600 μm long (rarely to 1 mm); longer than, equal to, or shorter than the prostrate filaments 17
4. Erect filaments mostly less than 12 μm in diameter in lower portions 5
4. Erect filaments mostly more than 12 μm in diameter in lower portions 12
5. Monosporangia mostly less than 15 μm long 6
5. Monosporangia mostly more than 15 μm long 7
6. Cells of erect filaments commonly over 5 diameters long 10
6. Cells of erect filaments rarely over 5 diameters long 20
7. Erect filaments mostly 10 μm or less in diameter in lower portions 8
7. Erect filaments mostly 10–12 μm in diameter in lower portions 11
8. Monosporangia mostly more than 18 μm long 9
8. Monosporangia mostly less than 18 μm long 10
9. Erect filaments simple or sparingly branched, commonly less than 7 μm in diameter in lower portions; monosporangia almost always sessile ..... *C. tenuissima*, p. 51
9. Erect filaments generally richly branched, mostly 7–10 μm in diameter in lower portions; monosporangia sessile or stalked ..... *A. thuretii*, p. 36
10. Cells of erect filaments 2–4 diameters long in lower portions, 5–20 diameters long in upper portions; filaments mostly simple or sparingly branched; prostrate system filamentous; pyrenoids present ..... *A. repens*, p. 35
10. Cells of erect filaments (2–)5–8 diameters long throughout; filaments richly branched; prostrate system pseudoparenchymatous; pyrenoids absent ..... *A. pectinata*, p. 24
11. Monosporangia arranged in part at least in groups of 4–8 on branched stalks..... *A. daviesii*, p. 28
11. Monosporangia solitary or in pairs, sessile or on unicellular stalks ..... *A. thuretii*, p. 36
12. Sporangia 3–8 μm wide and 6–12 μm long; erect filaments more or less distichously branched ..... *C. plumosa*, p. 48
12. Sporangia 8 μm or more wide and 12 μm or more long; erect filaments irregularly to secundly branched 13
13. Erect filaments commonly over 15 mm long and over 18 μm in diameter; cells with 3–10 parietal more or less stellate chromoplasts each with a single pyrenoid..... *A. floridula*, p. 30
13. Erect filaments less than 10 mm long and mostly less than 20 μm in diameter (occasionally to 30 μm wide); cells with a single chromoplast with one or more pyrenoids 14
14. Monosporangia 8–13 μm wide and 14–19(–24) μm long, arranged in part at least in groups of 4–8 on branched stalks ..... *A. daviesii*, p. 28
14. Monosporangia (10–)12–18 μm wide and 16–25(–40) μm long, mostly solitary or in pairs (rarely in groups of 3 or more) 15
15. At least some monosporangia with distinctly apically thickened walls; chromoplasts each with only one pyrenoid ..... *C. phacelorhiza*, p. 48
15. Monosporangia with walls not thickened at the apex; chromoplasts with one to several pyrenoids 16

16. Erect filaments mostly 10–16 μm in diameter in lower portions and normally not ending in hair-like prolongations; monosporangia commonly sessile; carposporophytes usually producing 10 or fewer globose, thick-walled carposporangia 18–30 μm in diameter ..... *A. dictyotae*, p. 38

16. Erect filaments mostly (10–)15–20(–30) μm in diameter in lower portions and sometimes ending in hair-like prolongations; monosporangia mostly stalked; carposporophytes producing 12–30 or more ovoid, thin-walled carposporangia up to 35 μm long and 25 μm wide ..... *A. botryocarpa*, p. 37

17. Cells of prostrate filaments generally distinctly narrower than cells of erect filaments; pyrenoids absent ..... *A. blumii*, p. 23

17. Cells of prostrate filaments generally equal to or greater in diameter than cells of erect filaments; pyrenoids present 18

18. Monosporangia mostly 3–9 μm wide and 6–14 μm long 19

18. Monosporangia mostly 8–20 μm wide and 15–35 μm long 21

19. Erect filaments 300–800 μm long; cells of erect filaments commonly over 20 μm long 20

19. Erect filaments rarely over 100 μm long; cells of erect filaments less than 20 μm long 29

20. Erect filaments mostly 4–7 μm wide and irregularly branched; sporangia scattered on the erect filaments ..... *C. pacifica*, p. 47

20. Erect filaments mostly 9–11 μm wide and distichously branched; sporangia largely opposite ..... *C. plumosa*, p. 48

21. Monosporangia mostly 8–11 μm wide and 12–18 μm long; cells of erect filaments generally 10 μm or less in diameter 22

21. Monosporangia mostly 12–14(–18) μm wide and 13–35 μm long; cells of erect filaments (3–)8–18(–24) μm in diameter 23

22. Cells of erect filaments 4–7 μm wide and 5–20 diameters long in upper portions; carposporangia mostly 14–20 μm long ..... *A. repens*, p. 35

22. Cells of erect filaments 7–10(–18) μm wide and rarely more than 5 diameters long; carposporangia mostly 12–15 μm long ..... *A. barbadense*, p. 26

23. Cells of prostrate filaments (12–)18–24 μm in diameter and generally wider than cells of erect filaments ..... *C. polyidis*, p. 49

23. Cells of prostrate filaments (3–)8–15 μm in diameter and more or less equal to the diameter of cells of the erect filaments ..... *A. liagorae*, p. 31

24. Monosporangia 8–15(–18) μm long; erect filaments commonly 1–2 mm long ..... *A. pectinata*, p. 24

24. Monosporangia 5–10 μm long; erect filaments under 300 μm long 25

25. Cells of erect filaments 5–25 μm (1–5 diameters) long; holdfast cell generally hemispherical or pyriform and flattened on the side in contact with the substrate; erect filaments commonly procumbent ..... *A. australis*, p. 25

25. Cells of erect filaments 3–12 μm (0.75–2 diameters) long; holdfast cell cylindrical or globose and not distinctly flattened on side in contact with the substrate; erect filaments upright or arcuate, only rarely procumbent 26

26. Cells 3–12 μm wide, barrel-shaped, commonly isodiametric or broader than long; erect filaments often arcuate ..... *A. microscopica*, p. 33

26. Cells 3–6 μm wide, cylindrical, commonly isodiametric or longer than broad; erect filaments upright and more or less straight ..... *C. nakamurai*, p. 46

27. Cells of prostrate filaments 1–3 diameters long 28

27. Cells of prostrate filaments frequently more than 3 diameters long 31

28. Monosporangia 6–9 μm wide and 8–15 μm long; cells of erect filaments 4–9 μm wide and 8–18 μm long 29

28. Monosporangia 3–6 μm wide and 4–8 μm long; cells of erect filaments 2–5 μm wide and 3–6(–9) μm long 30

29. Cells of prostrate filaments 4–6 μm wide and 5–7 μm long; prostrate system usually pseudoparenchymatous ..... *C. humilis*, p. 44

29. Cells of prostrate system (2–)5–12(–42) μm wide and 12–30(–100) μm long; prostrate system filamentous ..... *C. porphyrae*, p. 50

30. All cells 3–5 μm wide and 4–6(–8) μm long; monosporangia 4–5 μm wide and 5–7 μm long ..... *C. macula*, p. 45
30. All cells 2–3 μm wide and 3–6 μm long; monosporangia 3–4 μm wide and 4–6 μm long ..... *Acrochaetium subreductum*, p. 52
31. Cells of prostrate system nearly always less than 30 μm long 32
31. Cells of prostrate system commonly more than 30 μm long 34
32. Prostrate system composed of both non-confluent filaments and pseudoparenchymatous regions ..... *C. spiculiphila*, p. 40
32. Prostrate system entirely filamentous 33
33. Monosporangia 4–6 μm wide and 4–6 μm long; cells of prostrate filaments 2–4 μm wide ..... *C. deliseae*, p. 43
33. Monosporangia 6–12 μm wide and 8–14 μm long; cells of prostrate filaments 2.5–12(–42) μm wide 34
34. Cells of prostrate filaments mostly 3–8 μm wide and 1–20 diameters long 35
34. Cells of prostrate filaments (2.5–)6–12(–42) μm wide and 1–5(–8) diameters long 36
35. Cells of prostrate filaments 6–45 μm (2–8 diameters) long; pyrenoids present ..... *C. bonnemaisoniae*, p. 42
35. Cells of prostrate filaments 20–135 μm (3–20 diameters) long; pyrenoids absent ..... *C. spongiocola*, p. 41
36. Monosporangia 10–14(–18) μm wide and 13–24(–35) μm long; erect filaments (3–)8–15 μm wide ..... *A. liagorae*, p. 31
36. Monosporangia 6–13 μm wide and 6–14 μm long; erect filaments 3–9 μm wide 37
37. Monosporangia globose to lenticular, 9–13 μm wide and 6–13 μm long, commonly in clusters of 2–6 ..... *C. americana*, p. 42
37. Monosporangia ovoid, 6–9 μm wide and 8–14 μm long, mostly solitary ..... *C. porphyrae*, p. 50

V. Descriptions of Taxa

AUDOUINELLACEAE nom. nov.

Plants composed of monosiphonous simple or branched filaments, generally less than 5 mm (rarely to 25 mm) tall. Asexual reproduction by monospores, bispores, tetraspores, and/or multipartite spores. Carpogonia sessile on cells of vegetative filaments, intercalary in vegetative filaments, or one to several together terminating one (rarely more)-celled stalks. Gonimoblast, when present, formed directly from the fertilized carpogonium; pericarp absent.

Type Genus.–*Audouinella* Bory.

Genus AUDOUINELLA Bory

Audouinella Bory 1823: 340 (as *Auduinella*). *Acrochaetium* Naegeli 1861: 402. *Balbiania* Sirodot 1876: 149. *Chromastrum* Papenfuss 1945: 320. *Grania* Kylin 1944: 26. *Rhodochorton* Naegeli 1861: 355. *Thamnidium* Thuret in Le Jolis 1863: 110. *Trentepohlia* Pringsheim 1862: 29.

Note.–Species now referable to *Audouinella* have also been placed in the past in *Byssus*, *Callithamnion*, *Ceramium*, *Chantransia*, *Conferva*, *Kylinia*, and *Trentepohlia* Martius. In addition, some species hitherto placed in *Acrochaetium*, *Audouinella*, *Chromastrum*, and *Rhodochorton* are referable here to the form genus *Colaconema* (p. 40).

Plants epiphytic, endophytic, epizoic, endozoic, or saxicolous; attached to or suspended in the substrate by a single basal cell or by a prostrate system of simple or branched filaments which may or may not become pseudoparenchymatous. Erect filaments simple or branched, up to 25 mm long; cells containing one or occasionally several variously shaped chromoplasts with or without pyrenoids.

Asexual reproduction by monosporangia, bisporangia, and/or tetrasporangia; sporangia sessile or stalked and borne on erect or prostrate filaments.

Plants monoecious or dioecious. Spermatangia in clusters or occasionally single or in pairs, terminal or lateral on simple or branched stalks or sessile on ordinary vegetative cells. Carpogonia sessile or terminating 1–2-celled stalks, solitary or rarely in groups of 2–3; remaining undivided or dividing transversely after fertilization, and eventually giving rise to gonimoblast filaments and/or carposporangia.

Type Species.–*Audouinella hermanni* (Roth) Duby.

The 12 species of *Audouinella* recorded from southern Australia are divided into three sections based on the occurrence of pyrenoids; within each section the species are discussed in alphabetical order by specific epithet.

SECTION I

The species in this section are not known to contain pyrenoids in their chromoplasts. For brevity and greater clarity, the ratio of greatest cell length to greatest cell width is denoted by L/D in all species diagnoses. Thus L/D 2–4(–4.5) means cells 2–4(–4.5) diameters long.

Audouinella blumii sp. nov.

Fig. 1

Plantae plerumque vel omnino endophyticae; filamenta prostrata ramosa irregulariter et parce, non-confluentia, intra matricem gelatinam hospitis repenta; cellulae plus minusve cylindriceae, 3–5 μm diametro, 20–45 μm longae (L/D 6–10), cellula omnis chromoplasto uno lobato, interdum in partum aliquot discoideum irregularem dividenti; pyrenoides absentes. Filamenta erecta ad 300 μm longa (pili excludentes), ab cellulis filamentorum prostratorum in intervalis irregularibus orientia, simplicia vel ramis lateralibus brevis simplicibus. Cellulae cylindriceae, 5–8 μm diametro, 15–30 μm longae, L/D 2–4(–4.5), cellula omnis chromoplasto uno parietali lobato irregulari; pyrenoides absentes. Pili terminalis et pseudolateralis ad 300 μm longi ferentia.

Monosporangia ovata, 7–10 μm diametro, 15–18 μm longa, sessilia, lateralia, in filamentis erectis dispersis.

Carpogonia sessilis vel pedicellata, in filamentis prostratis vel erectis, post fecundatione transverse dividentia, filamenta brevia gonimoblasta carposporangiis terminalibus (4.5–)5–6(–7.5) μm diametro, 8–12 μm longis efferentia.

Plants largely or entirely endophytic; sporelings unknown. Prostrate system consisting of sparingly irregularly branched non-confluent filaments creeping within the gelatinous matrix of the host. Cells more or less cylindrical, 3–5 μm wide and 20–45 μm long, L/D 6–10; each cell containing an irregularly lobate chromoplast which sometimes becomes divided into several irregularly discoid portions; pyrenoids absent. Erect filaments up to 300 μm tall (exclusive of hairs), arising at irregular intervals from cells of the prostrate filaments; simple or with several short unbranched laterals. Cells cylindrical, 5–8 μm wide and 15–30 μm long, L/D 2–4(–4.5); each cell containing a parietal, irregularly lobate chromoplast; pyrenoids absent. Terminal and pseudolateral hairs up to 300 μm long occur.

Monosporangia ovoid, each 7–10 μm wide and 15–18 μm long, solitary, sessile, and scattered on the erect filaments.

Tetrasporangia and spermatangia unknown.

Carpogonia sessile or stalked, on prostrate and erect filaments; dividing transversely after fertilization and giving rise to short gonimoblast filaments bearing terminal carposporangia, each (4–)5–6(–8) μm wide and 8–12 μm long.

Type Locality.–Antechamber Bay, Kangaroo I., S.A.

Holotype.–ADU, A31980.

Distribution.–Type locality only.

Hosts.–*Helminthocladia australis* Harvey; *H. densa* (Harvey) Schmitz et Hauptfleisch.

Specimens Examined.–SOUTH AUSTRALIA: Antechamber Bay (Kangaroo I.), 20.xi.1967, *Woelkerling* (ADU, A31980, type); 20.xi.1967, *Woelkerling* (ADU, A32121). *Note*.–These specimens also contain plants of *Audouinella liagorae*.

This species is named in honor of Professor John L. Blum, University of Wisconsin–Milwaukee, who has contributed greatly to algal taxonomy and ecology and who guided my early algal studies.

Audouinella blumii is distinctive in having prostrate filaments narrower than erect filaments, most erect filaments simple and under 300 μm long, chromoplasts without pyrenoids, and sessile monosporangia. It appears quite distinct from other species lacking pyrenoids (*A. efflorescens* (J. Ag.) Papenfuss, *A. membranacea* (Magnus) Papenfuss, and *A. pectinata* (Kylin) Papenfuss) in features of cell dimensions, thallus size, habit, and development of prostrate and erect systems.

Audouinella pectinata (Kylin) Papenfuss 1945:. 326; 1947: 439. Norris et West 1967: 113.

Acrochaetium pectinatum (Kylin) Hamel 1927: 103; 1928: 197. Kylin 1944: 21, fig. 13. Sundene 1953: 185. West 1968: 89, figs. 1–28.

Chantransia pectinata Kylin 1906: 120, figs. 6, 7; 1907: 119. Rosenvinge 1909: 138, figs. 65, 66.

Rhodochorton pectinatum (Kylin) Rosenvinge 1935: 7.

Figs. 2, 3

Plants epiphytic, caespitose, up to 3 mm tall; original spore persisting as a more or less globular, thick-walled, unicellular holdfast (in sexual plants) 7–14 μm in diameter, giving rise to (1–)2–3(–5) sparsely to moderately branched erect filaments. Major laterals irregularly arranged, sometimes approaching the main axis in length; simple or bearing a few irregularly to fasciculately arranged branchlets. Cells cylindrical, 3–6 μm wide and 5–40 μm long, L/D (1–)3–6(–9); each cell containing a parietal lobate to stellate to spirally twisted chromoplast which may become dissected into several portions; pyrenoids absent. Terminal and pseudolateral hairs up to 100 μm long occur.

Monosporangia ovoid, 5–7(–10) μm wide and 8–15(–18) μm long, sessile or 1–2(–3) on unicellular stalks or occasionally in clusters of 4–10 on branched stalks, scattered over the erect filaments.

Spermatangia ovoid, up to 3 μm wide and 4 μm long, borne singly or in pairs in terminal or lateral clusters on branched stalks or singly or in pairs on 1–2-celled stalks.

Other reproductive structures unknown in southern Australian collections.

Type Locality.–Halland coast of Sweden.

Holotype.–?

Distribution.–Port Elliot, S.A. Denmark, Sweden, Pacific coast of North America.

Hosts.–*Audouinella daviesii* and *Dictyopteris nigricans* in southern Australia.

Specimens Examined.–SOUTH AUSTRALIA: Port Elliot, 31.i.1968, *Woelkerling* (ADU, A32233); 1.iii.1968, *Woelkerling* (ADU, A32249); 3.iv.1968, *Woelkerling* (ADU, A32259).

The southern Australian collections of *Audouinella pectinata* agree in vegetative features with plants described in the original account (Kylin 1907) and are referred to this species (not recorded previously from the field in the sexual state) because of their general similarity to gametophytes cultured by West (1968). West (1968) described female and carposporophytic structures from cultured plants, and Kylin (1907) recorded tetrasporangia.

The relationships of *A. efflorescens* (J. Agardh) Papenfuss and *A. pectinata* (Kylin) Papenfuss require clarification. Rosenvinge (1909) separated *A. pectinata* and *A. efflorescens* on differences in cell size and sporangial arrangement, but plants intermediate in both characters occur in southern Australian collections and in the cultures of West (1968).

Both *Acrochaetium dufourii* Collins and *A. hoytii* Collins (for descriptions, see Hoyt 1920) are similar in a number of features to *Audouinella pectinata*, but until the presence or absence of pyrenoids has been established for these taxa, no definite conclusions can be drawn, and they must be regarded as specifically distinct.

Chantransia baltica Rosenvinge (1909), *C. hallandica* Kylin (see Rosenvinge 1909, p. 93), *Rhodochorton ryukense* Nakamura (1941), *Acrochaetium sargassi* Boergesen (1915), and *Rhodochorton simplex* Drew (1928) also resemble sexual plants of *Audouinella pectinata* but differ in the possession of pyrenoids.

SECTION II

Species in this section have chromoplasts with only one pyrenoid each.

Audouinella australis (Levring) comb. nov.

Kylinia australis Levring 1953: 487, figs. 21*A–G*. Boney and White 1967: 595.

Figs. 4, 5

Plants epiphytic, (15–)40–100(–350) μm tall; original spore persisting as a hemispherical, unicellular base appressed to the substrate, 6–9 μm wide and 7–12 μm long, rarely dividing to form a two-celled prostrate system or occasionally becoming obscured by the erect filaments. Filaments of erect system usually 1–3, procumbent to semi-upright or occasionally coiling about the host; simple or with a few irregularly

arranged laterals. Cells cylindrical, 3–6(–8) μm wide and 5–25 μm long, L/D 1–5; each cell containing a single parietal lobate chromoplast and (Levring 1953) one pyrenoid. Terminal hairs up to 75 μm long occur.

Monosporangia ovoid, 4–6 μm wide and 6–10 μm long, terminal or lateral, single or rarely in pairs, sessile or occasionally on 1–2-celled stalks, scattered or occasionally restricted to the lower portions of the plants. Tetrasporangia unknown.

Spermatangia globose, up to 3 μm in diameter, terminal or rarely lateral in groups of 1–3, sessile on vegetative filaments. Carpogonia terminal or lateral, sessile or stalked; immediate post-fertilization stages unknown. Mature carposporophytes consisting of several short gonimoblast filaments bearing terminal carposporangia, each 5–7 μm wide and 8–12 μm long.

Type Locality.–Pennington Bay, Kangaroo I., S.A.

Holotype.–Herbarium T. Levring, Goteborg, Sweden (private collection). *Isotype*.–ADU, A31373.

Distribution.–Venus Bay to Robe, S.A. including Kangaroo I.

Hosts.–*Audouinella* spp., especially *A. daviesii*.

Representative Specimens Examined.–SOUTH AUSTRALIA: Venus Bay, 12.ii.1954, *Womersley* (ADU, A32110). Seal Bay (Kangaroo I.), 20.xi.1967, *Woelkerling* (ADU, A32103). Stanley Beach (Kangaroo I.), 7.ii.1956, *Womersley* (ADU, A32119); 27.i.1957, *Womersley* (ADU, A32112). Pennington Bay (Kangaroo I.), 7.i.1947, *Womersley* (ADU, A31373, isotype). Marino (Adelaide), 21.v.1953, *Womersley* (ADU, A32111). Robe, 19.viii.1966, *Woelkerling* (ADU, A32100).

The characteristic pyriform basal cell of *Audouinella australis* develops soon after attachment to the substrate (Figs. 4*A–F*) and occasionally divides to form a two-celled prostrate system (Figs. 4*G*, *H*). Pyrenoids have not been observed in material of this species examined during the present study, but Levring (1953, p. 487) recorded one pyrenoid per chromoplast. Freshly collected plants are needed before this matter can be clarified more fully.

Levring (1953, p. 488, Figs. 21*D–F*) described and illustrated male plants bearing terminal spermatangia on so-called "androphore cells", but in all material examined (including liquid-preserved isotype material) spermatangia occur in sessile groups of one to three on ordinary vegetative cells (Figs. 5*A–C*). Consequently this taxon is transferred from *Kylinia*, originally established for taxa producing "androphores", to *Audouinella*.

Short gonimoblast filaments develop after fertilization (Figs. 5*I*, *J*) and bear terminal carposporangia; Levring (1953) stated that carposporangia formed directly from the fertilized carpogonium, but this has not been observed during the present study.

Monosporangial plants of *Acrochaetium unifilum* Jao (1936; non Levring 1953, p. 472) appear to be identical with those of *Audouinella australis* except for minor differences in cell size, but until the type collections can be compared the two are left as distinct species.

Audouinella barbadense (Vickers) comb. nov.

Acrochaetium barbadense (Vickers) Boergesen 1915: 45. Abbott 1962: 83, figs. 1, 2*a*; 1968: 518. Collins et Hervey 1917: 97. Hamel 1927: 70, 88, fig. 41; 1928: 164, 181, fig. 41. Papenfuss 1945: 312.

Chantransia barbadensis Vickers 1905: 60. Bornet 1904: XX (nom. nud.). Collins 1906: 195. De Toni 1924: 47.

Acrochaetium angustum (Drew) Papenfuss 1945: 312.
Rhodochorton angustum Drew 1928: 185, pl. 44, figs. 54–56.
Chantransia liagorae Weber van Bosse 1914: 275. De Toni 1924: 62. Non *Chantransia liagorae* Boergesen 1915: 57.
Acrochaetium liagorae (Weber van Bosse) Hamel 1927: 92; 1928: 185. Non *Acrochaetium liagorae* Boergesen 1915: 58.
Acrochaetium vanbosseae Papenfuss 1945: 318.
Acrochaetium trichogloeae auct. non Boergesen: Abbott 1962: 94 (Australian collection only).

Fig. 6

Plants largely endophytic, developing from persistent spores 12–16(–24) μm in diameter. Prostrate system consisting of creeping, simple to sparingly and irregularly branched non-confluent filaments. Cells irregular to cylindrical in shape, 7–13 μm wide and (12–)20–30(–36) μm long. Erect filaments simple or sparingly and irregularly branched, up to 600 μm long. Cells cylindrical, 7–10(–18) μm wide and (12–)18–35(–75) μm long, L/D 2–4(–8); cells occasionally 5–6 μm wide in laterals; each cell containing a parietal lobate chromoplast and a single pyrenoid. Hairs unknown.

Monosporangia ovoid, 8–10 μm wide and 13–18 μm long, sessile or stalked, single or in pairs, situated on the lowermost cells of the laterals. Tetrasporangia unknown.

Spermatangia ovoid, up to 4 μm wide and 6 μm long, solitary or in groups of 2–3 on 1–2-celled stalks, mostly situated on the lower cells of lateral branches but occasionally scattered or terminal. Carpogonia sessile or stalked, axillary or scattered on the erect filaments; dividing transversely after fertilization and forming short gonimoblast filaments with terminal carposporangia 8–9 μm wide and 12–15 μm long.

Type Locality.–Barbados.

Holotype.–PC.

Distribution.–Marino (Adelaide), S.A. Barbados, Bermuda, Channel I. (California), Guadalupe I. (Mexico), Hawaii.

Hosts.–*Liagora* spp.

Specimens Examined.–SOUTH AUSTRALIA: Marino (Adelaide), 21.v.1953, *Womersley* (ADU, A30880). *Note*.–This collection is recorded by Abbott (1962, p. 94) as *H. B. S. Womersley* A18634; the latter number is now that of the ADU sheet of the host, *Liagora farinosa* Lamouroux.

Southern Australian plants of *Audouinella barbadense* have aseptate spores, but Abbott (1962) recorded both aseptate and septate spores in this species. The massively thickened lateral walls reported in some prostrate filaments by Abbott (1962) do not occur in southern Australian plants, but atypical erect branches composed of almost isodiametric cells are present in several of the plants examined (Fig. 6*B*).

The southern Australian collection of this species was referred by Abbott (1962, p. 94) to *Acrochaetium trichogloeae*, but the plants examined during this study differ from those described in her account of that species in having aseptate spores, lacking hairs, having prostrate filaments 7–13 μm wide and more or less equal in diameter to the erect filaments, and in cell length in both prostrate and erect filaments. These apparent differences may reflect ecological variation within a single taxon, and when possible, the types and other collections of *A. trichogloeae* and *Audouinella barbadense* should be compared. Since southern Australian material agrees more closely with *Audouinella barbadense*, it is referred to that species.

Abbott (1962, 1968) found the holotype specimens of *Rhodochorton angustum* Drew (1928) and *Acrochaetium liagorae* (Weber van Bosse) Hamel (= *A. vanbosseae* Papenfuss) to be identical with *Acrochaetium* (= *Audouinella*) *barbadense*, and her findings are accepted here.

The type collections of *Acrochaetium bornetii* Papenfuss (1945) (= *A. corymbiferum* (Thuret) Batters), *A. comptum* Boergesen (1915), and *A. occidentale* Boergesen (1915), which have not been available for study, also should be compared with *Audouinella barbadense* to determine whether they are specifically distinct from one another. Collins and Hervey (1917, p. 97) suggested that the first may be conspecific with *Audouinella barbadense*, and Abbott (1962) considered the other two to be identical with *A. barbadense.*

Audouinella daviesii (Dillwyn) comb. nov.

Acrochaetium daviesii (Dillwyn) Naegeli 1861: 405, figs. 26, 27. Baardseth 1941: 42, fig. 18. Blackler 1951: 28; 1956: 69, 70. Boergesen 1927: 25, fig. 15. Hamel 1927: 39, 98, fig. 31; 1928: 192; 1928*a*: 133, fig. 31. Levring 1953: 476. Sundene 1953: 183. Taylor 1957: 221, pl. 31, figs. 8–10.

Callithamnion daviesii (Dillwyn) Lyngbye 1819: 129 (excl. var. *secundatum* = *Acrochaetium secundatum* (Lyngbye) Naegeli 1861: 405, non *Chantransia secundata* Heydrich 1892: 475). J. Agardh 1851: 11; 1876: 8. Harvey 1851: pl. 314; 1853: 243. Koschtsug 1873: 13. Kuetzing 1849: 638.

Ceramium daviesii (Dillwyn) C. Agardh 1817: XXVII.

Chantransia daviesii (Dillwyn) Thuret in Le Jolis 1863: 106. Kylin 1907: 117, fig. 27. Levring 1937: 88. Rosenvinge 1909: 104, fig. 34.

Conferva daviesii Dillwyn 1809: 73, suppl. pl. F.

Rhodochorton daviesii (Dillwyn) Drew 1928: 172. Nakamura 1944: 106, fig. 5.

Trentepohlia daviesii (Dillwyn) Areschoug 1847: 338. Farlow 1881: 109.

Acrochaetium amphiroae (Drew) Papenfuss 1945: 312.

Rhodochorton amphiroae Drew 1928: 179, pl. 40, figs. 34–37.

Acrochaetium mirabile (Suhr) Naegeli 1861: 405. Newton 1931: 253.

Callithamnion mirabile (Suhr) Kuetzing 1849: 639. J. Agardh 1851: 15; 1876: 10.

Chantransia mirabilis (Suhr) Batters 1896: 9; 1902: 58. Non *Chantransia mirabilis* Heydrich 1892: 475 (= *C. lauterbachii* Schmitz et Heydrich in Schumann et Lauterbach 1901: 25).

Trentepohlia mirabilis Suhr 1839: 73, fig. 47.

Acrochaetium radicans (Harvey) J. Agardh 1892: 48. Chapman 1962: 134. Levring 1953: 477, figs. 10*E–G*(?); 1955: 414. Papenfuss 1945: 319.

Callithamnion radicans Harvey 1854: 563; 1863: synop., p. 1vi. J. Agardh 1876: 9.

Chantransia radicans (Harvey) De Toni 1897: 71; 1924: 73. Lucas 1909: 21.

Acrochaetium villiforme Levring 1953: 481, figs. 15*D*, *E*, 16, 17. Boney et White 1967: 591.

Acrochaetium botryocarpum auct. non (Harvey) J. Agardh: Womersley 1950: 162.

Callithamnion sparsum auct. non Harvey: Harvey 1854: 563; 1863: synop., p. 1vi.

Note.–J. Agardh (1851, p. 12) lists further possible synonymy and early records of probable misidentifications. Numerous other records of this species need checking.

Figs. 7, 22

Plants partly to entirely epiphytic, caespitose, up to 8 mm tall; original spore non-persistent. Prostrate system consisting of branched epiphytic or endophytic filaments forming a pseudoparenchymatous disc or an entangled funiform mass. Erect filaments freely and irregularly branched, sometimes attenuate and ending in multicellular hair-like prolongations. Cells of main axes and laterals cylindrical, (8.5–)10–17 (–24) μm wide and (17–)30–50(–90) μm long, L/D (1.5–)2–4(–6.5); cells sometimes tapering to 2.5–10 μm wide and 20–75 μm long (L/D up to 30) near the apices; each cell containing a single parietal lobate chromoplast with one pyrenoid.

Monosporangia ovoid, 8–13 μm wide and (12–)16–20(–24) μm long, in clusters of 4–8 on branched stalks or singly or in pairs on 1–2-celled stalks, situated on the lowermost cells of laterals or sometimes scattered or terminal. Tetrasporangia ovoid to subglobose, (13–)15–18 μm wide and 17–21 μm long, cruciately divided, borne in pairs on unicellular stalks or occasionally solitary or in clusters, on the lowermost cells of laterals or sometimes scattered.

Spermatangia ovoid to spherical, up to 3 μm wide and 4 μm long, borne terminally or laterally in dense clusters or occasionally in smaller groups on branched stalks. Carpogonia terminal on unicellular stalks; immediate post-fertilization stages unknown. Mature carposporophyte consisting of branched gonimoblast filaments bearing terminal, ovoid carposporangia 8–10 μm wide and 16–20 μm long.

Type Locality.–Bantry Bay, Ireland (*Hutchins*); locality for H. Davies collection not given by Dillwyn (1809).

Holotype.–NMW.

Distribution.–Cosmopolitan.

Hosts.–A wide variety of algae, marine angiosperms, and marine invertebrates.

Representative Specimens Examined.–WESTERN AUSTRALIA: Cottesloe (Perth), 14.xi.1968, *Woelkerling* (ADU, A32926). Fremantle, 1854, *Harvey* (ADU, A18536, isotype of *Callithamnion radicans* Harvey). Garden I., 1854, *Harvey* (ADU, A18482). Point Peron, 22.ix.1966, *Mitchell* (ADU, A30732). SOUTH AUSTRALIA: Head of Bight, 4.xi.1968, *Woelkerling* (ADU, A32924). Venus Bay, 12.ii.1954, *Womersley* (ADU, A19503). Daly Head, 26.iii.1967, *Gordon* (ADU, A31287). Pennington Bay (Kangaroo I.), 7.i.1948, *Womersley* (ADU, A6499, isotype of *Acrochaetium villiforme* Levring). Stanley Beach (Kangaroo I.), 7.ii.1956, *Womersley* (ADU, A20097). Marino (Adelaide), 21.v.1953, *Womersley* (ADU, A18644). Port Elliot, 28.vii.1967, *Woelkerling* (ADU, A32239). Petrel Cove (Victor Harbor), 1.xii.1967, *Woelkerling* (ADU, A31986). CALIFORNIA: White's Point (San Pedro), 15.ii.1908, Gardner (UC276411, holotype of *Rhodochorton amphiroae* Drew). IRELAND: Bantry Bay, prior to 1809, *Hutchins* (NMW, Dillwyn collection, type).

Audouinella daviesii usually grows in the upper sublittoral in southern Australia but has been recorded from the lower littoral and from depths of 10 m; Sundene (1953) reported that it occurs commonly in depths of 3–10(–25) m.

Cruciately divided tetrasporangia occur in plants from southern Australia and are recorded by most other authors (Baardseth 1941; Blackler 1951; Kylin 1907); Harvey's (1851, Plate 314) record of tetrahedral divisions, unknown in other audouinelloid algae, needs further checking.

Only three records of sexual populations are known: one from Western Australia (ADU, A32853), one from South Australia (ADU, A6499, isotype of *Acrochaetium villiforme* Levring), and one from North America (Aziz, unpublished data).

Rhodochorton amphiroae Drew (1928), *Trentepohlia mirabilis* Suhr (1839), *Callithamnion radicans* Harvey (1854), and *Acrochaetium villiforme* Levring (1953) are considered here as conspecific with *Audouinella daviesii*. Suhr's plants were examined by Hamel (1927) who confirmed the earlier opinions of Areschoug (1847, p. 338) and De Toni (1924, p. 56) about their relation to *A. daviesii*. Holotype or isotype material of the other three species has been examined during this study and found to agree in all essentials with *A. daviesii*, especially in the presence of clustered

monosporangia. The features by which Levring (1953) separated the latter two species from *A. daviesii* (cell size, extent of prostrate system, ramification, sporangial arrangement) are not considered taxonomically significant after isotype material in ADU was examined.

Two collections (ADU, A2828, A8721) from Pennington Bay (Kangaroo I.), S.A., which are probably those referred by Levring (1953, p. 477) to *Acrochaetium radicans*, do not contain any audouinelloid alga but are rich in *Sporocladopsis* (Chlorophyta).

Rhodochorton magnificum Drew (1928) is also probably conspecific with *Audouinella daviesii*. Drew (1928) distinguished the former species by the presence of endophytic filaments, but these occur in some southern Australian plants of *A. daviesii* (Fig. 22*A*) and were even reported by Drew (1928, p. 173) in a California collection of *A. daviesii*. Until the type specimen can be examined, *Rhodochorton magnificum* is maintained as a distinct species.

The relationships of *Rhodochorton elegans* Drew (1928) and *R. hyalosiphonae* Nakamura (1941) to *Audouinella daviesii* also require clarification. They apparently differ from *A. daviesii* in being partly endophytic and in growing on certain hosts, but these distinctions are of doubtful taxonomic value and a comparison of types may show that several or all are conspecific.

Audouinella floridula (Dillwyn) comb. nov.

Callithamnion floridulum (Dillwyn) Lyngbye 1819: 130, tab. 41.
Callithamnion floridulum (Dillwyn) C. Agardh in Harvey in W. J. Hooker 1833: 348. J. Agardh 1851: 19; 1876: 13. Harvey 1846: pl. CXX, A; 1849: 183; 1863: synop., p. 1v. Kuetzing 1849: 640. Tisdall 1898: 502.
Ceramium floridulum (Dillwyn) C. Agardh 1817: XXVII.
Chromastrum floridulum (Dillwyn) Papenfuss 1945: 323.
Conferva floridula Dillwyn 1809: 73, suppl., pl. F. C. Agardh 1828: 188.
Kylinia floridula (Dillwyn) Papenfuss 1947: 437.
Rhodochorton floridulum (Dillwyn) Naegeli 1861: 358, fig. 2. Baardseth 1941: 48, fig. 20*D*. Blackler 1956: 70. Dixon 1963: 241. Hamel 1927: 52, 106, figs. 37, 39*F*; 1928: 199; 1928*a*: 146, figs. 37, 39*F*. Knaggs 1964: 393; 1965: 478; 1967: 31. Knaggs et Conway 1964: 339, fig. 1. Kuckuck 1897: 345, fig. 6.
Rhodothamniella floridula nom. illeg. (Dillwyn) Feldmann 1954: 68. Gayral 1966: 359, pl. LXXVII. Magne 1964: 488, 497, pl. 1.
Thamnidium floridulum (Dillwyn) Thuret ex Le Jolis 1863: 111, tab. VI.
Trentepohlia floridula (Dillwyn) Harvey 1836: 218.

Figs. 8, 23*B*

Plants saxicolous or epiphytic, caespitose to matted, (3–)10–20(–25) mm tall; original spore non-persistent. Prostrate system consisting of branched non-confluent filaments or of more or less confluent filaments forming an irregularly shaped pseudoparenchymatous disc. Erect filaments simple to sparingly branched below, sparingly to moderately branched above; laterals secundly to irregularly arranged and sometimes tapering towards the tips. Cells cylindrical, 15–30 μm wide and (35–)50–120(–150) μm long, L/D 2–5(–6); cells tapering to 14–19 μm wide near the apices; cells of shorter laterals 8–12 μm wide, 12–36 μm long; all cells containing several (usually 3–8) parietal, more or less stellate chromoplasts each with a single pyrenoid.

Tetrasporangia ovoid to globose, each 18–30(–40) μm wide and (20–)25–40(–45) μm long, sessile or on 1–3-celled stalks, mostly arranged in adaxially secundate series

along the laterals; contents cruciately divided.

Other reproductive bodies unknown in southern Australian collections.

Type Locality.—Galway coast, Ireland.

Holotype.—NMW.

Distribution.—Christies Beach, S.A. to Western Port, Vic.; Europe, Tristan da Cunha.

Hosts.—Chaetomorpha aerea.

Specimens Examined.—SOUTH AUSTRALIA: Christies Beach, 14.x.1968, *Womersley* (ADU, A32869). Robe, 24.viii.1960, *Womersley* (ADU, A24423). VICTORIA: The Blowholes (Cape Bridgewater), 21.viii.1953, *Womersley* (ADU, A19057). Western Port, 1854, *Harvey* (ADU, A18476). Phillip I. (Western Port), 1854, *Harvey* (MEL 26394). IRELAND: Galway coast, 1809, *Scott* (NMW, Dillwyn collection, holotype).

Note.—ADU, A18476 is Harvey's Alg. Aust. Exsic. number 518*H*, and MEL 26394 bears Harvey's travelling set(?) number 401.

Audouinella floridula, which is easily distinguished from other species in the complex (even when sterile) by its chromoplast morphology, usually grows on sand-covered rock, but one occurrence of epiphytic plants (ADU, A19057) is recorded here on *Chaetomorpha* in a shaded pool over 30 m above sea-level on a very rough coast in Victoria.

Possible male and female plants have been described from cultures by Knaggs and Conway (1964), and cytological evidence (Knaggs 1964; Magne 1964) strongly indicates that an alternation of generations occurs in this species. Harvey's (1851) report of "roundish or lobed berry-like receptacles (favellae) seated on the main branches and containing numerous spores" should be checked to determine whether or not these might be carposporophytes.

Herbarium material of *A. floridula* is distinguished from that of *Rhodochorton purpureum* (Lightfoot) Rosenvinge, a species of similar habit but lacking pyrenoids (and recorded from New South Wales by Levring 1953, p. 489 as *R. rothii*), by the presence of mostly lateral solitary or paired tetrasporangia rather than mostly terminal clustered tetrasporangia.

Audouinella liagorae (Boergesen) comb. nov.

Acrochaetium liagorae Boergesen 1915: 58, figs. 60–62. Abbott 1962: 100, figs. 8, 9. Aziz 1966: 87, fig. 1 (in part; see Abbott 1968). Non *Acrochaetium liagorae* (Weber van Bosse) Hamel 1927: 92.

Chantransia liagorae Boergesen 1915: 57. Non *Chantransia liagorae* Weber van Bosse 1914: 275.

Chromastrum liagorae (Boergesen) Papenfuss 1945: 324.

Kylinia liagorae (Boergesen) Papenfuss 1947: 438.

Acrochaetium collinsianum Boergesen 1920: 454; 1937: 43; 1952: 15. Levring 1953: 486. Taylor 1928: 134, pl. 20, fig. 6.

Chantransia collinsiania (Boergesen) De Toni 1924: 69. Levring 1941: 633.

Fig. 9

Plants endophytic, developing from septate persistent or (Abbott 1962) aseptate non-persistent spores. Prostrate system consisting of sparingly and irregularly branched

non-confluent filaments creeping within the gelatinous matrix of the host, occasionally decumbent or bearing branches descending towards the centre of the host. Cells irregular to subcylindrical, (6–)8–12(–15) μm wide and (12–)25–40(–80) μm long, L/D (1–)2–4(–8); cells often widest in the middle. Erect filaments arising at irregular intervals from cells of the prostrate filaments, simple or sparingly and irregularly branched, up to 400 μm long. Cells irregular to cylindrical in shape, (3–)8–15 μm wide and 15–30(–50) μm long, L/D (1–)2–4(–5); each cell containing a lobate to stellate chromoplast and a single pyrenoid. Terminal and pseudolateral hairs up to 450 μm long occur.

Monosporangia ovoid, 10–14(–18) μm wide and 13–24(–35) μm long, terminal or lateral, sessile or stalked, on both prostrate and erect filaments, sometimes replaced by tetrasporangia which are 15–18 μm wide and 22–30(–35) μm long.

Spermatangia ovoid to globose, up to 5 μm wide and 6 μm long, borne singly or in groups of 2–3(–4) on simple or branched stalks in terminal or lateral positions. Carpogonia sessile or on 1–2-celled stalks on prostrate and erect filaments; dividing transversely after fertilization and giving rise to a few gonimoblast cells bearing terminal carposporangia 8–10 μm wide and 10–14 μm long.

Type Locality.–South coast of St. Croix, Virgin Is.

Holotype.–C.

Distribution.–Port Rickaby to Victor Harbour, S.A. including Kangaroo I. Bermuda, Dry Tortugas, Hawaii, Juan Fernandez Is., Philippines, Virgin Is.

Hosts.–*Helminthocladia* spp.; *Liagora* spp.

Representative Specimens Examined.–SOUTH AUSTRALIA: Pennington Bay (Kangaroo I.), 22.i.1947, *Womersley* (ADU, A30883); 16.i.1948, *Levring* (ADU, A19849). Antechamber Bay (Kangaroo I.), 20.xi.1967, *Woelkerling* (ADU, A32055; A32696). Barker's Rocks (Port Rickaby), 12.iii.1967, *Woelkerling* (ADU, A31371). Petrel Cove (Victor Harbour), 15.i.1968, *Woelkerling* (ADU, A32122).

Note.–ADU, A30883 is recorded by Abbott (1962, p. 102) as A4443; the latter number is now the ADU herbarium specimen of the host, *Liagora harveyiana* Zeh.

Persistent septate spores were found in most southern Australian collections (including ADU, A30883 studied by Abbott), but Abbott (1962) recorded only septate non-persistent spores.

The distinction between prostrate and erect filaments in *A. liagorae* at times becomes arbitrary. Occasionally prostrate filaments are decumbent, and sometimes what commences as an erect filament (in position and direction of growth) soon assumes a prostrate habit and gives rise to other erect filaments. The erect filaments of some plants are few in number, mostly simple, and under 75 μm long, but in other plants they are more numerous, up to 400 μm long, and irregularly branched. All intermediate forms occur, sometimes on the same plant of *A. liagorae*, and Abbott (1962, pp. 102, 103) noted similar variation in specimens from Bermuda, Hawaii, and the Philippines. Plants in uncalcified hosts are usually taller than those in calcified hosts, which suggests that the calcification may serve as a physical barrier to the development of the erect system.

Stellate and lobate chromoplasts occur randomly in cells of southern Australian plants, but Abbott (1962, p. 100) reported stellate plastids in cells 50 μm or more beneath the host surface and lobate plastids near to and above the host surface.

Monosporangia borne on plants with poorly developed erect filaments tend to be smaller (10–13 μm wide; 13–22 μm long) than those (12–14(–18) μm wide; 18–26(–35) μm long) borne on plants with well-developed erect filaments.

Carposporophytes of *Audouinella liagorae* have not been recorded previously. According to Abbott (1968), the carposporophytes described by Aziz (1966) belong to plants of *Acrochaetium laxum* Abbott rather than to *Acrochaetium* (= *Audouinella*) *liagorae*.

Tetrasporic plants of *Audouinella liagorae* from southern Australia agree well with plants described by Boergesen (1937) as *Acrochaetium liagoroides*. Abbott (1962) regarded the two taxa to be conspecific, and when an examination of type collection material can be made, it will probably confirm her opinion.

Eight other recorded taxa (*Acrochaetium antillarum* Taylor (1942, p. 78, Plate 2, Figs. 3, 4); *Rhodochorton brebneri* Batters (1897, p. 437); *Acrochaetium endophyticum* Batters var. *tristanese* Baardseth (1941, p. 45, Figs. 19*E–G*); *Chantransia immersa* Rosenvinge (1909, p. 130, Figs. 56–68); *Rhodochorton implicatum* Drew (1928, p. 190, Plate 46, Figs. 76–78); *Chantransia inclusa* Levring (1937, p. 96, Figs. 16*D*, *E*); *Chantransia stilophorae* Levring (1935, p. 39, Figs. 8*a–e*); *Rhodochorton vagum* Drew (1928, p. 188, Plate 45, Figs. 61–69)) appear to be morphologically similar to *Audouinella liagorae*, and a comparison of the types may show that some or all are conspecific.

The relationship of *Acrochaetium actinocladium* Abbott (1962) to *Audouinella liagorae* also requires further study. Plants intermediate in morphology occur in several southern Australian collections (ADU, A31980, A31981) and this supports Abbott's (1962, p. 112) opinion that the two taxa may represent forms of one species.

Audouinella microscopica (Naegeli) comb. nov.

Acrochaetium microscopicum (Naegeli) Naegeli 1861: 407, figs. 24, 25. J. Feldmann 1942: 211, fig. 5*A*. Hamel 1927: 15, 65, 79, fig. 16; 1928: 173; 1928*a*: 109, fig. 16. Schiffner 1931: 144, fig. 2.
Callithamnion microscopicum Naegeli in Kuetzing 1849: 640.
Chantransia microscopica (Naegeli) Batters in Schiffner 1916: 136, figs. 13–18.
Chromastrum microscopicum (Naegeli) Papenfuss 1945: 322.
Kylinia microscopica (Naegeli) Kylin 1944: 13. Papenfuss 1947: 437.
Rhodochorton microscopicum (Naegeli) Drew 1928: 151, 163.
Acrochaetium trifilum (Buffham) Batters var. *schiffneri* Hamel 1927: 80. Schiffner 1931: 145.
Acrochaetium catenulatum auct. non Howe: Levring 1953: 472, fig. 8.

Figs. 10, 23*A*

Plants epiphytic, up to 125 μm tall exclusive of hairs; original spore persisting as a unicellular base slightly smaller to slightly larger than other cells; rarely dividing to form a several-celled prostrate system. Filaments of erect system 1–3(–4), commonly arcuate, simple or with a few secundly to irregularly arranged laterals. Cells barrel-shaped to cylindrical, 3–12 μm wide and 3–10 μm long, with smaller cells near the apices, L/D 0.7–1.5(–2); each cell containing a single parietal to stellate (Levring 1953) chromoplast with one pyrenoid. Terminal and pseudolateral hairs up to 100 μm long occur.

Monosporangia ovoid, each 4–7 μm wide and 5–10 μm long, terminal or lateral, single or rarely in pairs, sessile or stalked, adaxially seriate or occasionally more scattered.

Other reproductive structures unknown in southern Australian collections.

Type Locality.—Bay of Naples, Italy.

Holotype.—?; according to Hamel (1927, p. 65) material from the type collection is distributed as specimen 454 in Hauck and Richter's "Phykotheka Universalis", but this material was collected in England rather than Italy.

Distribution. Cosmopolitan.

Hosts.—A wide variety of algae.

Representative Specimens Examined.—WESTERN AUSTRALIA: Radar Reef (Rottnest I.), 11.xi.1968, *Woelkerling* (ADU, A32931). SOUTH AUSTRALIA: Elliston, 24.viii.1967, *Woelkerling*, (ADU, A31995); 16.v.1968, *Gordon* (ADU, A32308). Wanna (Port Lincoln), 21.viii.1967, *Womersley* (ADU, A31370). Port Willunga, 3.xi.1967, *Woelkerling* (ADU, A31982). Port Elliot, 1.xii.1967, *Parsons* (ADU, A32202); 31.i.1968, *Parsons* (ADU, A32271); 1.iii.1968, *Woelkerling* (ADU, A32250). Petrel Cove (Victor Harbour), 1.xii.1967, *Woelkerling* (ADU, A31996); 17.iv.1967, *Woelkerling* (ADU, A31990).

Audouinella microscopica is distinguished from other audouinelloid algae in southern Australia by its unicellular holdfast, barrel-shaped cells, and commonly arcuate filaments under 125 μm long. Up to four erect filaments may arise from the basal cell of each plant (Figs. 10*A*–*H*), and when only one develops, the lowermost lateral may arise from any cell above the base. Irregularly lobate chromoplasts occur in cells of southern Australian plants (Fig. 10*I*); Hamel (1927) and Levring (1953), however, recorded stellate chromoplasts in this species. Sexual and tetrasporic plants have been recorded by Hamel (1927) and Schiffner (1931) respectively.

A number of taxa (Table 2) will probably be reduced to the synonymy of *Audouinella microscopica* when a comparison of the type collections can be made. Plants agreeing with the description of these taxa, which have been distinguished mainly on differences in habit, occur side by side in a single population (Fig. 23*A*) and almost certainly reflect only variation within *A. microscopica.*

Chantransia collopoda Rosenvinge (1909, p. 81) apparently differs from *Audouinella microscopica* by the presence of a much enlarged basal cell wall (Rosenvinge 1898, p. 34, Figs. 5*e*–*m*; Lund 1942, p. 54, Fig. 1). Further study is needed to determine whether this represents an ecological adaptation, since *Chantransia collopoda* is known only on *Chordaria* (Phaeophyta).

In addition, the relationships of *Rhodochorton arcuatum* Drew (1928), *Acrochaetium macropus* Kylin (1919), and *Chantransia parvula* Kylin (1906) to *Audouinella microscopica* require clarification to determine whether and in what ways they are distinct from one another.

Plants placed in *Chantransia* (= *Audouinella*) *microscopica* by Batters (1896), Kuckuck (1897), and Schiffner (1916) have been referred by Hamel (1927) respectively to *Acrochaetium battersianum* Hamel, *A. kuckuckianum* Hamel, and *A. trifilum* (Buffham) Batters. The type collections of these species as well as plants referred by Foslie (1890; see also Drew 1928; Kylin 1906, p. 126; Hamel 1927, p. 65) to *Chantransia microscopica* should be checked when possible against *Audouinella microscopica* for possible synonymy.

Lund (1959, p. 176) has discussed other collections which may be wrongly associated with Naegeli's "microscopica".

TABLE 2

TAXA POSSIBLY CONSPECIFIC WITH *AUDOUINELLA MICROSCOPICA*

1. *Acrochaetium catenulatum* Howe (1914, p. 84, pl. 31, figs. 12–18. See also Kylin and Skottsberg (1919), Nakamura (1941), and Weber van Bosse (1921). The material of Levring (1953, p. 472) from Burraneer, N.S.W. (ADU, A19855) has been examined and referred to *Audouinella microscopica.*
2. *Acrochaetium compactum* Jao (1936, p. 241, pl. 10, figs. 6–14). See also Abbott (1962, p. 92).
3. *Chantransia crassipes* Boergesen (1909, p. 1, fig. 1). See also Boergesen (1915, 1927, 1931), Baardseth (1941), and Taylor (1928).
4. *Acrochaetium microfilum* Jao (1936, p. 240, pl. 10, figs. 1–5). Non Levring 1945, p. 12 = *Acrochaetium levringii* Papenfuss (1947).
5. *Chantransia moniliforme* Rosenvinge (1909, p. 99, figs. 28, 29). See also Boergesen (1920*a*), Hamel (1927), Levring (1935), and Petersen (1918).
6. *Acrochaetium moniliforme* (Rosenvinge) Boergesen var. *mesogloiae* Jao (1936, p. 241, pl. 10, figs. 15–17). See also Abbott (1962, p. 92), who mistakenly recorded the alga as *A. unifilum* var. *mesogloiae.*
7. *Chantransia trifila* Buffham (1892, p. 25, pl. 3, figs. 1–4). See also Hamel (1927, pp. 12, 67, 80).

Audouinella repens (Boergesen) comb. nov.

Acrochaetium repens Boergesen 1915: 52, figs. 55, 56; 1920: 452, fig. 420. Papenfuss 1945: 317. Non *Rhodochorton repens* Jonsson 1901: 147 (= *Acrochaetium jonssonii* Papenfuss 1945: 309).

Fig. 11

Plants largely endophytic, developing from aseptate spores sometimes persisting in mature plants. Prostrate system consisting of sparingly and irregularly branched non-confluent filaments creeping within the host. Cells irregular to cylindrical in shape, commonly broadest in the middle, 6–12(–20) μm wide and 18–40 μm long, L/D (1–)2–4(–5); each cell containing a parietal lobate to stellate chromoplast with one pyrenoid. Erect filaments arising at irregular intervals from cells of the prostrate system, simple or sparingly branched, up to 800 μm tall. Cells cylindrical, 5–7(–9) μm wide and 10–25 μm long (L/D 2–4) in lower portions, 4–7 μm wide and 30–80 μm long (L/D 4–20) in upper portions, occasionally tapering to 2 μm wide and up to 30 diameters long near the apices; lower cells with a parietal lobate to stellate chromoplast and one pyrenoid; upper cells usually with feebly developed chromoplasts or none.

Monosporangia ovoid, 8–11 μm wide and 12–19 μm long, sessile or stalked, single or in pairs, scattered on the erect and occasionally on the prostrate filaments. Tetrasporangia unknown.

Spermatangia ovoid, up to 4 μm wide and 6 μm long, solitary or in groups of 2–3, sessile on vegetative cells or on 1–2-celled stalks, terminal or lateral on erect

filaments. Carpogonia sessile or stalked, on prostrate or occasionally on erect filaments; dividing transversely after fertilization and producing carposporangia directly or forming short gonimoblast filaments with terminal carposporangia 8–11 μm wide and 14–20 μm long.

Type Locality.–The Harbour, St. Thomas, Virgin Is.

Holotype.–C.

Distribution.–Point Sinclair and Victor Harbour, S.A. Virgin Is.

Hosts.–*Leptosomia* sp. and *Naccaria naccarioides* in southern Australia. *Hypnea musciformis* and *Griffithsia globifera* in the Virgin Is.

Specimens Examined.–SOUTH AUSTRALIA: Point Sinclair, 11.i.1961, *Oberlander* (ADU, A24701). Victor Harbour, 2.xi.1965, *Abbott* (ADU, A32256).

Although largely endophytic and occasionally producing persistent spores, southern Australian collections of *Audouinella repens* generally agree with the original description of Boergesen (1915; see also Boergesen 1920). In some carposporophytes, gonimoblast filaments are virtually absent and carposporangia form almost directly from the fertilized carpogonium, but in others on the same plant a more elaborate gonimoblast system with terminal carposporangia develops (Fig. 11*F*).

Audouinella repens is readily distinguished from other known southern Australian audouinelloid algae by the presence of progressively longer cells towards the apices of the erect filaments. In addition to lacking this feature *Audouinella thuretii* and *Colaconema tenuissima*, which also have main axes 10 μm or less in diameter, differ in having somewhat larger monosporangia.

Audouinella thuretii (Bornet) comb. nov.

Acrochaetium thuretii (Bornet) Collins et Hervey 1917: 98. Chapman 1962: 134. Hamel 1927: 37, 97, fig. 30; 1928: 191; 1928*a*: 131, fig. 30. Kylin 1944: 21, fig. 14. Levring 1953: 476. Papenfuss 1945: 311. Sundene 1953: 184. Taylor 1957: 222.
Chantransia thuretii Bornet. Collins 1900: 49 (nom. nud.).
Chantransia thuretii (Bornet) Kylin 1907: 119, fig. 28. Levring 1937: 88. Rosenvinge 1909: 100, figs. 30–33.
Rhodochorton thuretii (Bornet) Drew 1928: 171.
Chantransia corymbifera Thuret in Le Jolis 1863: 107 (in part; see Papenfuss 1945: 313 under *Acrochaetium bornetii*). Collins 1896: 5.
Chantransia efflorescens var. *thuretii* Bornet 1904: XVI, pl. 1. Collins 1906: 196.

Figs. 12, 24

Plants largely to entirely epiphytic, caespitose, up to 5 mm tall; original spore sometimes recognizable in younger thalli but eventually becoming obscured. Prostrate system consisting of short filaments forming a small pseudoparenchymatous disc. Erect filaments richly and irregularly branched with an occasional tendency towards alternate and secund arrangements. Cells cylindrical, 7–9(–13) μm wide and (20–)30–50 μm long (L/D 3–6) in lower portions of main axes, 6–9 μm wide and (15–)25–60 μm long (L/D 3–8) in laterals, sometimes tapering to 3–6 μm wide near the apices; each cell containing a single parietal lobate chromoplast with one pyrenoid. Hyaline hairs unknown.

Monosporangia ovoid, 10–14 μm wide and 18–22(–24) μm long, sessile or stalked, single or in pairs, in a secund series along the laterals or occasionally more scattered; sometimes replaced by tetrasporangia which are 17–24 μm wide and 23–35 μm long.

Other reproductive structures unknown in southern Australian collections.

Type Locality.–Cherbourg, France.

Holotype.–PC.

Distribution.–Nearly cosmopolitan.

Hosts.–A variety of algae and marine angiosperms.

Specimens Examined.–WESTERN AUSTRALIA: Point Walter (Swan R. estuary), 11.xi.1967, *Allender* (ADU, A32251). Crawley Bay (Swan R. estuary), 19.v.1968, *Allender* (ADU, A32291). South Perth, 20.viii.1949, *Royce* 223 (PERTH). SOUTH AUSTRALIA: Pelican Lagoon (Kangaroo I.), 10.i.1948, *Levring* (ADU, A19843).

Sexual plants of *Audouinella thuretii* have not been recorded from southern Australia but are described in detail by Kylin (1907).

Plants of *Audouinella daviesii* occasionally greatly resemble those of *A. thuretii*, but they differ in having somewhat smaller monosporangia which frequently occur on branched stalks.

SECTION III

Species in this section have chromoplasts with one to several pyrenoids each.

Audouinella botryocarpa (Harvey) comb. nov.

Acrochaetium botryocarpum (Harvey) J. Agardh 1892: 45. Chapman 1962: 133. Hamel 1927: 71, 91, fig. 42; 1928: 165, 184, fig. 42. Levring 1953: 484, figs. 18–20; 1955: 417. May 1947: 276. Papenfuss 1945: 313. Woelkerling 1970: 159, figs. 1–32. Non Womersley 1950: 162 (= *Audouinella daviesii*).

Callithamnion botryocarpum Harvey 1854: 563; 1860: 336; 1863: synop., p. lv. J. Agardh 1876: 10.

Chantransia botryocarpa (Harvey) De Toni 1897: 72; 1924: 73. Bornet 1904: XXI.

Acrochaetium polyrhizum (Harvey) J. Agardh 1892: 48. Bornet 1904: XX. Chapman 1962: 134. Cribb 1956: 185. Hamel 1927: 73, 92; 1928: 168, 186. Laing 1939: 137. Levring 1953: 481, figs. 14, 15*A–C*. Naylor 1954: 654 (author as Lagerheim). Papenfuss 1945: 317.

Callithamnion polyrhizum Harvey 1863: synop., p. lvi. J. Agardh 1876: 12. Boergesen 1915: 57. Tisdall 1898: 502. Wilson 1892: 187.

Chantransia polyrhiza (Harvey) De Toni 1897: 71. Laing 1905: 383; 1927: 147. Lucas 1909: 21.

Acrochaetium grande auct. non (Levring) J. De Toni: Levring 1953: 480.

Plants partly to entirely epiphytic or saxicolous, caespitose, up to 6 mm tall; original spore non-persistent. Prostrate system consisting of irregularly branched filaments remaining largely free from one another or forming an endophytic funiform mass of entangled filaments or a pseudoparenchymatous disc; sometimes supplemented by corticating rhizoidal filaments descending from the lower portions of the erect axes. Erect filaments freely and irregularly branched, sometimes terminating abruptly in multicellular hair-like prolongations or gradually tapering towards the tips. Cells of

erect filaments cylindrical, (10–)15–20(–30) μm wide and 30–120 μm long (L/D 1–6) in main axes, tapering to 6–15 μm wide near the apices; each cell with a parietal lobate chromoplast with (1–)2–6(–18) pyrenoids. Cells of hair-like prolongations 3–6 μm wide and up to 125 μm long with weakly developed chromoplasts with or without pyrenoids. Unicellular hairs unknown.

Monosporangia ovoid, 12–18(–24) μm wide and 18–25(–40) μm long, sessile or stalked, single, in pairs, or rarely in groups of 3–5, adaxial on the lower cells of laterals or more scattered. Tetrasporangia 18–24 μm wide and 25–40 μm long, usually on unicellular stalks, single or in pairs, on lower cells of laterals.

Spermatangia ovoid to globose, up to 6 μm wide and 6 μm long, borne singly, in pairs, or in clusters, sessile or stalked. Carpogonia terminal on 1–2-celled stalks usually situated near the axils of laterals; stalk cells occasionally giving rise to a short, unbranched sterile filament shortly before or after fertilization. Fertilized carpogonium dividing transversely or rarely remaining undivided after fertilization and giving rise to branched gonimoblast filaments bearing terminal carposporangia up to 25 μm wide and 35 μm long.

Type Locality.–King George's Sound, W.A.

Holotype.–Harvey No. 324, travelling collection; not in TCD.

Distribution.–Bunbury, W.A. to Point Lonsdale, Vic. and Tas. New Zealand.

Hosts.–A wide variety of algae. It also has been found on rock.

Representative Specimens Examined.–WESTERN AUSTRALIA: King George's Sound, 1854, *Harvey* (ADU, A18165, isotype). SOUTH AUSTRALIA: Elliston, 16.v.1968, *Woelkerling* (ADU, A32292). American River (Kangaroo I.), 25.i.1946, *Womersley* (ADU, A8795). Port Elliot, 28.vii.1967, *Woelkerling* (ADU, A32238). Petrel Cove (Victor Harbour), 15.vii.1968, *Woelkerling* (ADU, A32306); 14.viii.1967, *Woelkerling* (ADU, A31926); 1.xii.1967, *Woelkerling* (ADU, A31984). Robe, 10.ii.1968, *Woelkerling* (ADU, A32283); 9.ix.1968, *Woelkerling* (ADU, A32309); 26.i.1967, *Woelkerling* (ADU, A31242). VICTORIA: Pt. Lonsdale, 21.i.1967, *Woelkerling* (ADU, A30886). Port Fairy, 1854, *Harvey* (ADU, A8304, isotype of *Callithamnion polyrhizum* Harvey). Apollo Bay, 23.i.1967, *Woelkerling* (ADU, A31189). TASMANIA: White Beach (Wedge Bay), 29.ii.1964, *Wollaston* and *Mitchell* (ADU, A27681). Rolling Bay (Port Arthur), 29.ii.1964, *Wollaston* and *Mitchell* (ADU, A27787). Port Arthur, 29.iii.1950, *Cribb* (ADU, A20435).

For further details on the ecology, morphology, and taxonomy of *Audouinella botryocarpa*, consult Woelkerling (1970).

Audouinella dictyotae (Collins) comb. nov.

Acrochaetium dictyotae Collins 1906: 193. Papenfuss 1945: 314.
Chantransia dictyotae (Collins) Collins 1911: 186. De Toni 1924: 50.
Rhodochorton dictyotae (Collins) Drew 1928: 190, pl. 47, figs. 79, 80.

Figs. 13, 25

Plants largely epiphytic, caespitose, up to 4 mm tall; original spore non-persistent. Prostrate system consisting of a more or less discoid mass of branched epiphytic filaments with large single cells or short filaments penetrating the host tissue or occasionally without a superficial disc. Erect filaments irregularly to secundly branched and gradually tapering towards the apices. Cells cylindrical, (10–)12–15(–18) μm wide

and (24–)35–60(–90) μm long (L/D 1.5–5) in lower portions of main axes, 10–12 μm wide and 30–80 μm long (L/D 3–8) in laterals, tapering to 6–9 μm wide near the apices; each cell containing a parietal lobate chromoplast with 1–4 pyrenoids. Hyaline hairs unknown.

Monosporangia ovoid to subglobose, (10–)12–17 μm wide and 16–24 μm long, sessile and solitary or occasionally 1–2 together on unicellular stalks, situated mainly on the lowermost cells of lateral branches; occasionally replaced by bisporangia 12–16 μm wide and 14–22 μm long. Tetrasporangia unknown.

Spermatangia spherical to ovoid, up to 5 μm wide and 6 μm long, borne in small clusters on branched stalks or in groups of 1–3 on 1–2-celled stalks, commonly located in the axils of laterals but also scattered and occasionally on carpogonial stalk cells. Carpogonia sessile or stalked, solitary or occasionally in groups of 2–3; stalk cells sometimes producing a sterile filament prior to or after fertilization; fertilized carpogonium either dividing transversely or remaining undivided prior to gonimoblast formation; gonimoblast filaments short or absent; mature carposporangia globose and thick-walled, 18–30 μm in diameter, usually 3–10 per carposporophyte.

Type Locality.–La Jolla, California.

Holotype.–FH. Material from the type collection has been distributed in Phycotheca Boreali Americana, No. 1394.

Distribution.–Port Willunga, S.A. to Portland, Vic. San Diego County, California.

Hosts.–*Dictyota* spp.; *Glossophora nigricans*.

Specimens Examined.–SOUTH AUSTRALIA: Port Willunga, 25.x.1964, *Womersley* (ADU, A28372); 11.x.1965, *Womersley* (ADU, A29615); 3.xi.1967, *Woelkerling* (ADU, A16028). West Island (Victor Harbour), 1.i.1969, *Shepherd* (ADU, A33259). Port MacDonnell, 25.i.1967, *Womersley* (ADU, A31667). VICTORIA: Portland, 13.i.1954, *Beauglehole* (ADU, A20551). CALIFORNIA: La Jolla, 21.vii.1899, *Snyder* (ADU, A32705, isotype). La Jolla, 21.vii.1899, *Snyder* (FH, holotype).

Plants in southern Australian collections of *Audouinella dictyotae* are more robust but otherwise agree with holotype material from California. Bisporangia occurred in small numbers on sexual plants in one collection (ADU, A31667).

Sexual plants, recorded for the first time, may produce one or several carpogonia on a single stalk cell (Figs. 13*H*, *I*) and once fertilized, they may or may not divide (Fig. 13*J*) and may or may not produce gonimoblast filaments (Figs. 13*L*–*N*). Usually fewer than 10 carposporangia develop at any one time on a single carposporophyte, but occasionally several successive carposporangia are produced (Fig. 13*N*).

Carposporophyte-bearing plants of *Audouinella dictyotae* are readily distinguished from those of *A. botryocarpa*, but non-sexual plants of the two species occasionally are very similar and could be confused. However, *A. dictyotae* seldom exceeds 3 mm in height, may have secund branching, lacks multicellular hair-like prolongations, has cells which rarely exceed 15 μm in diameter, and has monosporangia under 25 μm long that are often sessile. *A. botryocarpa*, in contrast, often reaches 4–5 mm in height, has irregularly branched erect filaments which sometimes end in hair-like prolongations, has erect filaments which frequently exceed 15 μm in diameter, and has mostly stalked monosporangia up to 40 μm long.

Genus COLACONEMA Batters

Colaconema Batters 1896: 8. Non *Colaconema* Schmitz in Schmitz et Falkenberg 1897: 452.

Species now referable to *Colaconema* have been placed in the past in *Acrochaetium*, *Audouinella*, *Callithamnion*, *Chantransia*, *Chromastrum*, *Conferva*, *Kylinia*, *Rhodochorton*, and *Trentepohlia.*

Plants epiphytic or endophytic, epizoic or endozoic, or saxicolous; attached to or suspended in substrate by a single-celled holdfast or more commonly by a prostrate system of simple or branched filaments which may or may not become pseudoparenchymatous. Erect filaments, when present, simple or branched, up to 10 mm tall; cells containing one or occasionally several chromoplasts with or without pyrenoids.

Asexual reproduction by sessile or stalked monosporangia, bisporangia, tetrasporangia, and/or multipartite sporangia borne on the erect and/or prostrate filaments.

Sexual reproduction unknown.

Type Species.—*Colaconema bonnemaisoniae* Batters.

Colaconema as used here includes all audouinelloid algae unknown in the sexual state and is regarded as a form genus (p. 8). The 14 southern Australian form species are divided into sections based on pyrenoid numbers and are discussed alphabetically within each section. In several cases somewhat arbitrary species limits are drawn, mainly because collections and morphological information are inadequate. Following accepted mycological practice, *Colaconema* could still be used as a form genus even if and after *C. bonnemaisoniae*, the type species, were shown to reproduce sexually.

SECTION I

The species in this section are not known to contain pyrenoids in their chromoplasts.

Colaconema spiculiphila (Dawson) comb. nov.

Acrochaetium spiculiphilum Dawson 1953: 22, pl. 10, figs. 2–4.

Figs. 14*G–L*

Plants endozoic, forming a network in the host tissue; sporelings unknown. Prostrate system consisting of irregularly branched, creeping filaments, sometimes becoming confluent and forming pseudoparenchymatous patches in which individual filaments become indistinct. Cells irregular to cylindrical in shape, 3–7(–12) μm wide and 6–30(–50) μm long; L/D 1–5(–10); each cell containing a parietal more or less dissected chromoplast which rarely becomes divided into several portions; pyrenoids unknown. Erect system (Dawson 1953) of upright or semi-upright filaments of 2–7 cells. Cells ellipsoid to ovoid, 4–6 μm in diameter.

Reproduction unknown.

Type Locality.—Bahia de San Quintin, Mexico.

Holotype.—Dawson 9672 in vial 2294 and on slides 1688–1689 in AHFH.

Distribution.—Elliston and Port Elliot, S.A. Type locality.

Hosts.—Sponges.

Specimens Examined.—SOUTH AUSTRALIA: Elliston, 2.xi.1968, *Woelkerling* (ADU, A32857). Port Elliot, 15.i.1968, *Woelkerling* (ADU, A32127); 8.v.1968, *Woelkerling* (ADU, A32288; A32289); 15.vi.1968, *Woelkerling* (ADU, A32709).

Southern Australian material of *Colaconema spiculiphila* agrees with the original diagnosis except that cells up to 12 μm wide occur in the prostrate system.

Acrochaetium ascidiophilum Dawson (1953) and *A. epispiculum* Joly et Cordeiro (1963) appear very similar to *Colaconema spiculiphila* and a comparison of types will probably show them to be conspecific. The relationship of *Rhodochorton membranaceum* (Magnus) Hauck to *Colaconema spiculiphila* requires further study to determine whether or not the latter merely represents the prostrate system stage of the former.

The plants from England which Boney and White (1967*a*) first characterized and later (White and Boney 1967) referred to *Acrochaetium infestans* Howe et Hoyt appear very similar to plants of *Colaconema spiculiphila* and apparently differ from true *Acrochaetium infestans* in lacking pyrenoids and in cell length.

The relationships of *Colaconema spiculiphila* to *C. bonnemaisoniae* and *C. spongiocola* are discussed under those species.

Colaconema spongiocola (Weber van Bosse) comb. nov.

Acrochaetium spongiocolum Weber van Bosse 1921: 195, figs. 56, 57. Papenfuss 1945: 317.

Figs. 14*A*–*F*

Plants endozoic, forming a network in the host skeleton; sporelings unknown. Prostrate system consisting of irregularly branched, creeping filaments which rarely become confluent. Cells either more or less cylindrical, 3–9 μm wide and 20–135 μm long (L/D 3–20) or irregularly shaped and more or less isodiametric, 6–14 μm wide and 6–14 μm long; each cell containing a parietal chromoplast which sometimes becomes dissected into several portions; pyrenoids unknown. Erect system virtually absent, consisting of an occasional cell arising from the prostrate system and just reaching the surface of the host.

Reproduction unknown.

Type Locality.—Aru Is., Indonesia.

Holotype.—L.

Distribution.—Elliston and Port Elliot, S.A. Type locality.

Hosts.—Sponges.

Specimens Examined.—SOUTH AUSTRALIA: Elliston, 2.xi.1968, *Woelkerling* (ADU, A32858). Port Elliot, 15.i.1968, *Woelkerling* (ADU, A32125; A32126); 8.v.1968, *Woelkerling* (ADU, A32290); 30.vi.1968, *Woelkerling* (ADU, A32301).

Southern Australian plants of *Colaconema spongiocola* agree well with the original diagnosis of Weber van Bosse (1921). Anastamoses occur occasionally and secondary pit connections develop (Fig. 14*C*).

C. americana differs from *C. spongiocola* in not having cells more than 5 diameters long and in possessing pyrenoids; *C. bonnemaisoniae* differs in possessing pyrenoids; and *C. spiculiphila* differs in forming pseudoparenchymatous patches. All of these taxa are very inadequately known, and when further collections are made, a critical comparison may show that two or more of these taxa are conspecific.

SECTION II

Species in this section have chromoplasts each with only one pyrenoid.

Colaconema americana Jao 1936: 237, pl. 13, fig. 8. Levring 1937: 94; 1953: 489. de Valera 1939: 3.

Acrochaetium americanum (Jao) Papenfuss 1945: 312.

Plants endophytic. Prostrate system consisting of irregularly to oppositely branched filaments creeping between the cortical cells of the host. Cells irregular in shape, sometimes greatly swollen, 5–10(–32) μm wide and (16–)22–38(–55) μm long, mostly 3–5 μm wide at the cross-walls; each cell containing a parietal slightly lobate chromoplast and a pyrenoid(?). Erect filaments 2–3 cells long, tapering somewhat towards the apices. Cells 3–5 μm wide and 13–32 μm long.

Monosporangia globose to hemispherical, 9–13 μm wide and 6–13 μm long, sessile, solitary or in clusters, terminal or lateral.

Other reproductive structures unknown.

Type Locality.–Gay Head, Martha's Vineyard, Massachusetts.

Holotype.–MICH.

Distribution.–Pennington Bay (Kangaroo.I.), S.A.; Murchison River mouth, W.A. Type locality.

Hosts.–*Asparagopsis* spp.

Specimens Examined.–No material has been available for examination.

The above diagnosis is based on information in the original description (Jao 1936); Levring (1953) recorded the species from two localities in southern Australia. Numerous plants of *Asparagopsis*, including ADU, A6613 which was collected at the same time and place (Pennington Bay) as one of the specimens of Levring, have been examined without finding *C. americana*.

According to Jao (1936), *C. americana* is distinguished from *C. bonnemaisoniae* by the occurrence of greatly swollen cells, but further study is needed to determine whether or not such cells are typical and of taxonomic significance. Similarly swollen cells have been found in some plants of *C. porphyrae* (p. 50), but these appear to be atypical and of no systematic significance.

Colaconema bonnemaisoniae Batters 1896: 8. Batters 1902: 57. Chemin 1926: 1561, figs. 1–3. Cotton 1912: 97. Hamel 1930: 31, fig. 54. Howe et Hoyt 1916: 113. Kylin 1944: 29. Levring 1953: 489. Newton 1931: 250, fig. 154. Sundene 1953: 186.

Acrochaetium bonnemaisoniae (Batters) J. et G. Feldmann 1939: 458. Dawson 1953: 24. Dixon 1959: 67; 1961: 75. J. Feldmann 1954: 66. Ginsburg-Ardre 1963: 378. Jorde et Klavestad 1963: 76.

Chantransia bonnemaisoniae (Batters) Levring 1937: 94, figs. 16*a–c*. de Valera 1939: 3, fig. 1.

Fig. 17*E*

Plants endophytic; sporelings unknown. Prostrate system consisting of freely and irregularly branched filaments creeping between the cortical cells of the host. Cells irregularly shaped, 2.5–8 μm wide and 8–30(–45) μm long, L/D 2–8; each cell containing (Chemin 1926) a parietal irregularly lobate chromoplast and (Levring 1937) one pyrenoid. Erect filaments 1–2 cells long, arising at irregular intervals from cells of the prostrate system.

Monosporangia globose to more or less hemispherical, 8–12 μm wide and 8–12 μm long, solitary or (Batters 1896) in clusters of 2–6, terminating erect filaments or situated directly on cells of the prostrate filaments.

Other reproductive structures unknown.

Type Locality.–Plymouth or Berwick-on-Tweed, England.

Holotype.–BM.

Distribution.–Pennington Bay, Kangaroo I., S.A. Europe, Algeria, Mexico.

Hosts.–*Bonnemaisonia* spp.; *Ceramium* sp.

Specimens Examined.–SOUTH AUSTRALIA: Pennington Bay (Kangaroo I.), 29.viii.1948, *Womersley* (ADU, A32120).

Sporangia are sparse, and details of chromoplast and pyrenoid structure are not well preserved in the southern Australian material examined. Levring (1937) found terminal hairs, but such hairs do not occur in southern Australian material and have not been reported by other authors.

Colaconema deliseae Levring (1953, p. 489, Figs. 21*H–J*), described from southern Australia is probably conspecific with *C. bonnemaisoniae* as shown on p. 44.

Colaconema asparagopsidis Chemin (1926*a*) and *C. simplex* Inagaki (1935) (= *Acrochaetium japonicum* Papenfuss 1945; non *Rhodochorton simplex* Drew 1928), which are distinguished from *C. bonnemaisoniae* on minor differences in sporangial size and arrangement, will, when the types can be compared, probably be found to be conspecific with *Colaconema bonnemaisoniae*. The relationships of *Chantransia emergens* Rosenvinge (1909) and *Acrochaetium endophyticum* Batters (1896) to *C. bonnemaisoniae* also need clarification since all three taxa appear to be similar morphologically.

Colaconema spiculiphila (p. 40) also appears similar to *C. bonnemaisoniae* but differs in the absence of pyrenoids and in the occurrence of pseudoparenchymatous patches in the prostrate system. The relationship of *C. bonnemaisoniae* to *C. spongiocola* (p. 41) and *C. americana* (p. 42) is further discussed under those species.

Colaconema deliseae Levring 1953: 489, Figs. 21*H–J*.

Plants endophytic. Cells irregular in shape, 2–4 μm wide, L/D 2–6; each cell containing a parietal lobate chromoplast and one pyrenoid.

Monosporangia globose, 4–6 μm in diameter.
Other reproductive structures unknown.

Type Locality.–Blow Hole, Eaglehawk Neck, Tas.

Holotype.–Herbarium T. Levring, Goteborg, Sweden (private collection).

Distribution.–Type locality only.

Hosts.–*Delisea fimbriata* (= *D. pulchra*).

Specimens Examined.–See below.

No recognizable plants of *Colaconema deliseae* were found in a fragmentary portion of the type collection in ADU (A19844). The above diagnosis is, therefore, based on the original account of Levring (1953).

Colaconema deliseae is almost certainly conspecific with *C. bonnemaisoniae*. The differences in dimensions cited by Levring (1953) are very minor, and the descriptions of *C. bonnemaisoniae* from elsewhere (e.g. Chemin 1926; Levring 1937) indicate that such differences have no taxonomic significance. The two taxa have been kept distinct pending a comparison of type material which has not been available for study.

Colaconema humilis (Rosenvinge) comb. nov.

Acrochaetium humile (Rosenvinge) Boergesen 1915: 23. Baardseth 1941: 41. Jao 1936: 247. Jorde et Klavestad 1963: 76. Kylin 1944: 22, fig. 17. Levring 1953: 478. Schiffner 1931: 143. Sundene 1953: 185.
Chantransia humilis Rosenvinge 1909: 117, figs. 44, 45. Boergesen 1927: 21. Levring 1953: 37, figs. 7*F–S*; 1937: 89; 1940: 78, figs. 23*A*, *B*; 1942: 8.
Chromastrum humile (Rosenvinge) Papenfuss 1945: 323.
Kylinia humile (Rosenvinge) Papenfuss 1947: 437.
Rhodochorton humile (Rosenvinge) Drew 1928: 151, 169.

Fig. 15*J–O*

Plants epiphytic, more or less pulvinate, 40–75(–225) μm tall (exclusive of hairs); developing from septate or occasionally aseptate spores. Prostrate system consisting of simple or branched more or less confluent filaments forming a pseudoparenchymatous disc. Cells cylindrical to irregular, 4–6 μm wide and 5–7 μm long. Erect filaments simple or with a few irregularly arranged laterals. Cells cylindrical, 3–7 μm wide and 8–12(–15) μm long, L/D 1.5–3; each cell containing a lobate to stellate chromoplast and one pyrenoid. Terminal and pseudolateral hairs up to 150 μm long occur.

Monosporangia ovoid, 6–9 μm wide and 11–15 μm long, sessile or stalked, single or in pairs, terminal or lateral and irregularly arranged.

Other reproductive structures unknown.

Type Locality.–Spodobjerg, Langeland, Denmark.

Holotype.–C.

Distribution.–Robe and Port MacDonnell, S.A.; Victoria. Atlantic and Mediterranean shores of Europe.

Hosts.–*Audouinella botryocarpa* in South Australia. A variety of algae in Europe.

Specimens Examined.–SOUTH AUSTRALIA: Robe, 26.i.1967, *Woelkerling* (ADU, A32118). Port MacDonnell, 25.i.1967, *Womersley* (ADU, A32114).

The relationship of *Colaconema humilis* to *C. macula* needs clarification. Although the two taxa apparently differ in length of erect filaments and cell and sporangium size, six other taxa (*Acrochaetium boergesenii* Schiffner (1931, p. 143); *A. cymopoliae* Boergesen (1927, p. 22); *A. pulchellum* Boergesen (1915, p. 23); *A. radiatum* Jao (1936, p. 246); *Chantransia reducta* Rosenvinge (1909, p. 120); *Acrochaetium subreductum* Levring (1953, p. 480)) are intermediate in regard to these features, and a comparison of the types and other collections may show that most or all are conspecific. Baardseth (1941, p. 41) already has suggested that several of these taxa belong to the same species.

The type collections of *Rhodochorton densum* Drew (1928) and *Acrochaetium mahumetanum* Hamel (1927) also should be compared with *Colaconema humilis.* Levring (1942) regarded the last two as conspecific, and differences in cell size, branching, and chromoplast shape which have been used to separate all three do not now appear to be taxonomically significant.

Rarely, plants of *Audouinella australis* (p. 25) have a habit somewhat similar to that of *Colaconema humilis*, but they differ in the absence of pyrenoids, in cell dimensions, and in having a unicellular holdfast. *Chantransia polyblasta* Rosenvinge (1909) and *Acrochaetium pulvinatum* Levring (1953) share some features with *Colaconema humilis* but are taller and have larger cells and sporangia. Until better understood, the latter two taxa are best regarded as distinct from *C. humilis.*

Colaconema macula (Rosenvinge) comb. nov.

Acrochaetium macula (Rosenvinge) Hamel 1927: 97; 1928: 191. Jao 1936: 247.
Chantransia macula Rosenvinge 1909: 114, fig. 42. Hygen et Jorde 1935: 37. Levring 1937: 88.
Chromastrum macula (Rosenvinge) Papenfuss 1945: 323.
Kylinia macula (Rosenvinge) Papenfuss 1947: 437.
Rhodochorton macula (Rosenvinge) Rosenvinge 1935: 7.

Figs. 15*A–I*

Plants epiphytic, up to 30 μm tall; original spore not persistent. Prostrate system at first a small parenchyma-like group of cells, later producing short and mostly simple filaments which commonly but not always become confluent to form an irregularly shaped pseudoparenchymatous disc. Cells 3–5 μm wide and 4–6(–9) μm long, L/D 1–2(–3). Erect filaments simple, up to 5 cells long. Cells of erect filaments similar in size to those of the prostrate system; each cell containing (Rosenvinge 1909, p. 114) a single stellate chromoplast and one pyrenoid. Hyaline hairs unknown.

Monosporangia spherical to ovoid, 4–5 μm wide and 5–7 μm long, sessile, terminal on erect filaments or arising from cells of prostrate filaments.

Other reproductive structures unknown.

Type Locality.–Gjenild Klint, Kattegat, Denmark.

Holotype.–C.

Distribution.–Daly Head, Yorke Peninsula, S.A. Denmark, Norway.

Hosts.–*Audouinella daviesii* in South Australia. *Polysiphonia* spp. in Europe.

Specimens Examined.–SOUTH AUSTRALIA: Daly Head (Yorke Peninsula), 27.iii.1967, *Woelkerling* (ADU, A31372).

Germinating spores of southern Australian plants may either first divide by a median wall and then undergo further divisions to produce a parenchymatous disc (Figs. 15*C*, *D*) or they may produce filaments directly which remain largely non-coherent (Figs. 15*A*, *B*, *I*). Rosenvinge (1909) recorded only the former type of development. In addition, monosporangia of southern Australian plants are somewhat smaller than those of Danish plants, possibly owing to age differences in the two collections.

Colaconema macula may represent a depauperate form of *C. humilis*, but since plants of intermediate morphology have not been found in southern Australian collections, the two taxa have been maintained as distinct species until better understood.

Acrochaetium subreductum Levring (p. 52), described from southern Australia, agrees well with *Colaconema macula* and when a comparison of the type collections can be made, it will almost certainly show the two to be conspecific.

Acrochaetium desmarestiae Kylin (1925) (see also Drew 1928) shares many features with *Colaconema macula* but differs in the absence of pyrenoids and in having prostrate system cells 3.5–6 diameters long.

Colaconema nakamurai nom. nov.

Acrochaetium unifilum Levring 1953: 472, fig. 9. Non Jao 1936: 239, pl. 10, figs. 26–32.

Fig. 16

Plants epiphytic; attached to the substrate by means of a single cell the same size as or smaller than other cells; producing a single erect filament up to 175 μm long with or without short, unbranched laterals. Cells cylindrical, 3–5 μm wide and (4–)6–9 μm long, L/D 1–1.5(–2); each cell containing (Levring 1953) a single parietal chromoplast with one pyrenoid. Terminal hyaline hairs occur.

Monosporangia ovoid, 4–6 μm wide and 6–9 μm long, sessile or rarely on one-celled stalks, seriate, lateral or occasionally terminal.

Other reproductive structures unknown.

Type Locality.–Cape du Couedic (Kangaroo I.), S.A.

Holotype.–Herbarium T. Levring, Goteborg, Sweden (private collection). Isotype: ADU, A19847.

Distribution.–Type locality only.

Hosts.–*Delisea hypneoides.*

Specimens Examined.–The isotype in ADU.

The specific epithet of *Acrochaetium unifilum* Levring (1953) must be rejected under Article 64 of the "Botanical Rules" since Jao (1936, p. 239) used the name earlier for another species of the genus *Acrochaetium*. The specific epithet "nakamurai" is proposed in its place, to honour Y. Nakamura who monographed the Japanese members of this complex (Nakamura 1941, 1944).

Contrary to the report of Levring (1953), branched plants occur as commonly as unbranched ones, and hairs are seldom found in the isotype material examined.

Acrochaetium erectum Boergesen (1932) is similar in some respects to *Colaconema nakamurai*, but apparently differs in height of erect filaments, larger cell dimensions, and several other minor respects. Authentic material of the two should be compared when possible in order to clarify their relationships more fully.

Acrochaetium spathoglossi Boergesen (1937) and *Rhodochorton hancockii* Dawson (1944) appear to be more distinct from *Colaconema nakamurai*. The former produces several erect filaments from the base and has cells 3–4 μm wide and 20–25 μm long in the upper portions of the erect filaments while the latter is 3–8 times as tall and has cells 3–4 diameters (up to 25 μm) long.

Colaconema pacifica (Kylin) comb. nov.

Acrochaetium pacificum Kylin 1925: 11, figs. 4*g–i*. Papenfuss 1945: 310; 1947: 435. *Rhodochorton pacificum* (Kylin) Drew 1928: 169, pl. 38, fig. 25.

Figs. 17*A–D*, 26*A*

Plants epiphytic, caespitose, 300–750(–1000) μm tall; sporelings unknown. Prostrate system consisting of creeping, branched, more or less confluent filaments forming an irregular pseudoparenchymatous disc. Erect filaments simple to moderately branched; laterals arising mostly from the upper portions of the main axes, irregularly to secundly arranged, and occasionally tapering towards the tips. Cells cylindrical, 4–7(–12) μm wide and 8–30(–36) μm long, L/D 1.5–6; each cell containing (Drew 1928) a single parietal chromoplast and one pyrenoid. Terminal and pseudolateral hairs up to 200 μm long occur.

Monosporangia ovoid, 6–9 μm wide and 8–12(–15) μm long, sessile or stalked, single or in pairs, lateral or rarely terminal on main axes and laterals. One tetrasporangium, cruciately divided, observed.

Other reproductive structures unknown.

Type Locality.–Not specified. Kylin (1925) lists three localities near Friday Harbour, Washington: Brown I., Shaw I., and Peavine Pass.

Holotype.–?

Distribution.–Garden I., W.A. and Elliston, S.A. San Juan County, Washington.

Hosts.–*Cladophoropsis* and *Sargassum* in Australia. Various algae in Washington.

Specimens Examined.–WESTERN AUSTRALIA: Garden I., 22.ix.1966, *Mitchell* (ADU, A30884). SOUTH AUSTRALIA: Elliston, 24.viii.1967, *Woelkerling* (ADU, A31994).

Acrochaetium iyengarii Boergesen (1933) reportedly differs from *Colaconema pacifica* in having cells of the erect filaments all about 15 μm long, but a comparison of the type collections will probably show the two taxa to be conspecific.

Other taxa of similar morphology to, but for the present regarded as distinct from, *Colaconema pacifica* include *Chantransia attenuata* Rosenvinge (1909) (see also Jao 1936, p. 244; Nakamura 1944, p. 103), *Acrochaetium flexuosum* Vickers (1905) (see also Boergesen 1915, p. 34; Hamel 1927, p. 77), and *Acrochaetium gracile* Boergesen (1915) (see also Boergesen 1927, p. 23; Abbott 1962, p. 115).

The relationship of *Colaconema pacifica* to *C. plumosa* (p. 48) is discussed under the latter species.

Colaconema phacelorhiza (Boergesen) comb. nov.

Acrochaetium phacelorhizum Boergesen 1915: 54, figs. 57–59; 1920*a*: 274; 1927: 37. Papenfuss 1945: 317. Taylor 1960: 313.
Chantransia phacelorhiza (Boergesen) De Toni 1924: 65.
Rhodochorton phacelorhizum (Boergesen) Drew 1928: 152.

Figs. 17*F–I*, 26*B*

Plants partly endophytic, up to 5 mm tall; sporelings unknown. Prostrate system consisting of a funiform mass of branched, confluent filaments penetrating the host tissues. Erect filaments moderately to richly branched; laterals irregularly to secundly arranged and generally tapering towards the tips. Cells cylindrical, (10–)16–24 μm wide and 25–75(–90) μm long (L/D 2–5) in lower portions of erect filaments, 7–16 μm wide and 25–60 μm long in upper portions of erect filaments; each cell containing a single parietal chromoplast with one pyrenoid. Hyaline hairs unknown.

Monosporangia ovoid, 10–15 μm wide and 22–30 μm long, sessile or occasionally stalked, solitary, seriate along the lower portions of laterals or more scattered; monosporangial wall sometimes with a distinct apical thickening. One tetrasporangium, 22 μm wide and 25 μm long, cruciately divided, observed.

Other reproductive structures unknown.

Type Locality.–Virgin Is.

Holotype.–C.

Distribution.–Head of Great Australian Bight, S.A. Virgin Is.

Hosts.–*Codium* spp.

Specimens Examined.–SOUTH AUSTRALIA: Head of Great Australian Bight, 4.xi.1968, *Woelkerling* (ADU, A32925).

Southern Australian plants of *Colaconema phacelorhiza* agree in general with the original description of Boergesen (1915) but are somewhat more robust and bear more sporangia. Tetrasporangia are recorded here for the first time. Non-apically thickened monosporangial walls occur more frequently than apically thickened ones.

Colaconema phacelorhiza and some plants of *Audouinella botryocarpa* (p. 37) superficially appear very much alike but are readily distinguished by differences in pyrenoid numbers. In addition, the latter species has mostly stalked monosporangia without apically thickened walls.

The type collections of *Colaconema phacelorhiza* and *Acrochaetium nemalionis* (De Notaris) Boergesen (see Rosenvinge 1909) should be compared in order to clarify their relationships more fully. Judging from the literature, the two taxa have many features in common.

Colaconema plumosa (Drew) comb. nov.

Acrochaetium plumosum (Drew) Smith 1944: 180. Papenfuss 1945: 310.
Rhodochorton plumosum Drew 1928: 173, pl. 39, fig. 29. Nakamura 1944: 108, figs. 6, 7.

Fig. 18

Plants epiphytic, caespitose, up to 800 μm tall. Prostrate system consisting of creeping, branched filaments more or less confluent in the centre. Erect filaments moderately branched; laterals opposite, alternate, or secund and tending to lie in a single plane. Cells cylindrical or occasionally fusiform, (6–)8–11(–17) μm wide and 18–36 μm long (L/D 1.5–4) in lower portions of main axes, gradually tapering to 2–4 μm wide near the apices; each cell containing a single parietal chromoplast and one pyrenoid. Terminal and pseudolateral hairs up to 250 μm long occur.

Monosporangia ovoid, 3–8 μm wide and 6–12 μm long, mostly distichous along the main axes and laterals, sessile or stalked; contents of subtending vegetative cells sometimes developing into monosporangia after release of the terminal monospore.

Other reproductive structures unknown.

Type Locality.–Fort Point, San Francisco, California.

Holotype.–UC 294559 (*Gardner* 4441).

Distribution.–Port Elliot, S.A.; Western Port, Vic. California, Japan.

Hosts.–*Petalonia fascia* and *Porphyra* sp. in southern Australia. Larger brown and red algae elsewhere.

Specimens Examined.–SOUTH AUSTRALIA: Port Elliot, 8.xi.1967, *Woelkerling* (ADU, A31279). VICTORIA: Crawfish Rock (Western Port), 15.ix.1968, *Watson* (ADU, A32707).

The southern Australian specimens of *Colaconema plumosa* are so few in number and in the Victorian collection so young, that they can be referred to this species only provisionally. In general, the plants agree with the descriptions given by Drew (1928) and Nakamura (1944).

Successive production of monosporangia has not been recorded previously in this species. Unlike other species, monosporangia form from the entire contents of stalk or subtending vegetative cells, and these spores eventually escape through the original sporangial walls (Figs. 18*C*, *D*). In Figure 18*D*, six spores have been released already, and the contents of two other vegetative cells have formed spores.

Drew (1928) and Nakamura (1944) discussed the difficulties of separating *Rhodochorton* (= *Colaconema*) *plumosa* from *R. variable* Drew (1928), but both authors maintained the two as distinct taxa.

Colaconema pacifica (p. 47) and *C. plumosa* share a number of similar features, but they apparently differ in the width of erect filaments, arrangement of laterals, and arrangement of sporangia and thus are maintained as distinct species for the present.

Colaconema polyidis (Rosenvinge) comb. nov.

Acrochaetium polyidis (Rosenvinge) Boergesen 1915: 59. Kylin 1944: 26. Papenfuss 1945: 317.

Chantransia polyidis Rosenvinge 1909: 132, figs. 59, 60. Levring 1935*a*: 460, fig. 2.

Figs. 19, 27*A*

Plants endophytic; sporelings unknown. Prostrate system consisting of sparingl and irregularly branched non-confluent filaments creeping within the gelatinous matr

of the host. Cells or prostrate filaments cylindrical, (12–)18–24(–36) μm wide and 40–75(–120) μm long, L/D 1.5–5(–6); each cell containing a single parietal lobate to highly dissected chromoplast with one pyrenoid. Erect filaments up to 500 μm tall, simple or sparingly and irregularly branched. Cells cylindrical, (6–)10–18(–24) μm wide and (12–)20–60(–100) μm long, L/D 1.5–5(–8), with smaller cells near the apices. Hyaline hairs unknown.

Monosporangia ovoid, 12–14 μm wide and 18–23 μm long, solitary or in pairs, terminal or lateral, sessile or stalked. Tetrasporangia ovoid, (13–)18–21 μm wide and (19–)25–30 μm long, cruciately divided.

Other reproductive structures unknown.

Type Locality.–Tonneberg Banke, Denmark.

Holotype.–C.

Distribution.–Wanna to Nora Creina, S.A.; Rocky Cape, Tas. Denmark.

Hosts.–*Codium* spp. in Australia. *Polyides* in Denmark.

Representative Specimens Examined.–SOUTH AUSTRALIA: Wanna (Pt. Lincoln), 15.v.1968, *Woelkerling* (ADU, A32307). Daly Head, 26.iii.1967, *Parsons* (ADU, A31445). Christies Beach, 2.iii.1968, *Woelkerling* (ADU, A32260). Marino (Adelaide), 21.v.1953, *Womersley* (ADU, A18860). Port Elliot, 6.x.1967, *Woelkerling* (ADU, A31302). Nora Creina, 26.i.1967, *Woelkerling* (ADU, A31992); 9.ii.1968, *Woelkerling* (ADU, A32254). TASMANIA: Rocky Cape, 24.ii.1964, *Wollaston* and *Mitchell* (ADU, A27654).

Southern Australian plants of *Colaconema polyidis* are more robust than those originally described by Rosenvinge (1909), but otherwise appear to be identical with them. Chromoplast structure is quite complex (Figs. 19*C–E*, *I*, *J*) and some chromoplasts are so dissected as to appear reticulate.

Chantransia immersa Rosenvinge (1909) was separated from *Colaconema polyidis* primarily on differences in chromoplast shape, but this difference may not be taxonomically significant and a comparison of the type collections may show that the two taxa are conspecific.

The relationship of *Colaconema polyidis* and *Chantransia interposita* Heydrich (1893, p. 78, Plate XXI, Fig. 8) requires clarification. Isotype material of the latter (in NY) has been examined and found to be similar in habit to but in all respects smaller than Australian plants of *Colaconema polyidis*. Further comparison of New Zealand and Australian populations, when collected, may reveal intermediate forms thus indicating that the two taxa may be conspecific.

Colaconema porphyrae (Drew) comb. nov.

Acrochaetium porphyrae (Drew) Smith 1944: 177, pl. 40, figs. 8, 9. Chapman 1962: 134.
Chromastrum porphyrae (Drew) Papenfuss 1945: 325.
Kylinia porphyrae (Drew) Papenfuss 1947: 438. Dawson 1953: 30.
Rhodochorton porphyrae Drew 1928: 188, pl. 46, figs. 70–75. Nakamura 1941: 280.

Figs. 20, 27*B*

Plants largely endophytic; developing from septate or occasionally aseptate spores. Prostrate system consisting of irregularly branched non-confluent filaments; cells irregular to cylindrical in shape, (2.5–)5–12(–42) μm wide and 12–30(–100) μm

long, L/D 1–5; each cell containing (Drew 1928) an axial stellate chromoplast and one pyrenoid. Erect filaments mostly simple and 2–3 cells long but occasionally up to 100 μm long and simple or with short irregularly arranged laterals; cells (4–)6–9 μm wide and 8–18 μm long. Terminal and pseudolateral hairs up to 200 μm long occur.

Monosporangia ovoid, 6–9 μm wide and 8–14 μm long, sessile or stalked, solitary or occasionally in pairs, terminal or lateral on the erect filaments.

Other reproductive structures unknown.

Type Locality.–Lands End, San Francisco, California.

Holotype.–UC 294552 (*Gardner* 3276).

Distribution.–Port Lincoln, S.A. to Western Port, Vic. California, Mexico, New Zealand.

Hosts.–*Porphyra* sp.; *Epiphloea* sp.

Specimens Examined.–SOUTH AUSTRALIA: Wanna (Pt. Lincoln), 21.viii.1967, *Womersley* (ADU, A31808). Troubridge Light (Coobowie), 4.ii.1969, *Shepherd* (ADU, A33399). Ellen Point (Vivonne Bay, Kangaroo I.), 24.viii.1963, *Womersley* (ADU, A27025). Robe, 24.viii.1960, *Womersley* (ADU, A24432). VICTORIA: Crawfish Rock (Western Port), 15.ix.1968, *Watson* (ADU, A32708). CALIFORNIA: Lands End (San Francisco), 1.ix.1917, *Gardner* (ADU, A16908).

Note.–A24432 and A31808 show good erect filaments; A27025 has poorly developed erect filaments; A27025 and A31808 have greatly swollen cells in the prostrate system.

Unfortunately Drew (1928) gave no information on cell size in the prostrate system for this species. Dawson (1953) found cells up to 10 μm wide, and plants from the type locality (ADU, A16908) contain cells 5–12(–18) μm wide. Most southern Australian collections have plants with cells of this width, but occasionally cells up to 42 μm wide occur.

Variation in height of erect filaments in populations of *C. porphyrae* may be due to age differences of plants. Drew (1928) suggested possible seasonal differences as the cause, but both tall and short plants occur in southern Australian populations collected in August.

The relationship between *Colaconema americana* (p. 42) and *C. porphyrae* requires clarification when additional material becomes available. Greatly swollen cells occur in both taxa and they share a number of other features, but they apparently differ in width of erect filaments and in sporangium size and shape.

The relationship of *C. porphyrae* to *C. bonnemaisoniae* also requires clarification. Except for apparent differences in sporangium size and shape and in cell dimensions of the prostrate filaments, the two taxa appear to be very similar.

Colaconema tenuissima (Collins) comb. nov.

Acrochaetium tenuissimum (Collins) Papenfuss 1945: 319.
Chantransia tenuissima (Collins) Kylin 1941: 5, figs. 1*e*, *f*.
Rhodochorton tenuissimum (Collins) Drew 1928: 170, pl. 38, figs. 26, 27.
Acrochaetium virgatulum f. *tenuissima* (Collins) Collins 1906: 194.
Chantransia virgatula f. *tenuissima* Collins in Collins, Holden, and Setchell, P.B.A., No. 741 (nom. nud.).
Acrochaetium subsimplex Levring 1953: 473, figs. 10*A–D*, 11. Non *Rhodochorton subsimplex* (Harvey) De Toni 1897: 1515.

Fig. 21

Plants epiphytic, caespitose, up to 4 mm tall; original spore dividing into 3 or occasionally 2 portions which are recognizable in young but not older thalli. Prostrate system parenchyma-like at first but soon producing short, distinct, more or less confluent filaments. Erect filaments simple or sparingly and irregularly branched, tapering slightly towards the apices. Cells cylindrical, (4–)6–8(–10) μm wide and (15–)24–40 (–50) μm long, L/D 3–6(–8); each cell containing (Drew 1928) a parietal star-shaped chromoplast and one pyrenoid. Terminal and pseudolateral hairs up to 300 μm long occur.

Monosporangia ovoid, 9–15 μm wide and 18–24 μm long, solitary, sessile or rarely stalked, scattered on the erect filaments or occasionally terminal.

Other reproductive structures unknown.

Type Locality.–San Pedro, California.

Holotype.–FH. Material from the type collection is distributed in Phycotheca Boreali Americana, No. 741.

Distribution.–Discovery Bay, Vic.; Musselroe Bay, Tas. Type locality.

Hosts.–*Zostera* spp.

Specimens Examined.–VICTORIA: Glenelg mouth (Discovery Bay), 26.i.1952, *Beauglehole* (ADU, A21725). TASMANIA: Musselroe Bay, 7.ii.1948, *Levring* (ADU, A19846, isotype of *Acrochaetium subsimplex* Levring). CALIFORNIA: San Pedro, xi.1898, *Monk* (ADU, A32706, isotype).

Germinating spores of *Colaconema tenuissima* frequently undergo two initial divisions to produce a distinctive 3-celled germling (Figs. 21*B–F*). Unicellular hairs on the erect filaments may remain short (usually less than 60 μm long) permanently or may undergo marked elongation (to 300 μm).

Isotype plants of *Acrochaetium subsimplex* Levring (1953) and *Colaconema tenuissima* have been compared and found to be conspecific. They agree in all respects.

The relationship of *C. tenuissima* to *Acrochaetium virgatulum* (Harvey) Bornet requires further study. The latter species exhibits considerable variation (Rosenvinge 1909), and Collins (1906) originally described *Colaconema tenuissima* as a form of *Acrochaetium virgatulum*. Drew (1928), however, regarded the two as distinct species and was followed by Kylin (1941) and Papenfuss (1945). A further critical comparison of the type and other collections of the two taxa appears necessary and may show the two taxa to be forms of a single variable species.

Chantransia stricta Rosenvinge (1909) and *Acrochaetium gracile* Boergesen (1915; see also Boergesen 1927 and Abbott 1962) apparently differ from *Colaconema tenuissima* in several minor respects including having mostly stalked monosporangia of smaller dimensions, but the types should be compared when possible in order to clarify their relationships more fully.

Acrochaetium subreductum Levring 1953: 480, figs. 13*A–E*.

Plants epiphytic, up to 20 μm tall exclusive of hairs; arising from aseptate spores which remain recognizable in young thalli. Prostrate system consisting of creeping filaments growing more or less densely together and forming a small disc.

Cells 3 μm wide, L/D 1–2. Erect filaments 1–5 cells long. Cells 2.5–3 μm wide, L/D 1–2, cylindrical or slightly barrel-shaped; each cell containing a parietal chromoplast and one pyrenoid. Terminal hyaline hairs occur.

Monosporangia ovoid, 3–4 μm wide and 4–6 μm long, sessile on prostrate filaments or terminal or lateral on erect filaments.

Other reproductive structures unknown.

Type Locality.–Not specified. The alga was apparently first collected from Pennington Bay, Kangaroo I., S.A. (see Levring 1953, pp. 459, 480).

Holotype.–Herbarium T. Levring, Goteborg, Sweden (private collection).

Distribution.–South Australia; Victoria.

Hosts.–"... various filamentous algae such as Rhodomelaceae and *Halopteris*" (Levring 1953, p. 480).

Specimens Examined.–See below.

No plants of *Acrochaetium subreductum* were found on host plants of two fragmentary portions of Levring's collections in ADU (A19845, A19857); consequently the original name has been retained in this account. The above diagnosis is based on information in the account of Levring (1953).

As noted on p. 45, *A. subreductum* and *Colaconema macula* agree in all respects and are almost certainly conspecific.

VI. Audouinelloid Algae Recorded from Tropical and Subtropical Australia

Six audouinelloid algae are recorded from tropical and subtropical Australia (Table 3) but have not been dealt with in detail as adequate material has not been available. These regions remain almost entirely unknown as regards audouinelloid algae, and numerous other species probably occur.

Table 3

Audouinelloid Algae Recorded from Tropical and Subtropical Australia

Rhodochorton concrescens Drew 1928: 167, pl. 37, fig. 15. Levring 1953: 490.

Acrochaetium effusum Levring 1953: 479, figs. 13*F*, *G*.

Audouinella eugenea Skuja 1934: 179, pl. 1, figs. 3–5. Cribb 1965: 273, pls. 5, 6.

Acrochaetium pulvinatum Levring 1953: 477, fig. 12.

Rhodochorton purpureum (Lightfoot) Rosenvinge. Levring 1953: 489 (as *R. rothii* (Turton) Naegeli).

Chantransia subtilis Moebius 1894: 313, pl. 1, figs, 9, 10.

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INDEX TO SPECIFIC EPITHETS OF AUDOUINELLOID ALGAE CITED

Synonyms are italicized; misidentifications are indicated by an asterisk after the page number.

ADDENDUM

After this article had gone to press, two additional important papers have come to the author's attention. One (Chapman, V. J. (1969).–"The Marine Algae of New Zealand". Part III. Rhodophyceae. Issue I: Bangiophycidae and Florideophycidae (Nemalionales, Bonnemaisoniales, Gelidiales). 113 pp., 38 pl. Lehre, Germany.) includes an account of New Zealand audouinelloid algae based almost entirely on earlier publications, many of which are cited in the present Australian investigation. The New Zealand study not only leaves many points to be clarified but also includes a number of illustrations that are difficult to interpret. The second paper (Ramus, J. (1969).–The developmental sequence of the marine red alga *Pseudogloiophloea* in culture. *Univ. Calif. Publs Bot.* **52**, 1–28, pl. 1–12.) represents a detailed treatment of information contained in an abstract (Ramus 1968) that is cited in the present paper.

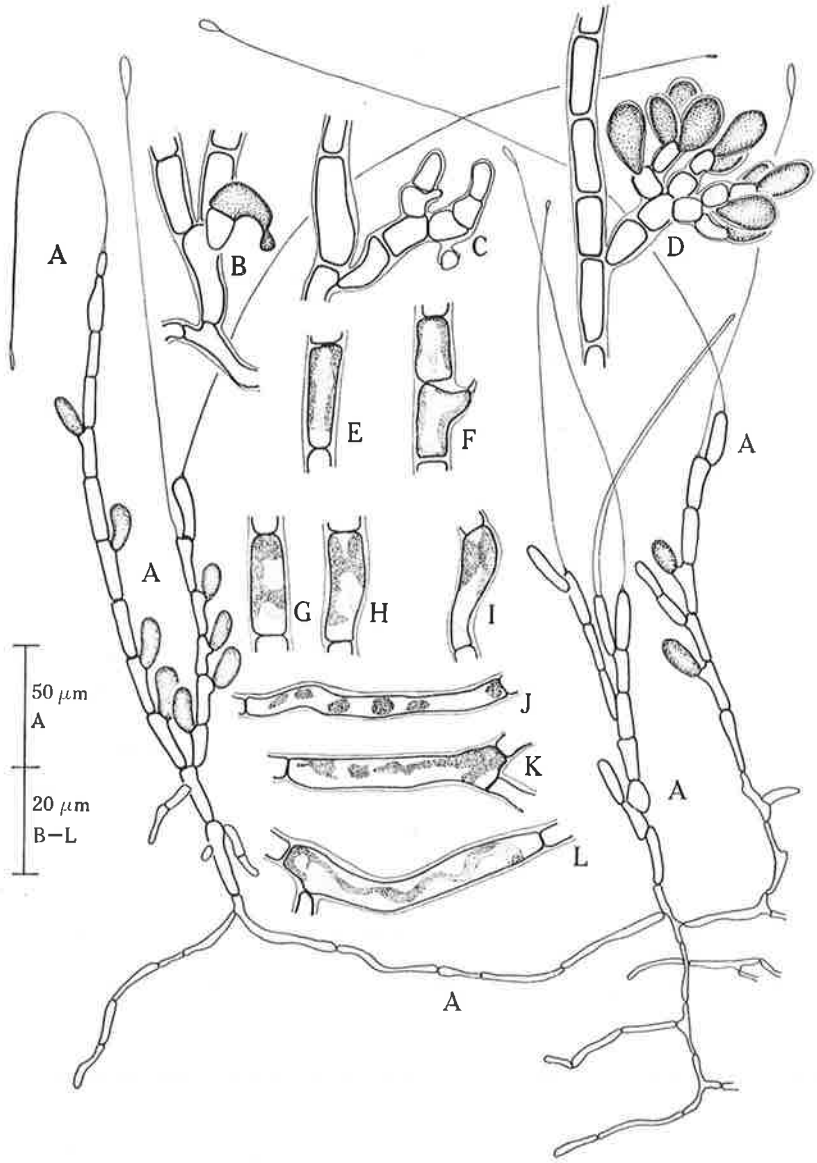


Fig. 1.—*Audouinella blumii* sp. nov.

A. Habit of mature monosporangial plant. Note terminal and pseudolateral hairs.

B. Unfertilized carpogonium on unicellular stalk.

C. Very young carposporophyte.

D. Nearly mature carposporophyte.

E–I. Variation in chromoplast shape in cells of erect filaments.

J–L. Variation in chromoplast shape in cells of prostrate filaments.

A–L. ADU, A32121 (Antechamber Bay, Kangaroo I., S.A., 20.xi.1967, *Woelkerling*).

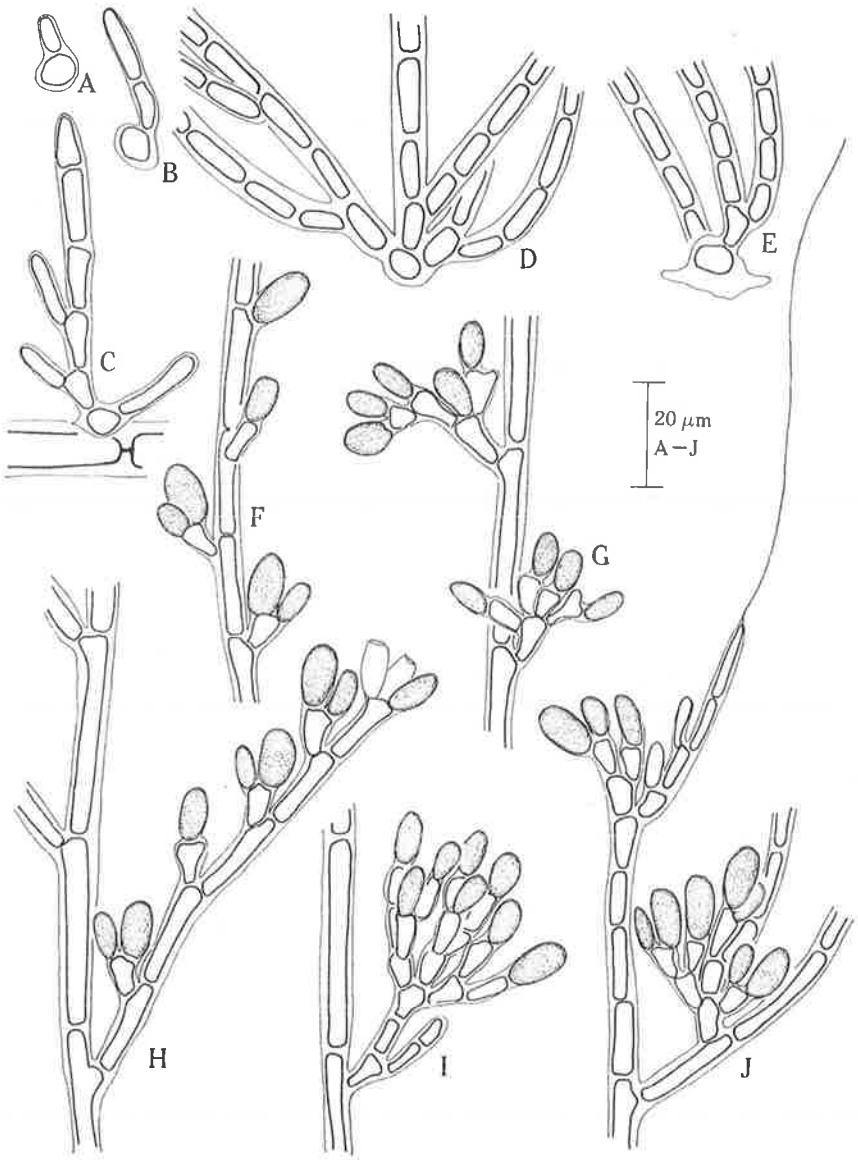


Fig. 2.—*Audouinella pectinata* (Kylin) Papenfuss

A–C. Sporelings.

D, E. Base of mature sexual plants. Note differences in the degree of development of the wall on the under-side of the cell.

F–J. Arrangement and position of monosporangia. Note the continuous intergrading series from solitary to clustered sporangia.

A–J. ADU, A32233 (Port Elliot, S.A., 31.i.1968, *Woelkerling*).

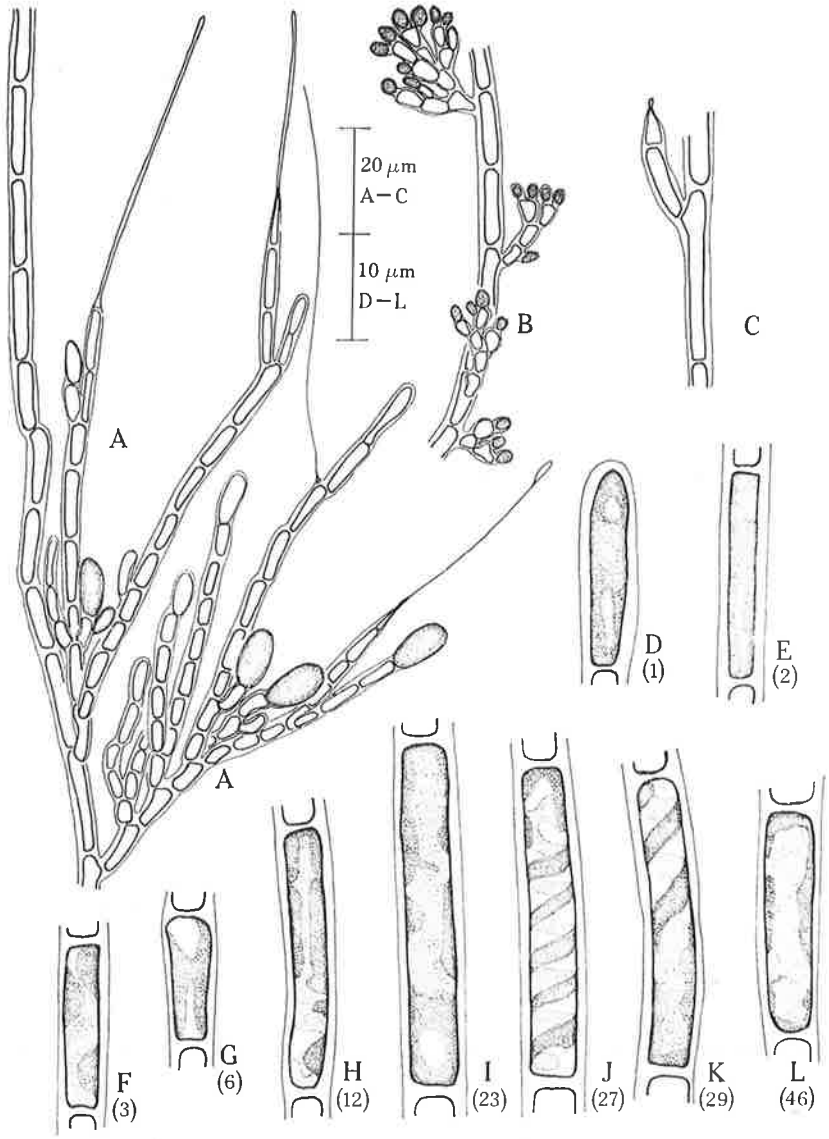


Fig. 3.—*Audouinella pectinata* (Kylin) Papenfuss

A. Upper portion of densely branched axis with monosporangia and terminal and pseudolateral hairs.

B. Spermatangia.

C. Possible unfertilized carpogonium.

D–L. Variation in chromoplast shape in cells of a single erect filament. Numbers denote position of the cell in the filament; i.e. 1 is the apical cell, 2 is the cell immediately behind the apex, etc.

A–C. ADU, A32233 (Port Elliot, S.A., 31.i.1968, *Woelkerling*); *D–L*. ADU, A32249 (Port Elliot, S.A., 1.iii.1968, *Woelkerling*).

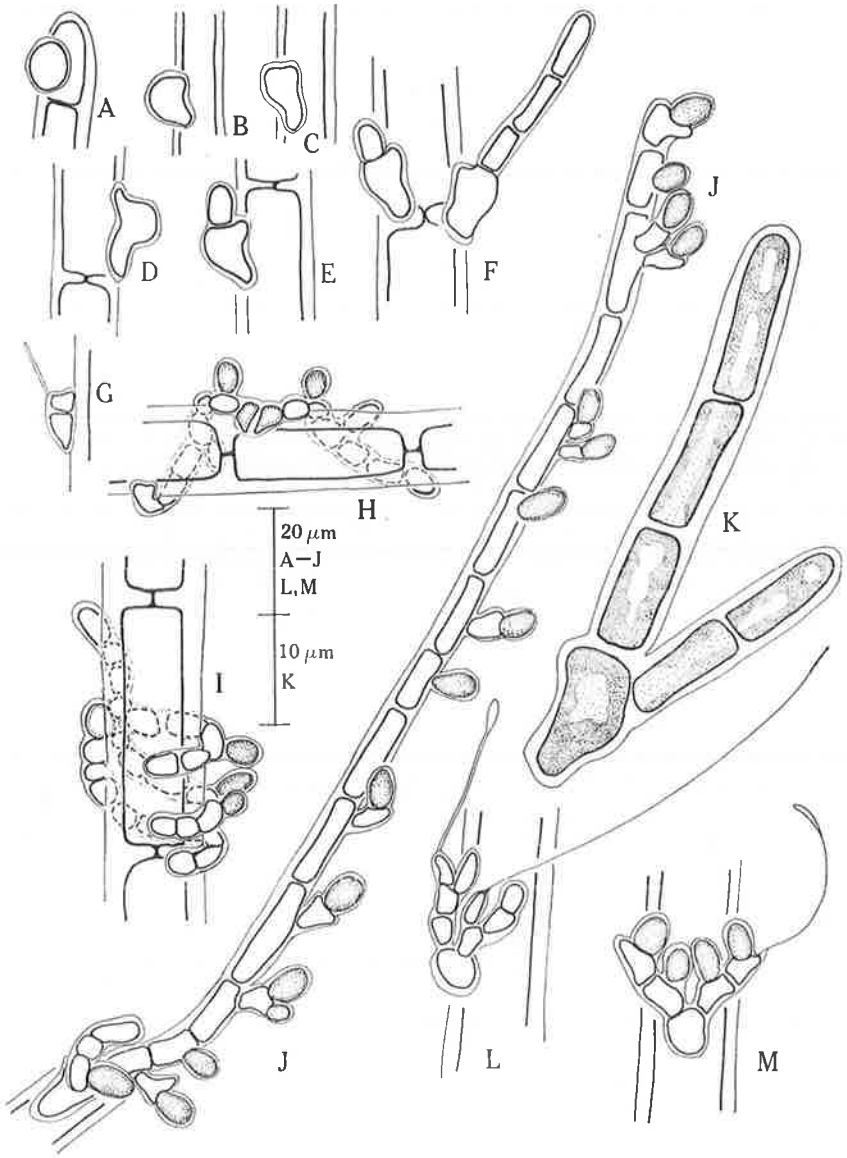


Fig. 4.—*Audouinella australis* (Levring) comb. nov.

A–D. Successive stages in the flattening of under-side of the germinating spore.

E, F. Sporelings.

G. Germinating spore divided to form a two-celled base.

H–J. Habit of mature plants. Note two-celled base in *H.*

K. Chromoplast shape in cells of erect filaments.

L, M. Minute mature plants with hairs and monosporangia.

A–F, K. ADU, A19503 (Venus Bay, S.A., 12.ii.1954, *Womersley*); *G–J, L, M.* ADU, A31373 (Pennington Bay, Kangaroo I., S.A., 7.i.1947, *Womersley*, isotype).

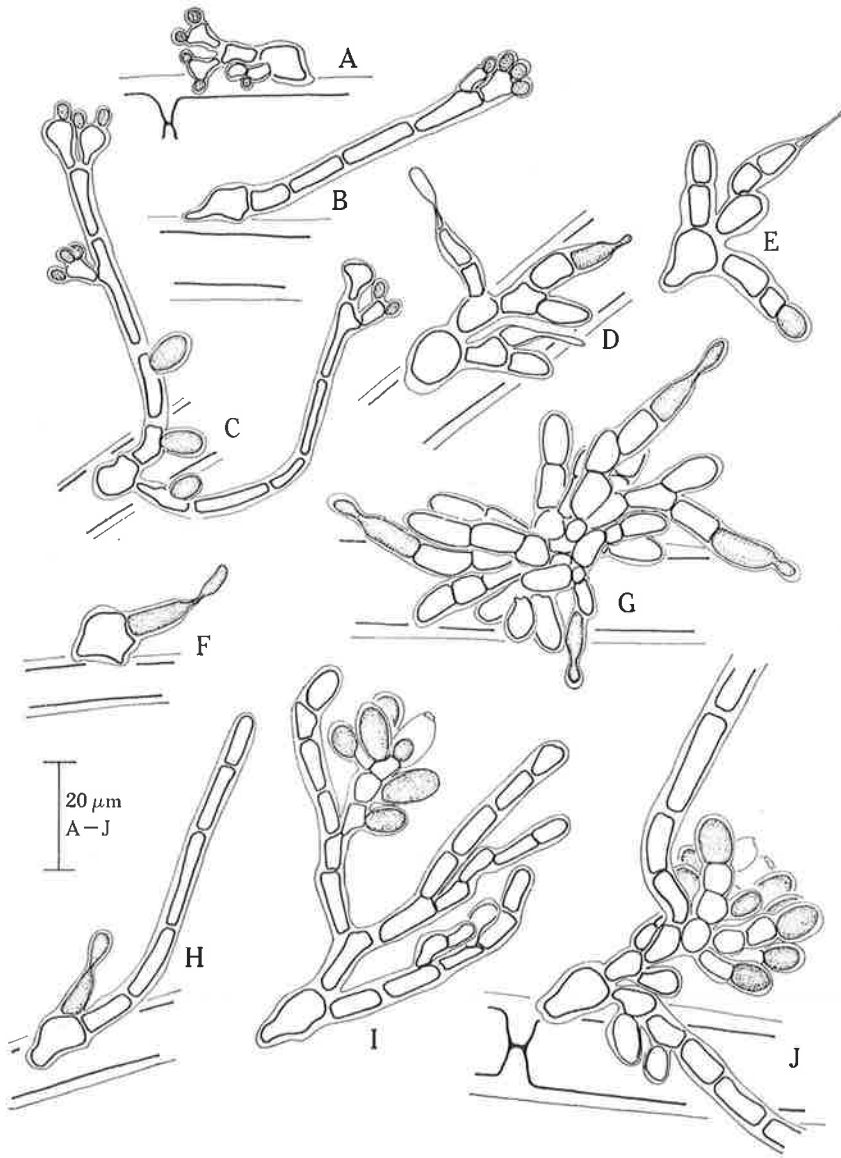


Fig. 5.—*Audouinella australis* (Levring) comb. nov.

A–C. Plants bearing spermatangia.

D, F–H. Plants with unfertilized carpogonia. Note pulvinate thallus in *G.*

E. Plant with terminal hair resembling a carpogonial trichogyne.

I, J. Plants with carposporophytes. Note successive sporangium production in *I.*

A–F, J. ADU, A31373 (Pennington Bay, Kangaroo I., S.A., 7.i.1947, *Womersley*); *G–I.* ADU, A19503 (Venus Bay, S.A., 12.ii.1954, *Womersley*).

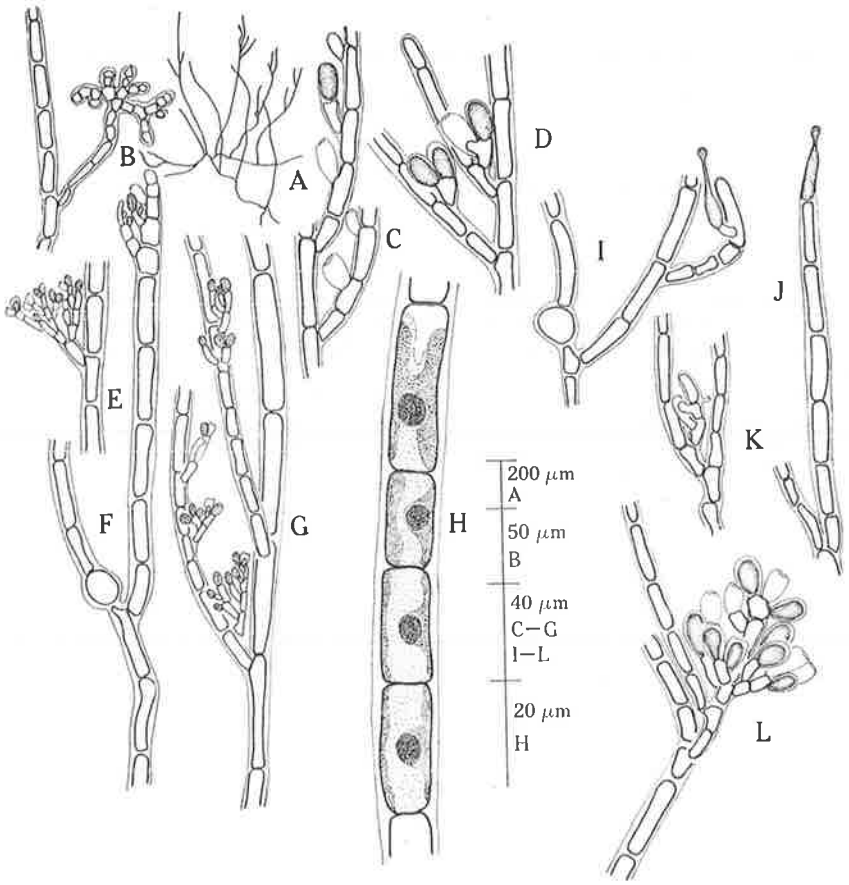


Fig. 6.—*Audouinella barbadense* (Vickers) comb. nov.

A. Habit of mature plant.

B. Apparently abnormal laterals composed of nearly isodiametric cells.

C, *D*. Erect filaments bearing monosporangia.

E–G. Spermatangia. Note clusters in lateral (*E*) and terminal (*F*) positions and paired spermatangia (*G*).

H. Chromoplasts in cells of erect filaments.

I, *J*. Unfertilized carpogonia. Note terminal carpogonium (*J*).

K. Recently fertilized carpogonium, showing an apparent initial transverse division.

L. Mature carposporophyte.

A–L. ADU, A30880 (Marino, S.A., 21.v.1953, *Womersley*).

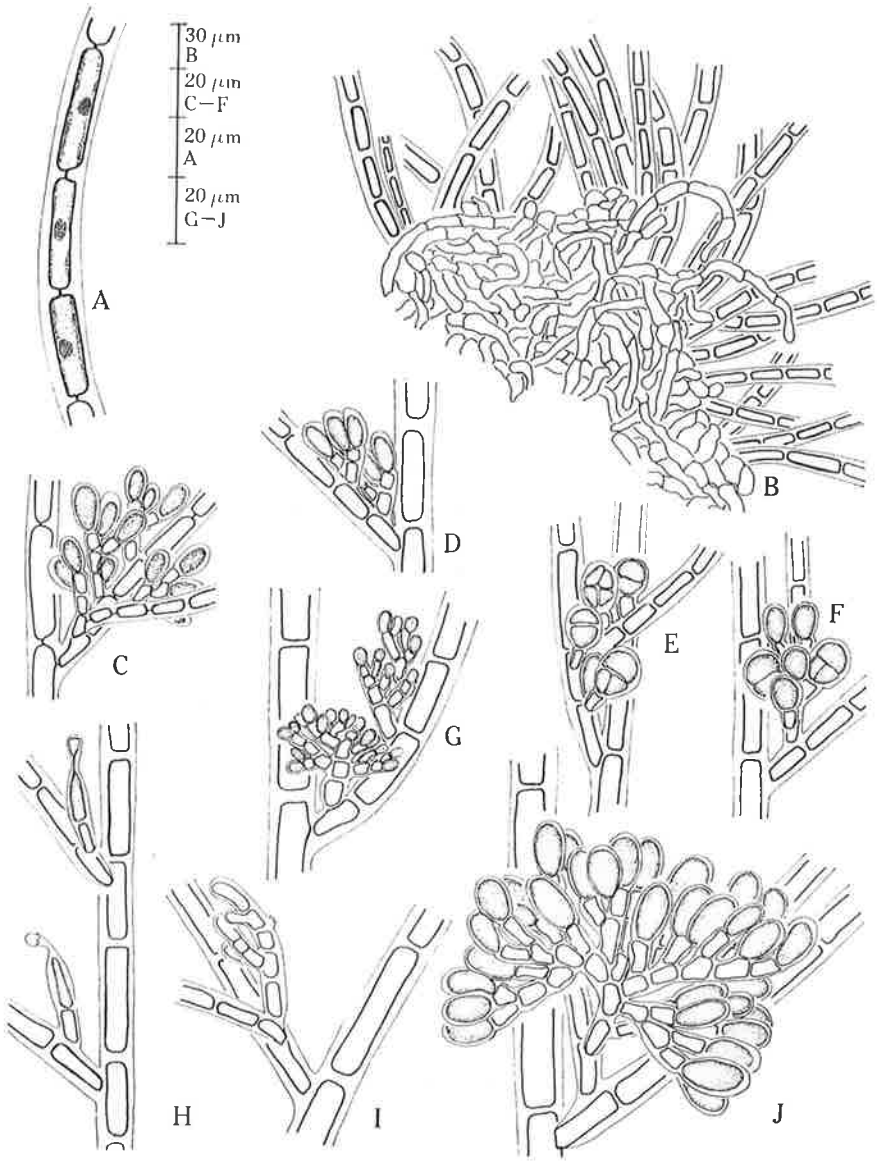


Fig. 7.—*Audouinella daviesii* (Dillwyn) comb. nov.

A. Chromoplasts in cells of erect filaments.

B Portion of prostrate system of plant on *Lenormandia*. Note pseudoparenchymatous nature.

C, *D*. Plants with monosporangia. Note how many are grouped into clusters on branched stalks.

E, *F*. Tetrasporangia on erect filaments.

G. Spermatangia.

H. Unfertilized carpogonia on unicellular stalks.

I. Young carposporophyte. *J*. Almost mature carposporophyte.

A–C, *E*. ADU, A31287 (Daly Head, Yorke Pen., S.A., 26.iii.1967, *Gordon*); *D*, *H–K*. ADU, A6499 (Pennington Bay, Kangaroo I., S.A., 7.i.1948, *Womersley*); *F*, *G*. ADU, A30732 (Point Peron, W.A., 22.ix.1966, *Mitchell*).

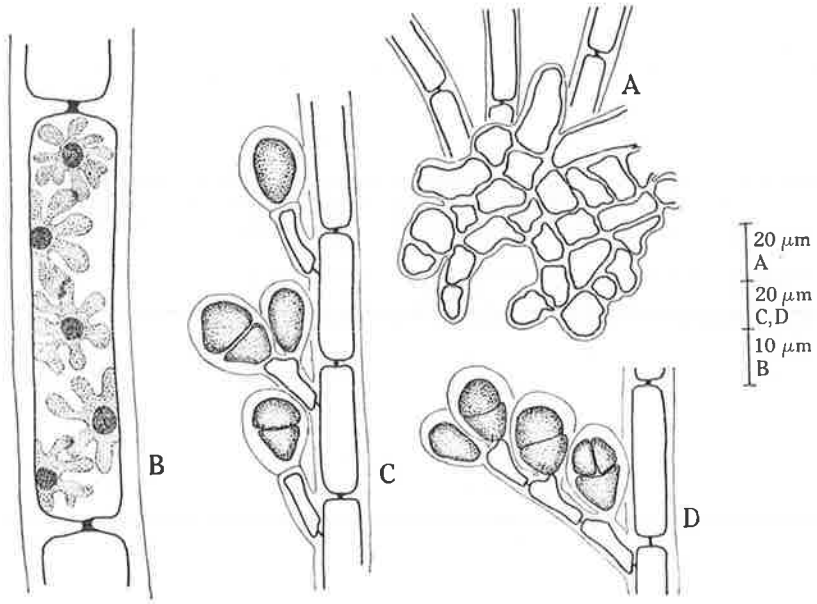


Fig. 8.—*Audouinella floridula* (Dillwyn) comb. nov.

A. Portion of prostrate system of epiphytic plant.

B. Chromoplasts in cell of erect filaments.

C, *D*. Tetrasporangia.

A, *B*. ADU, A19057 (The Blowholes, Cape Bridgewater, Vic., 21.viii.1953, *Womersley*); *C*, *D*. ADU, A24423 (Robe, S.A., 24.viii.1960, *Womersley*).

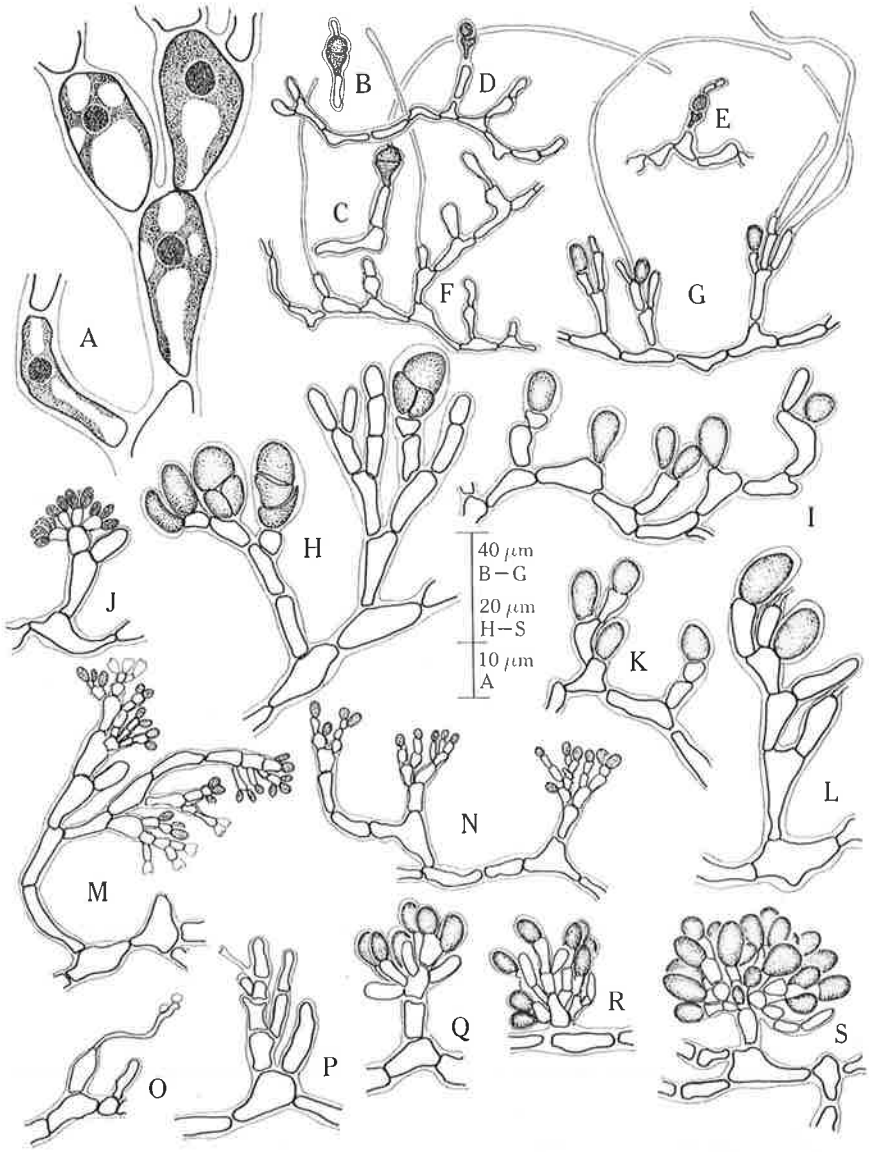


Fig. 9.—*Audouinella liagorae* (Boergesen) comb. nov.

A. Chromoplast shape in cells of erect filaments.

B–E. Sporelings. Note persistent, septate spore and favoured development from the lower product of the original spore.

F, G. Portions of thallus with terminal and pseudolateral hairs.

H. Tetrasporangia on erect filaments. *I, K, L*. Monosporangia. *J, M, N*. Spermatangia.

O. Carpogonium with attached spermatium.

P–S. Stages in the development of the carposporophyte.

A, D–G, I, J, M, N, P–S. ADU, A30883 (Pennington Bay, Kangaroo I., S.A., 22.i.1947, *Womersley*); *B, C, K, L*. ADU, A32696 (Antechamber Bay, Kangaroo I., S.A., 20.xi.1967, *Woelkerling*); *H*. ADU, A32055 (Antechamber Bay, Kangaroo I., S.A., 20.xi.1967, *Woelkerling*); *O*. ADU, A31371 (Barker's Rocks, Yorke Pen., S.A., 12.iii.1967, *Woelkerling*).

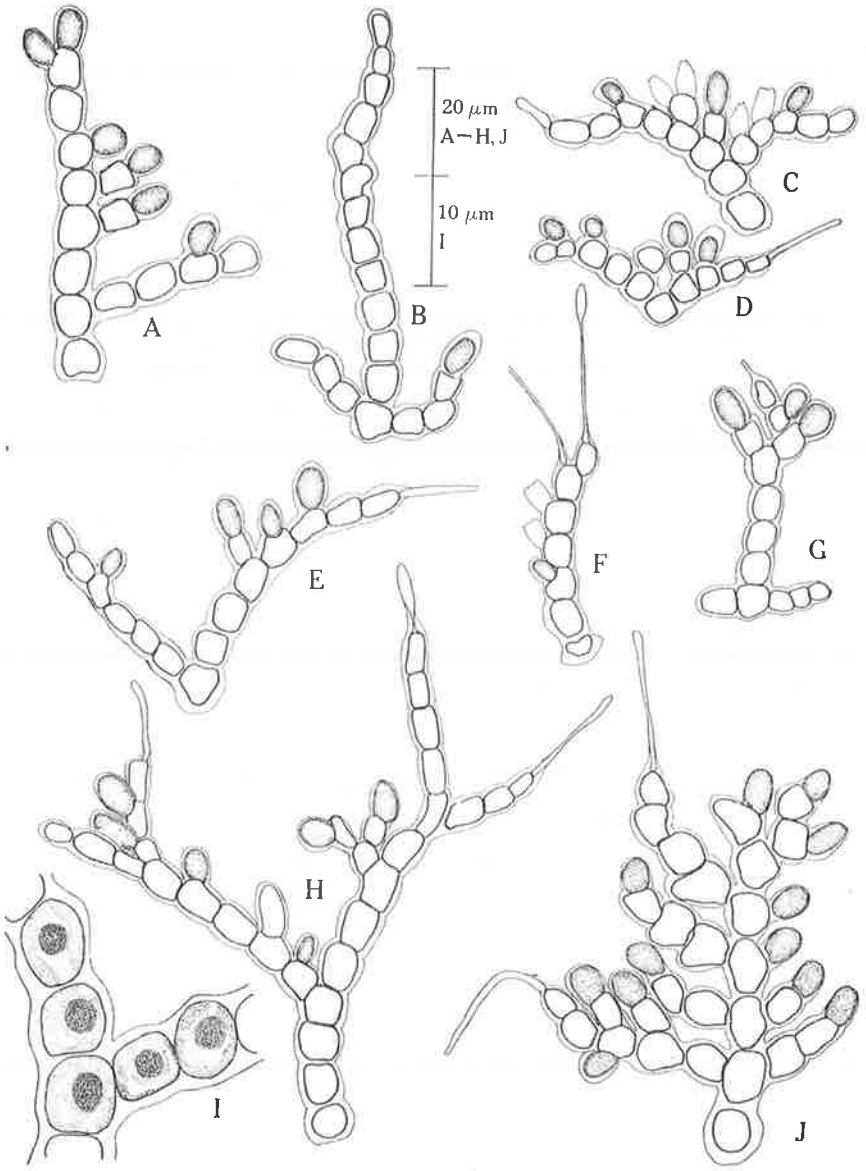


Fig. 10.—*Audouinella microscopica* (Naegeli) comb. nov.

A–H. Variation in habit of plants from a single population.

I. Chromoplast shape in cells of erect filaments.

J. Mature plant with dense branching.

A–H. ADU, A32710 (Port Elliot, S.A., 27.v.1967, *Woelkerling*); *J.* ADU, A19854 (Burraneer, N.S.W., 16.xi.1947, *Levring*); *I.* ADU, A32350 (Port Elliot, S.A., 1.iii.1968, *Woelkerling*).

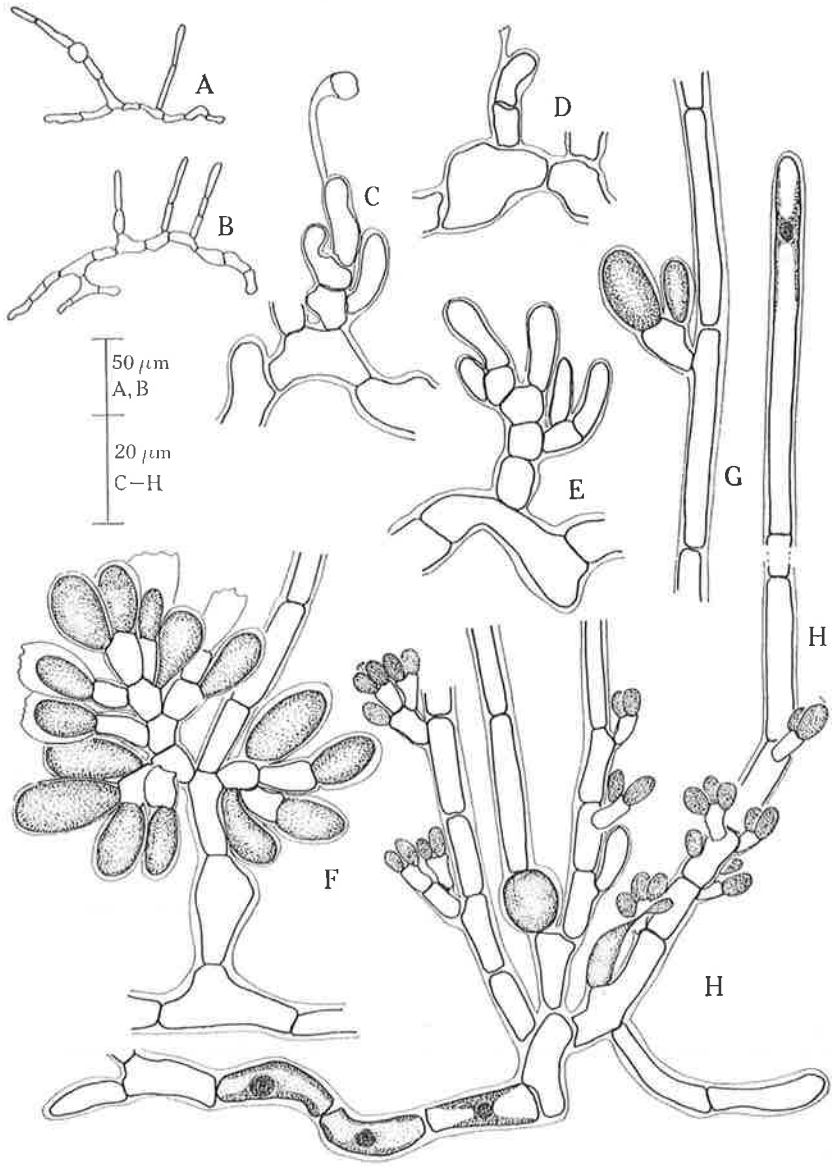


Fig. 11.—*Audouinella repens* (Boergesen) comb. nov.

A, *B*. Sporelings. Note both persistent and non-persistent spores.

C D. Recently fertilized carpogonia, showing initial transverse divisions.

E. Young carposporophyte.

F. Two mature carposporophytes on opposite sides of an erect filament.

G. Monosporangia on erect filaments.

H. Spermatangia. Note variation in shape of chromoplasts.

A–H. ADU, A32556 (Victor Harbour, S.A., 2.xi.1965, *Abbott*).

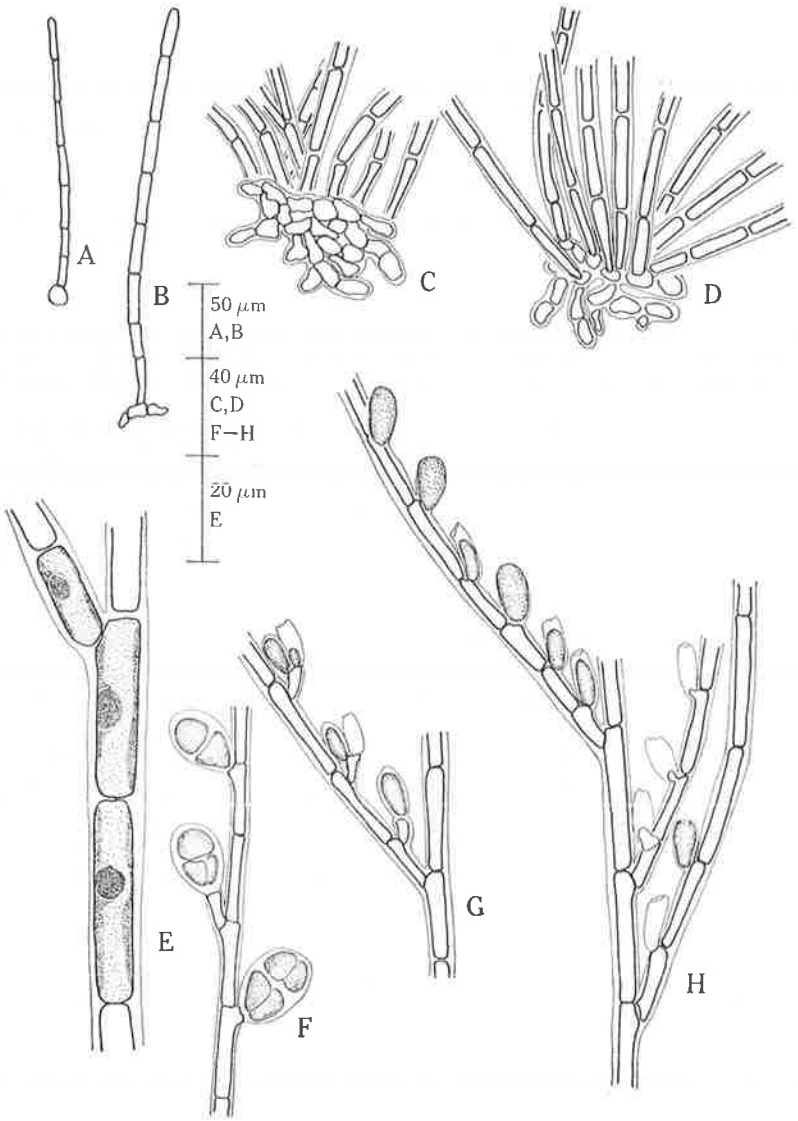


Fig. 12.—*Audouinella thuretii* (Bornet) comb. nov.

A, *B*. Sporelings.

C, *D*. Prostrate system of plants viewed from above and below.

E. Chromoplasts in cells of erect filaments.

F. Tetrasporangia.

G, *H*. Sessile and stalked monosporangia.

A–E, *H*. ADU, A32251 (Pt. Walter, Swan River Estuary, W.A., 11.xi.1967, *Allender*); *F*. ADU, A32291 (Crawley Bay, Swan River Estuary, W.A., 19.v.1968, *Allender*); *G*. ADU, A19843 (Pelican Lagoon, Kangaroo I., S.A., 10.i.1948, *Levring*).

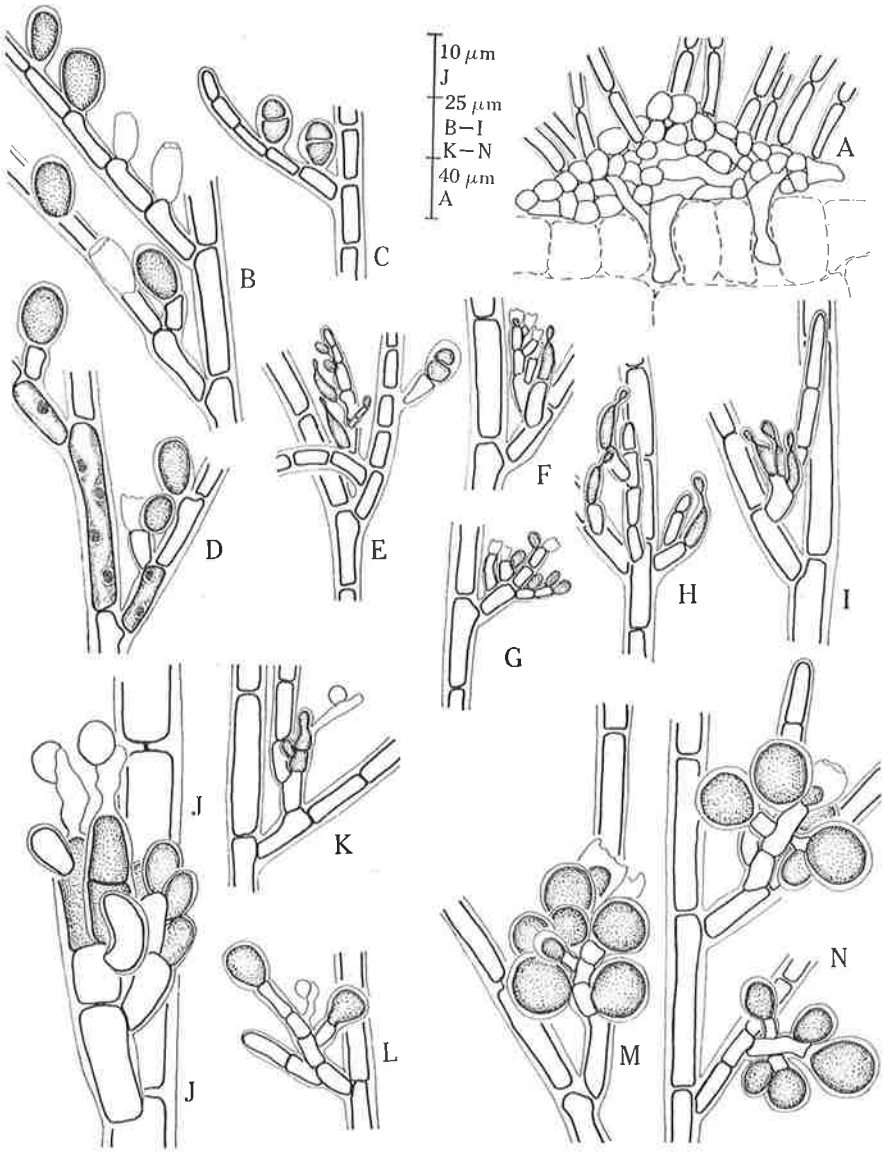


Fig. 13.—*Audouinella dictyotae* (Collins) comb. nov.

A. Cross section of endophytic and epiphytic prostrate system of mature plant.

B, *D*. Monosporangia. *C*, *E*. Bisporangia.

D. Chromoplasts in erect filaments. *E–G*. Spermatangia.

H, *I*. Unfertilized carpogonia. Note solitary and clustered arrangement.

J. Two fertilized carpogonia, one transversely divided and the other undivided with a cell cut off.

K, *L*. Young carposporophytes.

M, *N*. Mature carposporophytes. Note that neither cell representing the original fertilized carpogonium in *N* shows evidence of a preliminary transverse division, but the one in *M* does.

C, *E–N*. ADU, A28372 (Aldinga Beach, S.A., 25.x.1964, *Womersley*); *B*, *D*. ADU, A31667 (Port MacDonnell, S.A., 25.i.1967, *Woelkerling*).

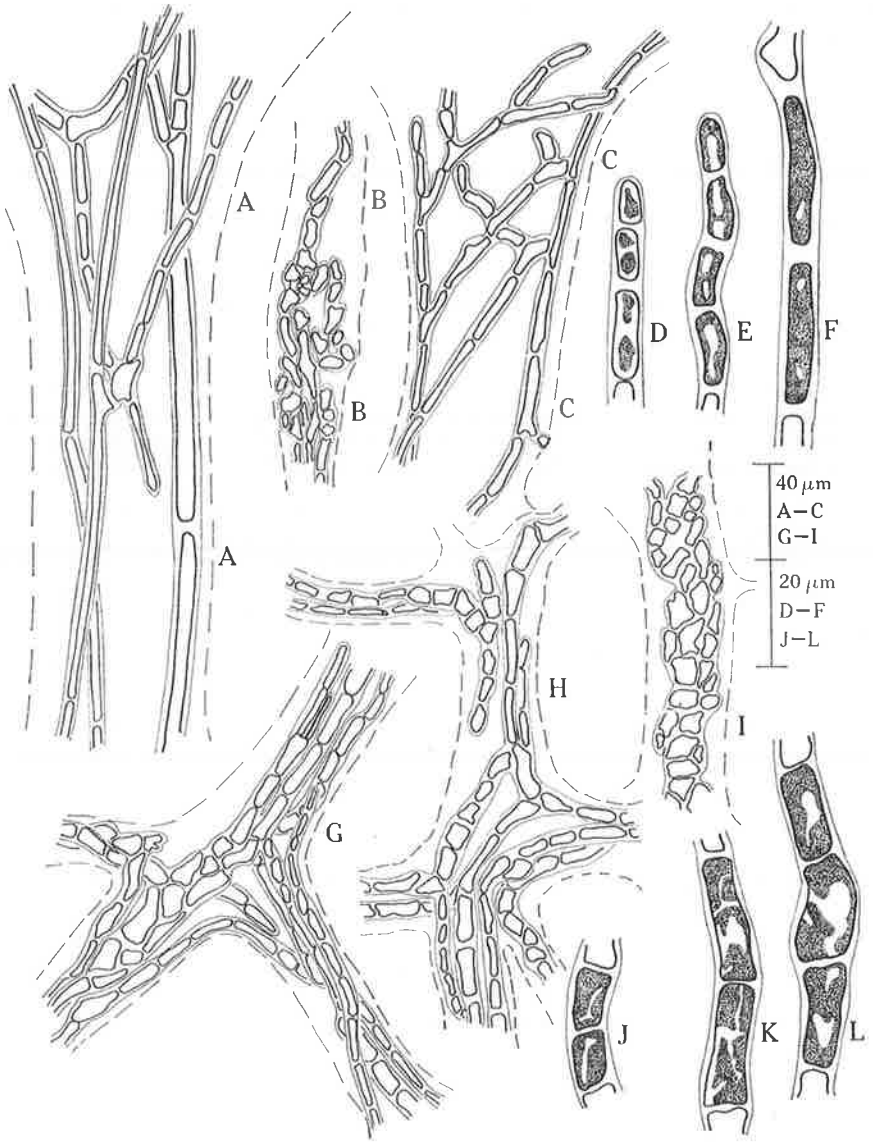


Fig. 14.—*Colaconema spongiocola* (Weber van Bosse) comb. nov.

A–C. Prostrate system. Note extremely elongate cells (*A*), more or less isodiametric cells (*B*), and anastomosing filaments (*C*).

D–F. Variation in chromoplast shape in cells of prostrate system.

Colaconema spiculiphila (Dawson) comb. nov.

G–I. Prostrate system. Note congested nature of filaments (*G*, *H*) and pseudoparenchymatous portion of thallus (*I*).

J–L. Variation in chromoplast shape in cells of prostrate system.

A, *B*, *D–F.* ADU, A32135 (Port Elliot, S.A., 15.i.1968, *Woelkerling*); *C.* ADU, A32136 (Port Elliot, S.A., 15.i.1968, *Woelkerling*); *G–K.* ADU, A32137 (Port Elliot, S.A., 15.i.1968, *Woelkerling*).

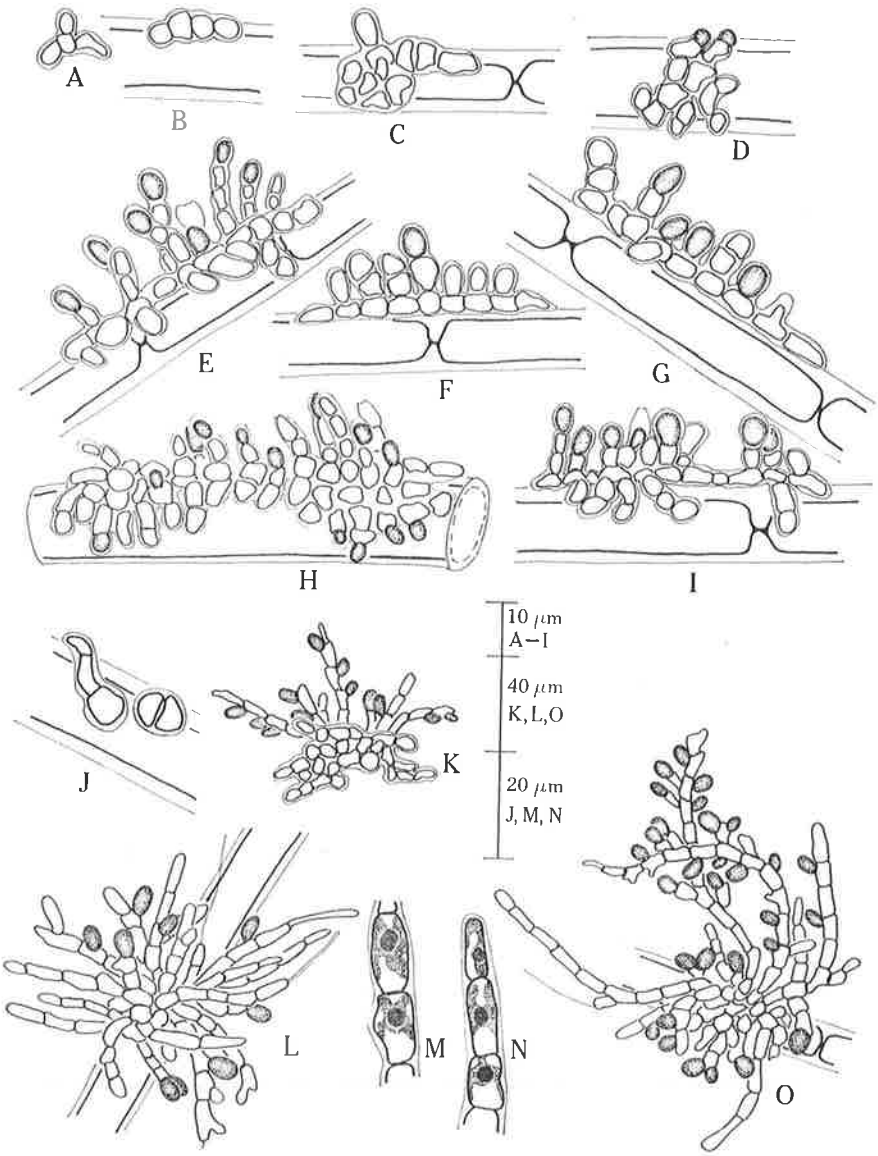


Fig. 15.—*Audouinella macula* (Rosenvinge) comb. nov.

A–D. Sporelings, showing development of parenchyma-like prostrate system.

E–I. Mature monosporangial plants.

Colaconema humilis (Rosenvinge) comb. nov.

J. Septate and aseptate germinating spores.

K. Prostrate system of plant viewed from below.

L, O. Mature monosporangial plants with well-developed erect filaments.

M, N. Chromoplasts in cells of erect filaments.

A–I. ADU, A31372 (Daly Head, Yorke Peninsula, S.A., 26.iii.1967, *Woelkerling*); *J–O.* ADU, A32114 (Port MacDonnell, S.A., 25.i.1967, *Womersley*).

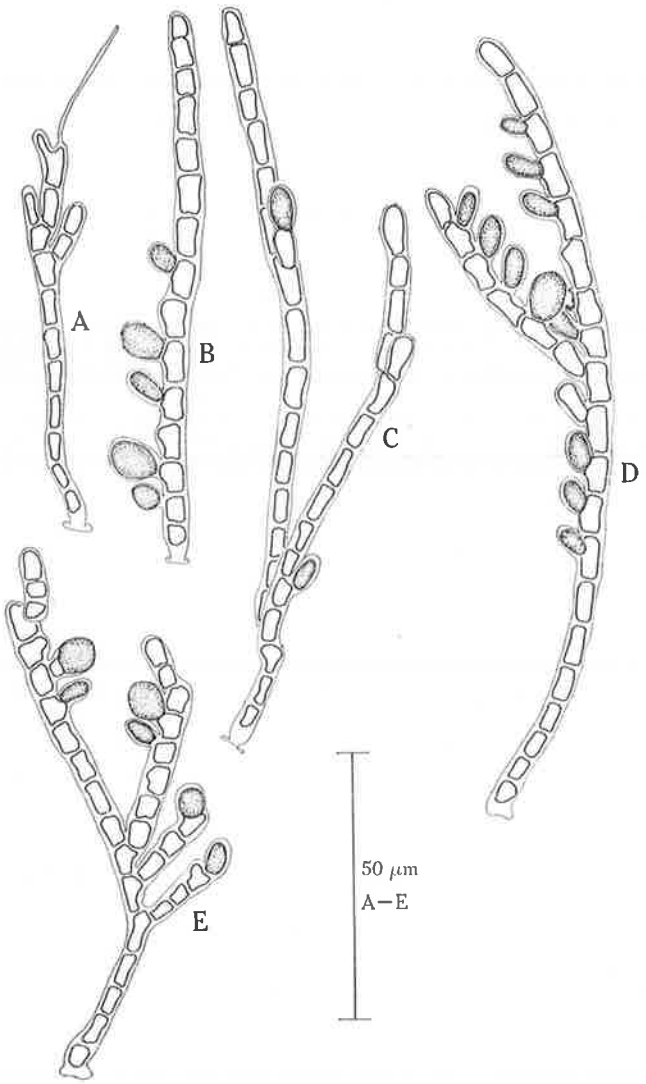


Fig. 16.—*Colaconema nakamurai* nom. nov.

A. Young plant with terminal hair. Note that the subterminal cell is dividing and that the terminal hair will be displaced to a lateral position.

B–E. Habit of mature monosporangial plants.

A–E. ADU, A19847 (Cape du Couedic, Kangaroo I., S.A., 12.i.1948, *Levring*).

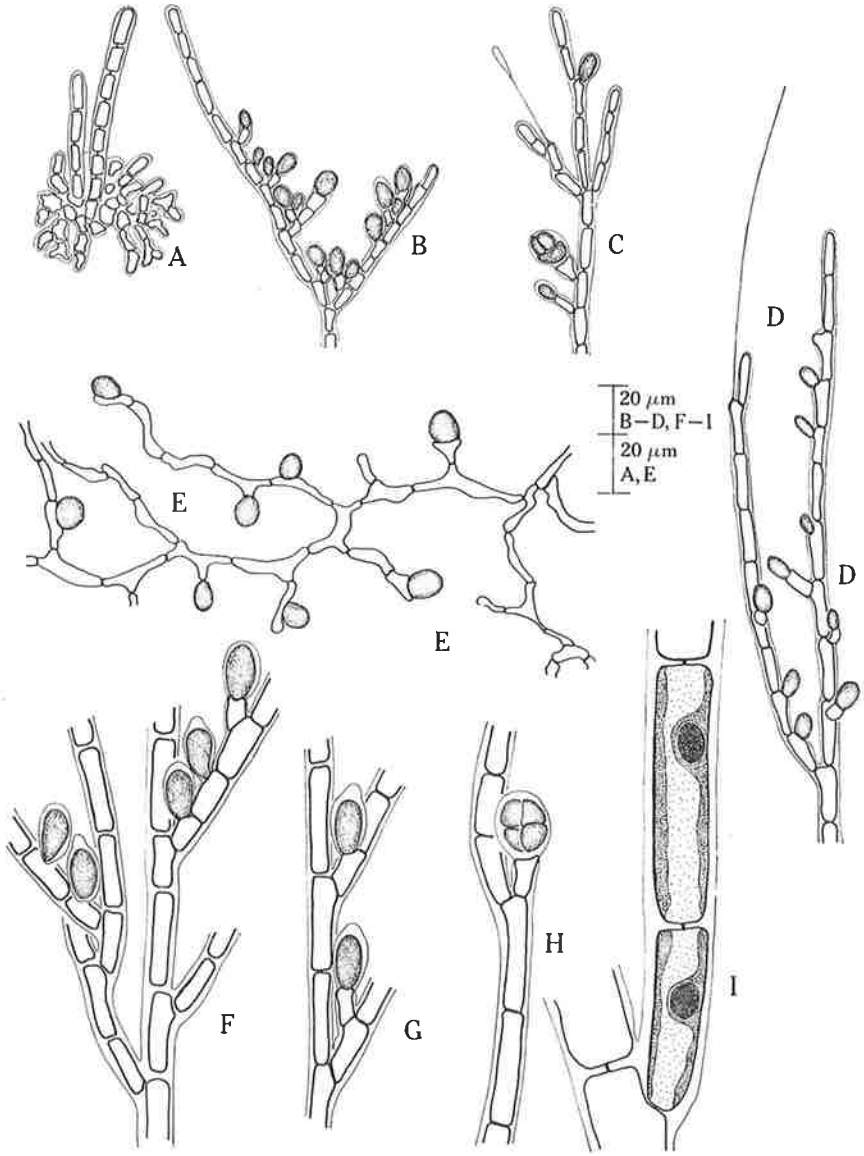


Fig. 17.—*Colaconema pacifica* (Drew) comb. nov.

A. Prostrate system of young plant.

B, *D*. Erect filaments with monosporangia and pseudolateral hairs.

C. Tetrasporangium.

Colaconema bonnemaisoniae Batters

E. Portion of mature plant with monosporangia.

Colaconema phacelorhiza (Boergesen) comb. nov.

F, *G*. Monosporangia on erect filaments. Note the apically thickened spore walls in some sporangia.

H. Tetrasporangium. *I*. Chromoplast shape in cells of erect system.

A–C. ADU, A31994 (Elliston, S.A., 24.viii.1967, *Woelkerling*); *D*. ADU, A30884 (Garden I., W.A., 22.ix.1966, *Mitchell*); *E*. ADU, A32130 (Pennington Bay, Kangaroo I., S.A., 29.viii.1948, *Womersley*); *F–I*. ADU, A32925 (Head of Bight, S.A., 4.xi.1968, *Woelkerling*).

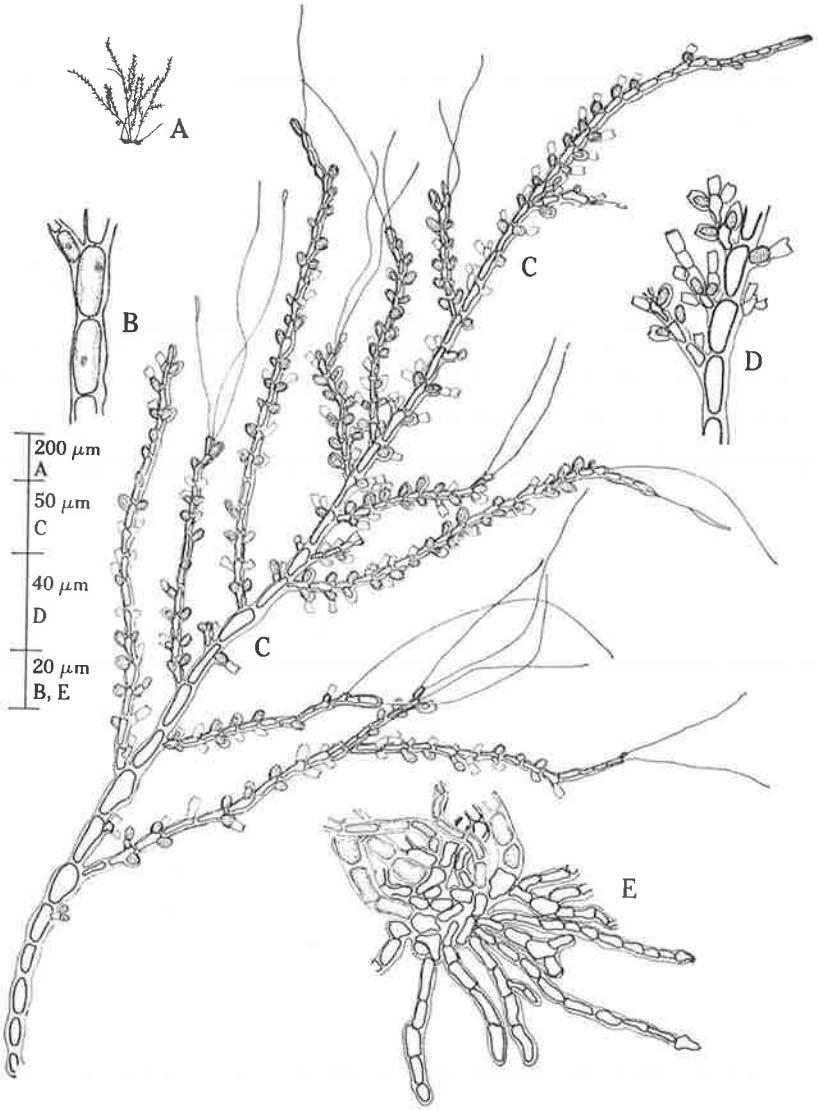


Fig. 18.—*Colaconema plumosa* (Drew) comb. nov.

A. Habit.

B. Chromoplasts in cells of erect filaments.

C. Erect system. Note percurrent main axis, terminal and pseudolateral hairs, arrangement and successive development of monosporangia.

D. Detailed view, showing successive development of monospores.

E. Portion of prostrate system. Erect filaments are shaded.

A–E. ADU, A31279 (Port Elliot, S.A., 8.ix.1967, *Woelkerling*).

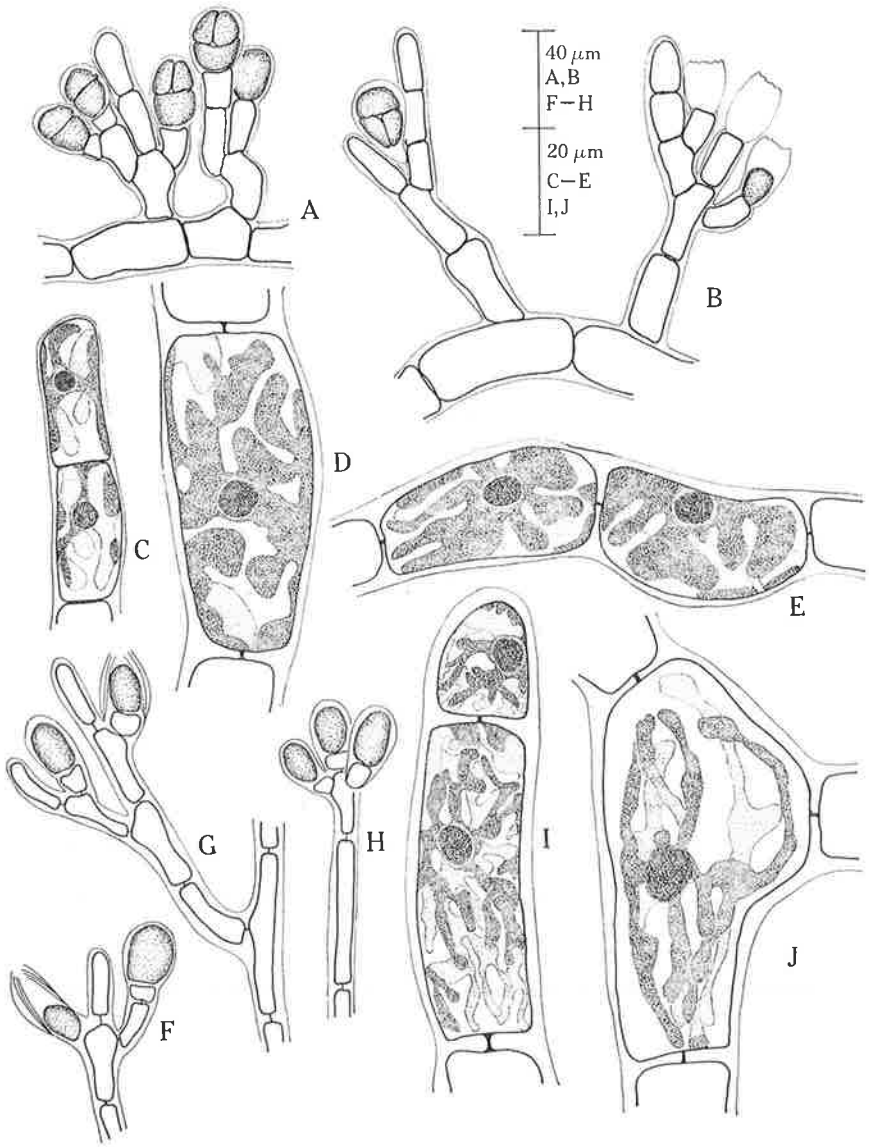


Fig. 19.—*Colaconema polyidis* (Rosenvinge) comb. nov.

A, B. Terminal and lateral tetrasporangia on erect filaments.

C–E, I, J. Variation in chromoplast shape in cells of erect filaments.

F–H. Terminal and lateral monosporangia on erect filaments. Note successive production of spores (*F, G*).

A–E. ADU, A18860 (Marino, S.A., 21.v.1953, *Womersley*); *F–J.* ADU, A32255, Nora Creina, S.A., 9.ii.1968, *Woelkerling*).

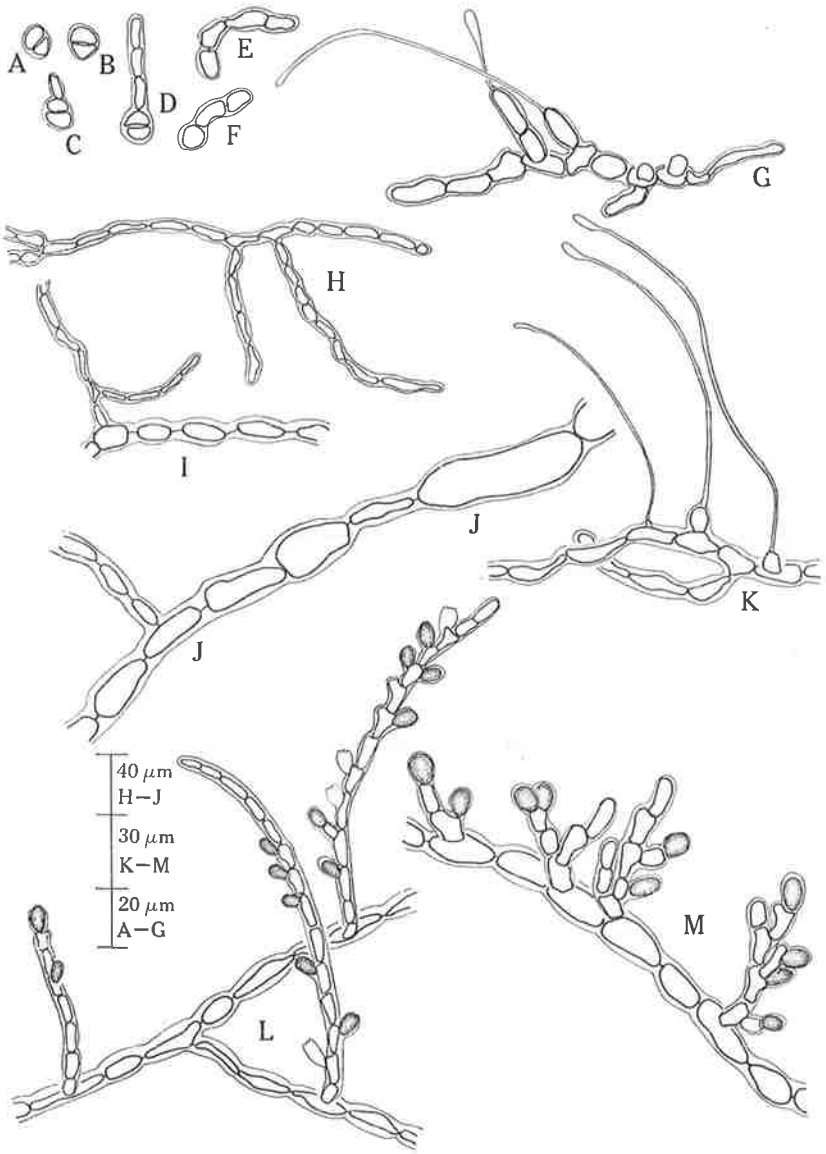


Fig. 20.—*Colaconema porphyrae* (Drew) comb. nov.

A–F. Septate and aseptate germinating spores.

G. Sporeling.

H–J. Prostrate filaments. Note great variation in cell size.

K. Unicellular hairs. Note hair directly on prostrate filament as well as those terminating one-celled erect filaments.

L, M. Long and short erect filaments bearing monosporangia.

A–D, L. ADU, A24432 (Robe, S.A., 24.viii.1960, *Womersley*); *E–H, K, M.* ADU, A31808, Wanna, Port Lincoln, S.A., 21.viii.1967, *Womersley*); *I, J.* ADU, A27025, Ellen Pt., Vivonne Bay, Kangaroo I., S.A., 24.viii.1963, *Womersley*).

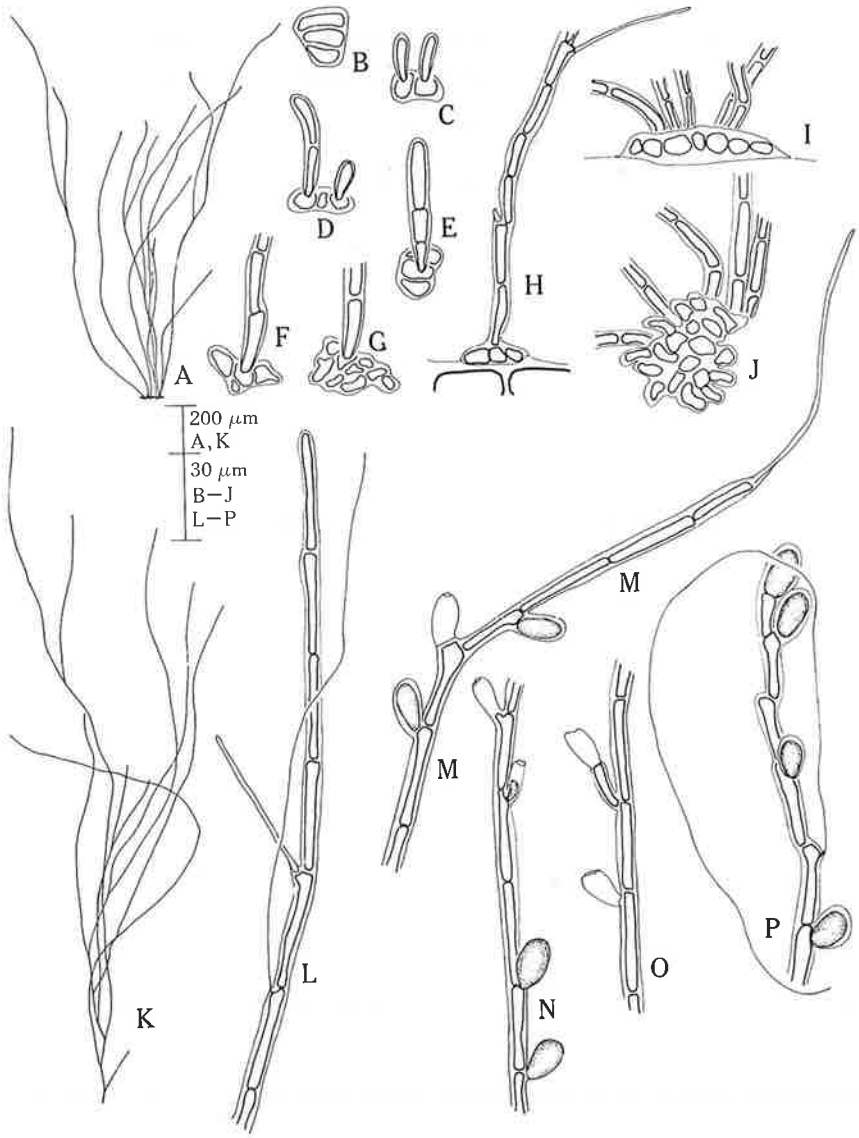


Fig. 21.—*Colaconema tenuissima* (Collins) comb. nov.

A. Habit.

B. Original spore divided into three cells.

C–H. Sporeling stages, showing successive divisions of the germinating spore and origin of the erect filaments.

I, J. Prostrate system of older plants.

K. Exceptionally well-branched erect filament.

L, M, P. Erect filaments with terminal and pseudolateral hairs. Note how some hairs become very thin and extremely elongate (*L*) and the sympodial-like axis (*P*) resulting from the displacement of several successively formed terminal hairs.

M–P. Monosporangia. Note terminal sporangium (*P*) and successive production of sporangia (*N*).

A, *H–P*. ADU, A19846 (Musselroe Bay, Tas., 7.ii.1948, *Levring*); *B–G*. ADU, A21725 (Glenelg Mouth, Discovery Bay, Vic., 26.i.1952, *Beauglehole*).

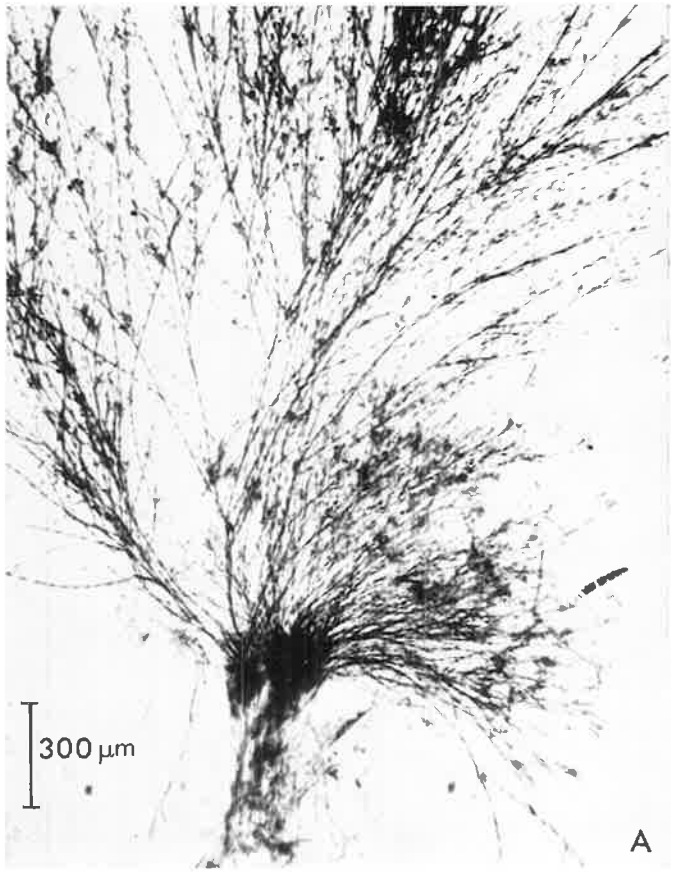
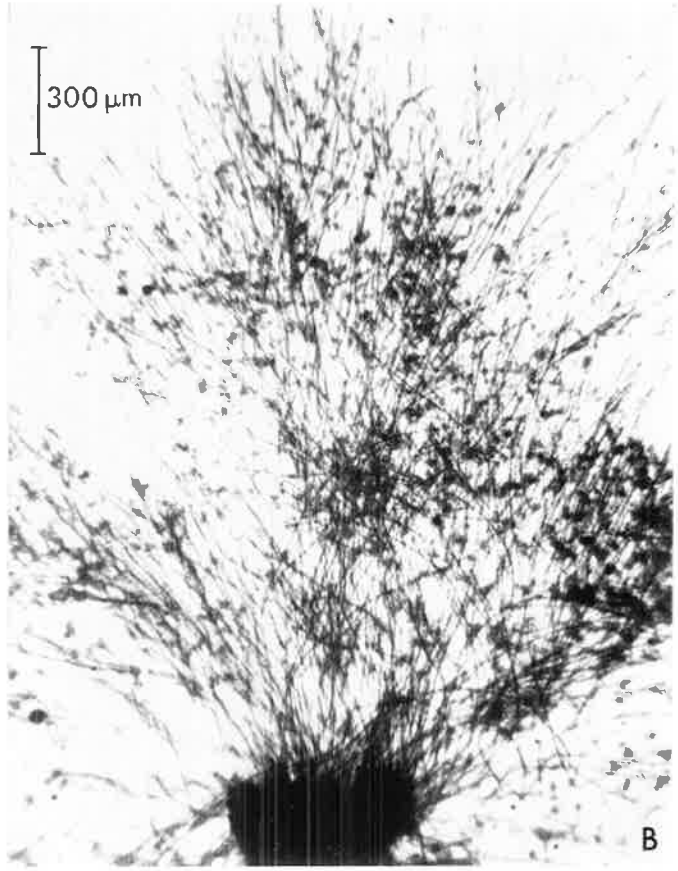
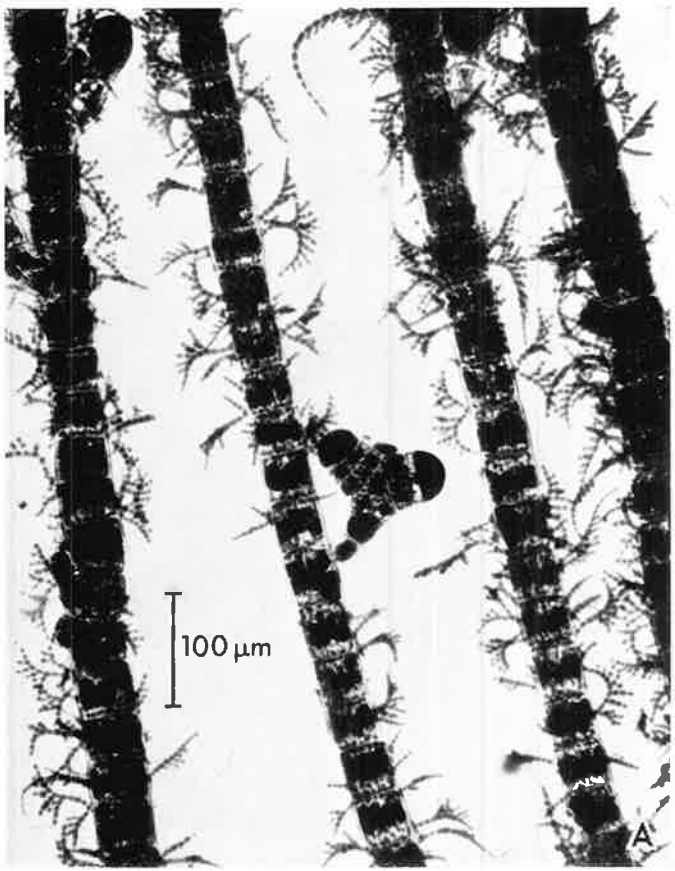


Fig. 22.—*A*. Habit of *Audouinella daviesii* (single plant removed from the host, *Codium*). Note the rope-like mass of entangled prostrate filaments. ADU, A32851 (Radar Reef, Rottnest I., W.A., 11.xi.1968, *Woelkerling*).



B. Habit of *Audouinella daviesii* (single plant removed from the host, *Amphibolis*). Note pseudoparenchymatous discoid prostrate system. ADU, A32922 (Head of Bight, S.A., 4.xi.1968, *Woelkerling*).



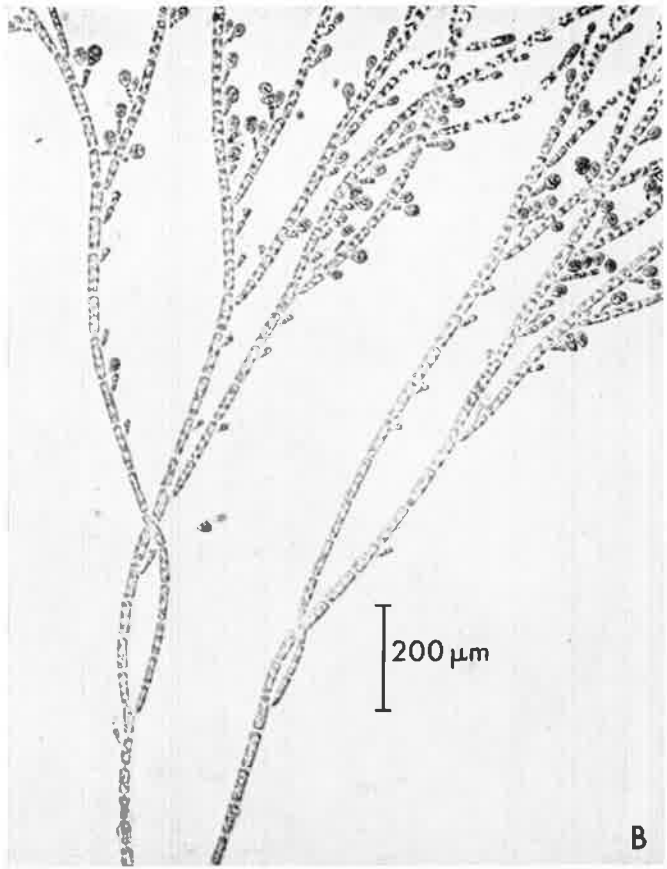


Fig. 23.—*A*. Population of *Audouinella microscopica* on *Sphacelaria*, showing variation in habit. ADU, A32250 (Port Elliot, S.A., 1.iii.1968, *Woelkerling*).

B. Erect filaments of *Audouinella floridula* bearing tetrasporangia. ADU, A24423 (Robe, S.A., 24.viii.1960, *Womersley*).

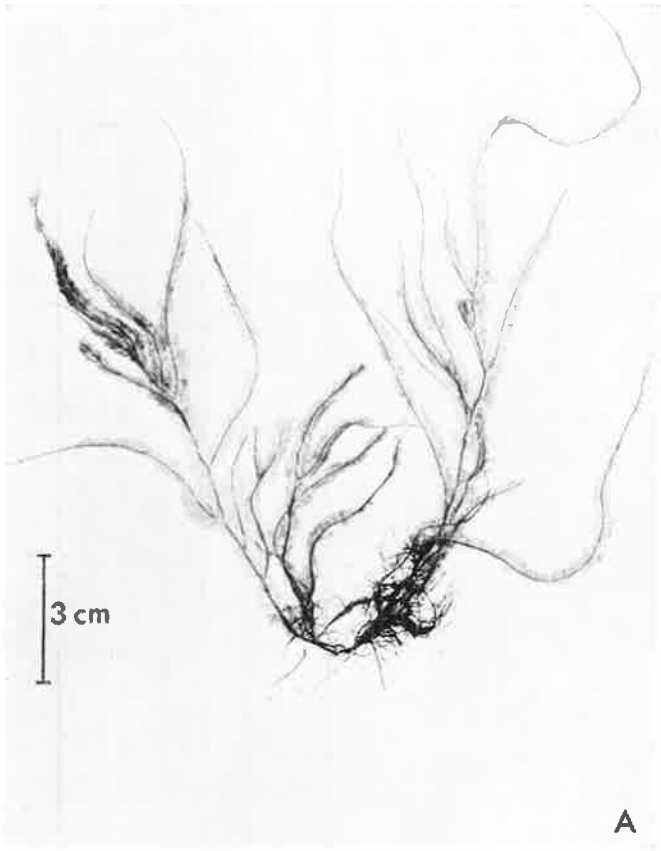
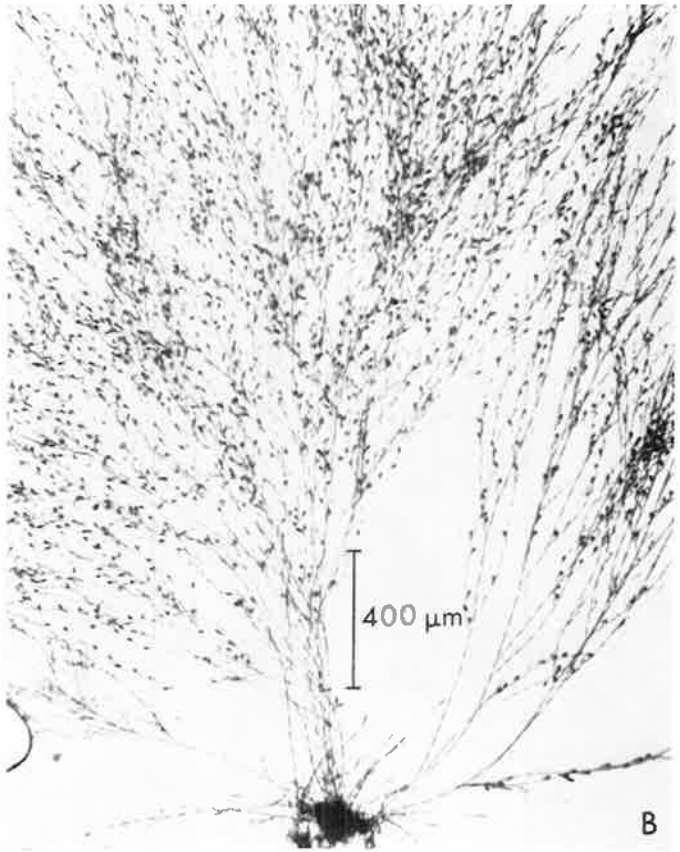


Fig. 24.—*A*. Population of *Audouinella thuretii* on *Gracilaria*. ADU, A32251 (Point Walter, Swan River Estuary, W.A., 11.xi.1967, *Allender*).



B. Habit of *Audouinella thuretii* (single plant removed from the host, *Gracilaria*). ADU, A32251 (Point Walter, Swan River Estuary, W.A., 11.xi.1967, *Allender*).

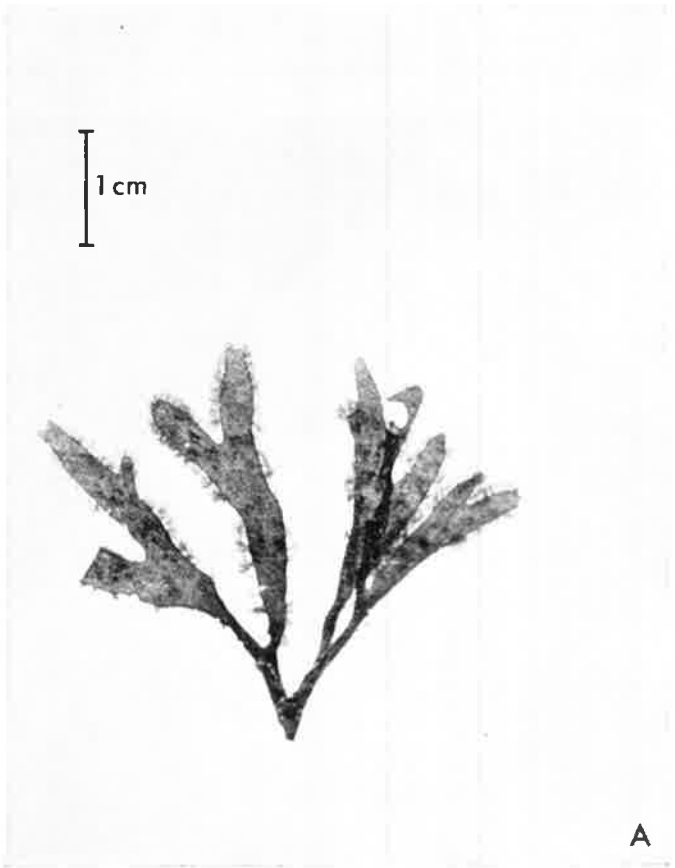
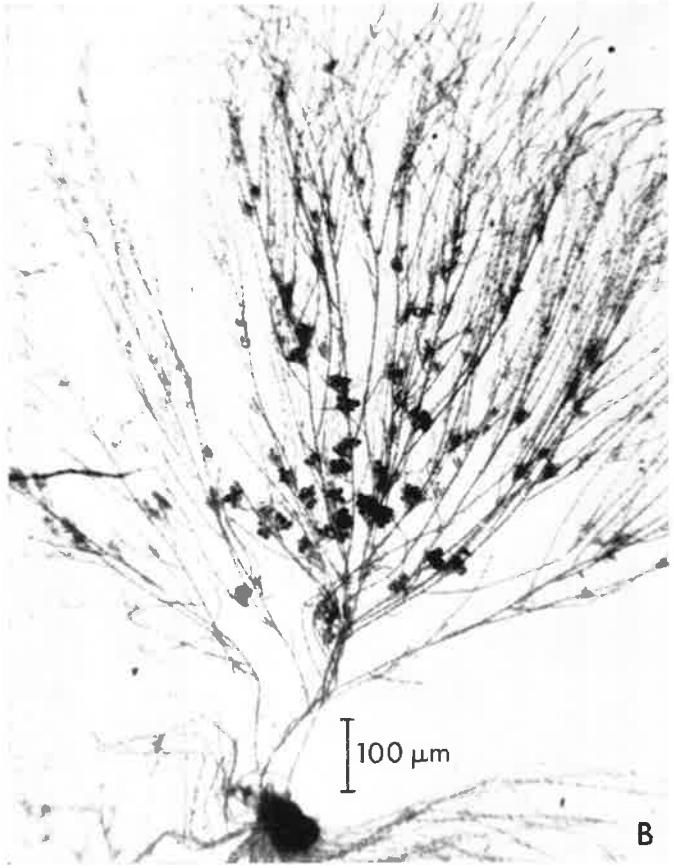


Fig. 25.—*A*. Population of *Audouinella dictyotae* on *Dictyota*. ADU, A29614 (Aldinga, S.A., 11.x.1965, *Womersley*).



B. Habit of female plant of *Audouinella dictyotae* bearing carposporophytes. ADU, A28372 (Aldinga, S.A., 25.x.1964, *Womersley*).

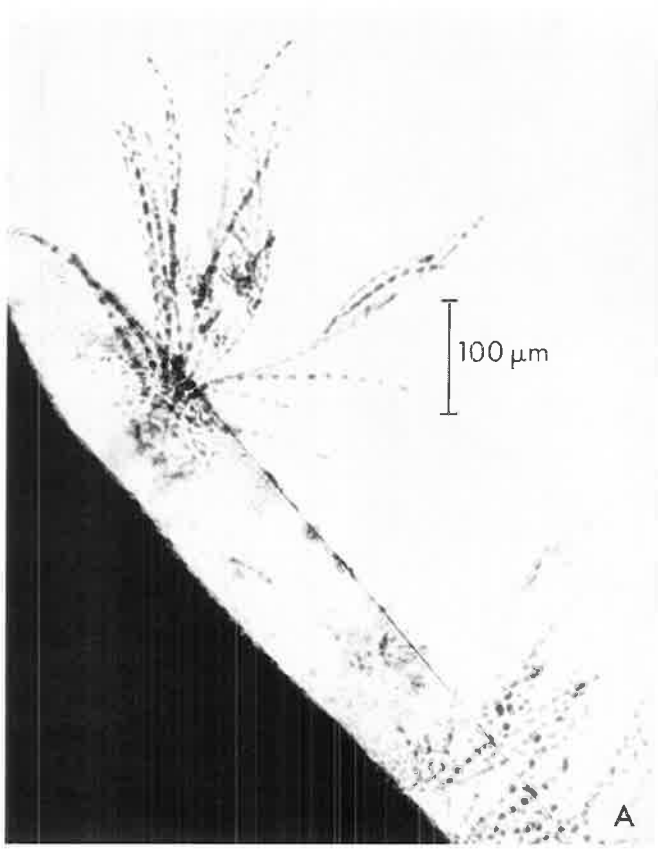
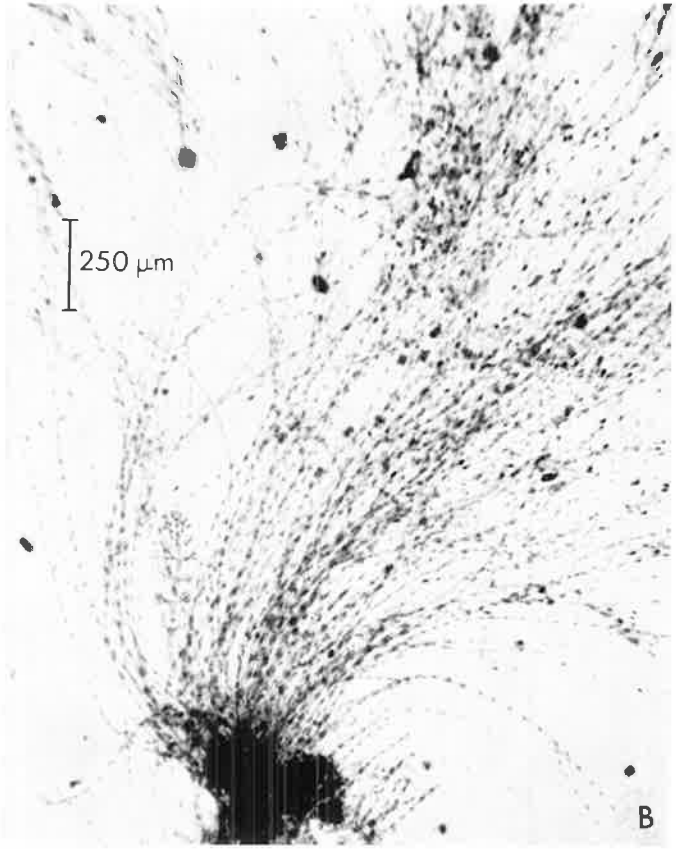


Fig. 26.—*A*. Habit of *Colaconema pacifica* on *Cladophoropsis*. ADU, A31994 (Elliston, S.A., 24.viii.1967, *Woelkerling*).



B. Habit of single plant of *Colaconema phacelorhiza*. Note the funiform prostrate system. ADU, A32925 (Head of Bight, S.A., 4.xi.1968, *Woelkerling*).

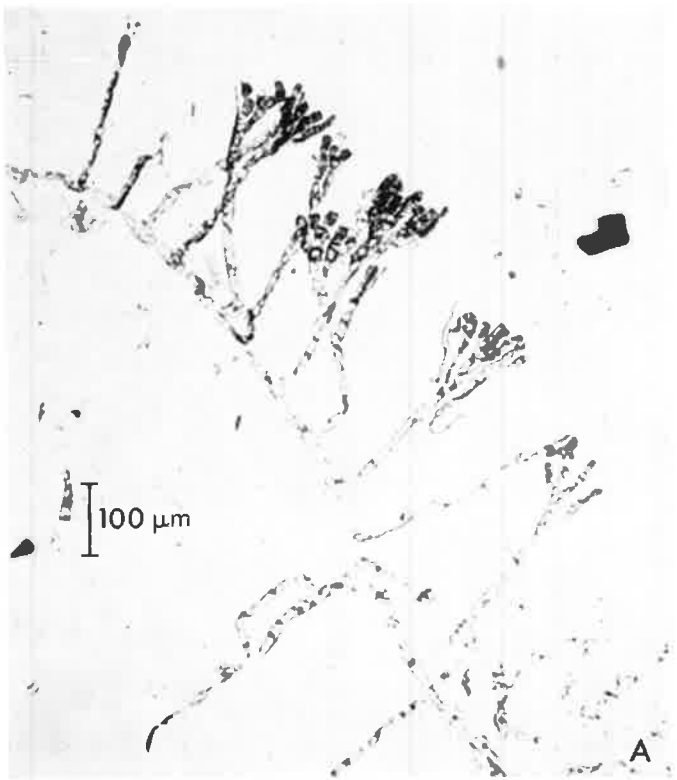
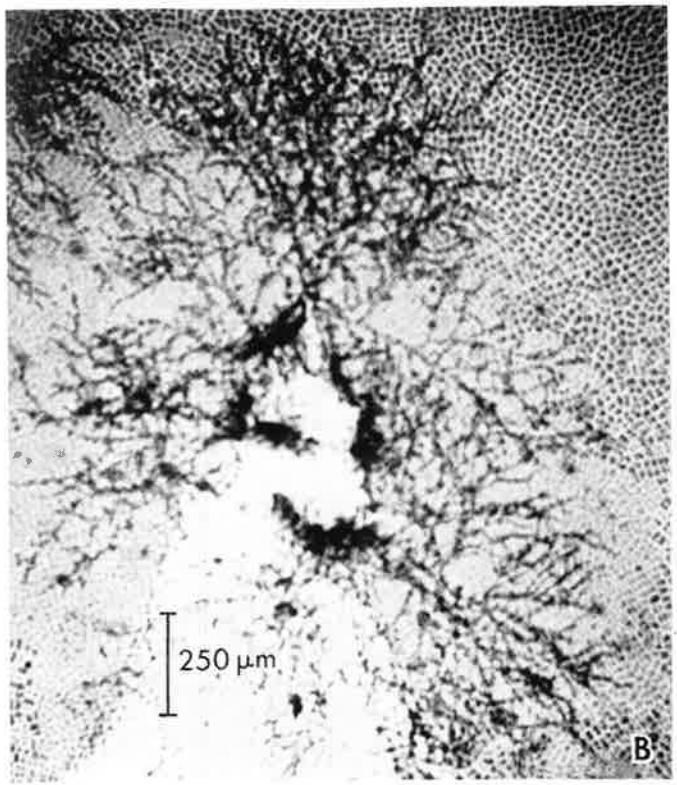


Fig. 27.—*A*. Habit of *Colaconema polyidis*. ADU, A32255 (Nora Creina, S.A., 9.ii.1968, *Woelkerling*).



B. Habit of *Colaconema porphyrae* growing in *Porphyra*. ADU, A31808 (Wanna, Port Lincoln, S.A., 21.viii.1967, *Womersley*).

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STUDIES ON THE AUDOUINELLA MICROSCOPICA (NAEG.) WOELK. COMPLEX (RHODOPHYTA)

WILLIAM J. WOELKERLING

Several recent studies (Abbott 1962, West 1968, Woelkerling 1970, 1971) have indicated that the taxonomic status of numerous species in the *Audouinella* complex (*Acrochaetium-Rhodochorton* complex) of the red algae is in need of review. Many of these taxa have been described from meagre material and (or) without regard for possible intraspecific variation, and recent work on several species (Abbott 1968, West 1969, Woelkerling 1970) has resulted in a reduction of some taxa to synonomy.

Preliminary work of the author on the audouinelloid algae of the New England coast of North America has led to a detailed consideration of the relationships of *Audouinella microscopica* (Naegeli) Woelkerling to six closely related taxa: *Acrochaetium crassipes* Boergesen (1909, p. 1, Fig. 1; 1915, p. 20, Figs. 11-13), *A. catenulatum* Howe (1914, p. 84, pl. 31, Figs. 12-18), *A. microfilum* Jao (1936, p. 240, pl. 10, Figs. 1-5), *Kylinia collopoda* (Rosenvinge) Kylin (see Rosenvinge 1898, p. 41, Figs. 10-11; 1909, p. 81), *K. compacta* (Jao) Papenfuss (see Jao 1936, p. 241, pl. 10, Figs. 6-14), and *K. moniliformis* (Rosenvinge) Kylin (see Rosenvinge 1909, p. 98, Figs. 28-29). (It should be noted here that although the taxonomic proposals of Woelkerling (1971) have been adopted in this study, older generic names have been employed in cases of probable synonomy in order to avoid making new and unnecessary nomenclatural combinations). *A. crassipes* and *A. catenulatum* were described respectively from material collected in the Virgin Islands (Boergeson 1909) and Peru (Howe 1914) while the other four taxa have been described from or are reported to occur along the New England and adjacent coasts.

These seven species have been distinguished from one another on slight differences in habit, branching, cell size,

chromoplast shape, and spore size. These apparent differences, however, may not be as taxonomically reliable as formerly thought, and Woelkerling (1971) has suggested that several or all of the taxa under discussion may be conspecific. The aims of the present investigation have been: 1) to critically examine and compare morphologically the type collections and other populations of these seven taxa, and 2) to clarify taxonomic limits within this species complex, particularly with reference to the New England flora.

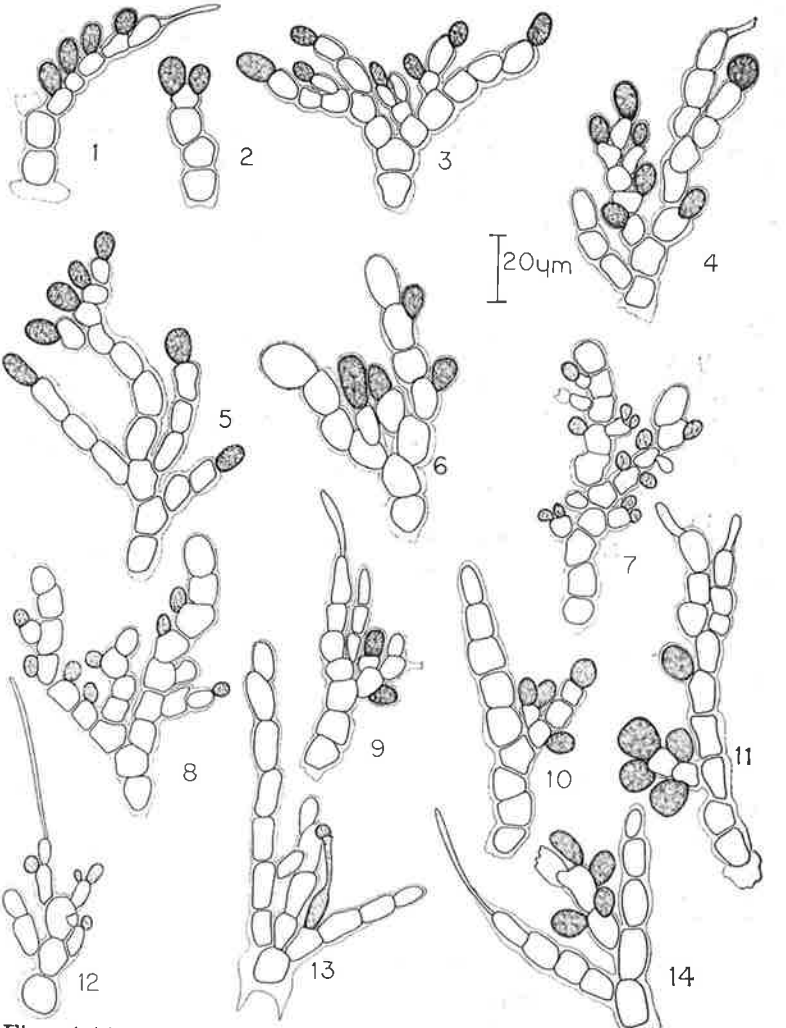
MATERIALS AND METHODS

The morphological techniques employed in these studies have been detailed elsewhere (Woelkerling 1970). Line drawings have been made with the aid of a Leitz drawing head microscope attachment; herbarium abbreviations follow Lanjouw and Stafleu (1964).

Wherever possible, results have been based on the study of populations (Table 1) rather than isolated individuals. This approach has been facilitated by the nature of the material; i.e., audouinelloid algae sometimes occur in large numbers on various substrates and by virtue of their small size, dozens or hundreds of individuals may be present in a single collection. The data presented here in most cases represents the results of study on numerous individuals within each population; an exception is the type collection of *Acrochaetium crassipes* Boergesen which is represented in C only by several drawings. Data on this taxon has been taken from the accounts of Boergesen (1909, 1915).

MORPHOLOGY

Audouinella microscopica, the earliest described member of this complex, was first characterized by Kuetzing (1849), and later Naegeli (1861) discussed and illustrated it in somewhat greater detail. Although Kuetzing (1849, p. 640) cited the Bay of Naples as the type locality, Hamel (1927; 1928) has indicated that the type collection came from Torquay, England and is represented by specimen 454 in Hauck and Richter's "Phykotheca Universalis" (as *Chan-*



Figs. 1-14. *Audouinella microscopica* (Naegeli) Woelkerling. Figs. 1-6. Monosporangial plants from type collection. Note variation in habit and in development of basal cell wall. Figs. 7-8. Spermatangial plants from type collection. Figs. 9-11. Cystocarpic plants from type collection. Note remains of trichogyne and an apparent transversely divided carpogonium (Fig. 9). Figs. 12-14. Sexual plants from Denmark removed from the host, *Chordaria*. Note variation in development of basal cell wall and carpogonium with attached spermatium (Fig. 13).

transia secundata (Lyngbye) Thuret). The type specimen in the Kuetzing collections at L contains only plants collected by Naegeli in England (identical to those distributed in Hauck and Richter) and none from the Bay of Naples. The location given by Kuetzing (1849) is, therefore, apparently in error.

Plants from the type collection of *A. microscopica* in L as well as isotypes in FH and NY have been examined during this study. The plants form a dense population on *Enteromorpha* (Chlorophyta), are 40-100 (-200) μ tall, and are attached to the host by unicellular bases with or without enlarged lower cell walls (Figs. 1-11). One or occasionally several erect filaments arise from the basal cell (Figs. 3, 4), and these may remain unbranched (Fig. 1-2) or bear several secundly or irregularly arranged laterals (Figs. 3-11). Cells are doliiform to cylindrical in shape, 6-8 (-12) μ wide and 6-12μ (1-2 diameters) long; terminal hairs up to 40μ long occur occasionally.

Both monosporangial and sexual plants are present in the material examined. The monosporangia occur singly or in pairs, are 7-10μ long and 5-7μ wide, are sessile or stalked, and are scattered over the erect filaments (Figs. 1-6). Spermatangia are ovoid, up to 4μ long, occur singly or in pairs, are sessile or stalked and are scattered over the erect filaments (Figs. 7-8). Unfertilized carpogonia have not been observed definitely in the type collection material, but the remains of at least one apparently transversely divided fertilized carpogonium has been seen (Fig. 9). Gonimoblasts are several celled and give rise to terminal or lateral carposporangia 7-10μ long and 6-8μ wide (Figs. 10-11). Only the clustered arrangement of the carposporangia distinguishes the gonimoblast from a monosporangial bearing branch. Tetrasporangial individuals have not been observed but are reported by Schiffner (1931).

Hamel (1927, 1928) previously reported sexual individuals, and Lund (1942) noted possible antheridia in Danish plants. One Danish collection on loan from Dr. Lund has been examined and found to contain numerous sexual in-

dividuals including specimens with carpogonia bearing attached spermatia (Figs. 12-14). Lund (1942) referred the Danish material to *Chantransia* (= *Kylinia*) *collopoda*, a taxon here considered conspecific with *Audouinella microscopica*.

Monosporangial plants more or less agreeing with the above description of *A. microscopica* occur along the New England and adjacent coasts, but up to the present time, they have been referred (Edelstein & McLachlan 1966; Edelstein et. al. 1967; Jao 1936; Taylor 1937, 1957) to four other species (see above) including two (*A. microfilum* and *K. compacta*) with type localities in the Cape Cod region. An analysis (Table 1) of a number of New England populations including those cited by the above authors, strongly indicates that they agree in all essential features with *A. microscopica* and are therefore justifiably referred to that species.

The analysis further indicates that while the range in basal attachment, height, branching, number of erect axes, chromoplast shape, cell size, and spore size may vary somewhat from one population to the next (probably attributable to variation in environmental factors and age), considerable overlap in these characters exists between various collections and in no cases can distinct specific limits be drawn. Consequently, it appears that all these plants are best regarded as members of a single, variable species — *A. microscopica*. Woelkerling (1971) has found similar variation in southern Australian populations of this species.

Ecological data on *A. microscopica* in New England remains scant. Specimens have been collected from July through February, but the species probably occurs throughout the year and has thus far escaped detection by virtue of its small size. Sexual plants have not been reported to date in New England, and indeed have been recorded only twice from European waters. *A. microscopica* has been found growing on a number of algae in New England waters (*Chaetomorpha, Chondria, Chondrus, Chordaria, Cladophora, Entromorpha, Polysiphonia, Porphyra*) all of which

occur in the sublittoral or in the drift. The species no doubt enjoys a much wider host distribution and is to be sought particularly on old and heavily epiphytized algae.

SYSTEMATIC IMPLICATIONS

The results of this study again (see Woelkerling 1971) raise the question as to whether a number of taxa closely related to *Audouinella microscopica* are really distinct species. The type collections of six of these taxa have been available for study, and a detailed analysis (Table 1) strongly indicates that taxonomic distinctions cannot be made among them on the bases of height, number of erect axes, cell size, or spore size. As is the case for the various New England collections, considerable overlap in the above characters is evident in the type collection populations, and specific limits cannot be clearly drawn. Moreover, a comparison of the type collection illustrations (see Boergesen 1909; Howe 1914; Jao 1936; and Rosenvinge 1909) also indicates the great similarity of these taxa.

In addition to the above characteristics, apparent differences in habit, development of the basal cell wall, degree of branching, origin of laterals, chromoplast shape, presence or absence of hairs, and position of sporangia have been used in making specific distinctions. As Woelkerling (1971) has shown in a lengthy review, the degree of branching, presence or absence of hairs, and sporangial position are not taxonomically reliable in general for making specific distinctions in the *Audouinella* complex, and the present study supports this view. Thus, for example, the type collection of *A. microscopica* contains plants which vary in the degree of branching, may or may not have unicellular hairs, and possess both terminal and lateral sporangia (Figs. 1-11).

Hamel (1927, 1928) attempted to distinguish *A. microscopica* from other members of this complex on the basis of lateral branch origin. Thus, according to Hamel, the first lateral branch in *A. microscopica* always arises from the first cell above the base. The type collection of this species,

however, also contains unbranched plants (Figs. 1-2) and plants in which the lateral arises from the basal cell (Fig 4) or from two or more cells above the base (Figs. 9-11). Woelkerling (1971) found similar variation in Australian populations of *A. microscopica*, and this variation also occurs in New England populations. Thus it appears that specific distinction based on origin of lateral branches is not taxonomically reliable.

The presence of a much enlarged basal cell wall has been used (Rosenvinge 1898, 1909; Lund 1942) to distinguish *Kylinia collopoda* from *Audouinella microscopica*. However, considerable variation in basal cell wall development occurs in the type collection of *A. microscopica* (Figs. 1-11) as well as collections made by Lund (Figs. 12-14), and Woelkerling (1971) reported a similar situation in southern Australian populations of this species. This variation suggests that this character also is not taxonomically reliable for delimiting species in this complex.

Chromoplast shape (parietal vs. stellate) has also been used (Taylor 1957) to distinguish these species. However, recent work (West 1968, p. 92, 95; Woelkerling 1971) has indicated that plastid shape shows considerable intraspecific variation and therefore is not a generally trustworthy taxonomic criterion. Some variation has already been recorded in plastids of *A. microscopica* (Woelkerling 1971), and studies (e.g., Abbott 1962, p. 100; Boergesen 1937, p. 39, 41; Drew 1928, p. 156, 176, 177, 182; Feldmann 1962, p. 220; Levring 1937, p. 94) have noted similar variation in other species. It appears, therefore, that the taxa under discussion cannot be distinguished from one another solely on apparent differences in chromoplast shape.

This study has not revealed any other criteria by which these taxa may be reliably separated into distinct species; consequently all are regarded here as conspecific with *Audouinella microscopica*.

The relationships of *A. microscopica* to four other taxa remain uncertain, primarily because the type collections have not been available for examination. The taxa include

Chantransia meditierranea Levring (1942, p. 30, Figs. 1a-g), *C. minutissima* Reinsch (1874-5, p. 33, tab. V, Fig. 2a, tab. XI, Fig. 3a; not of other authors), *C. trifila* Buffham (1892, p. 24, pl. 3, Figs. 1-4), and *Kylinia scapae* Lyle (1929, p. 245, Figs. 6-7). A comparative examination of the type collections of these taxa will almost certainly show them to be conspecific with *A. microscopica*. The androphores described and illustrated by Lyle (1929) probably represent young, unelongated unicellular hairs.

COLLECTIONS EXAMINED

Types and Isotypes: DENMARK: Kattegat Channel, 17. vii. 1890, *Rosenvinge* (C, Rosenvinge 863, Algae marinae Danicae, type of *Chantransia moniliformis* Rosenvinge). ENGLAND: Torquay, 1845, *Naegeli* (L 940285 . . . 306, type of *Audouinella microscopica* (Naegeli) Woelkerling). Torquay, 1845, *Naegeli* (FH, No. 454, "Phykotheka Universalis", isotype of *A. miscroscopica*). Torquay 1845, *Naegeli* (NY, No. 454, "Phykotheka Universalis", isotype of *A. microscopica*). GREENLAND: Holstenborg, 9. vii. 1895, *Hanson* (C, type of *Chantransia collopoda* (Rosenvinge) Rosenvinge). PERU: La Punta, region of Callao, 25. i. 1907, *Coker* (NY, type of *Acrochaetium catenulatum* Howe). UNITED STATES: Black Rock, Sconticut Neck, New Bedford, Massachusetts, 25. vii. 1934, *Jao* (MICH, Woods Hole, No. 275, type of *Acrochaetium compactum* Jao). Norton Point, Martha's Vineyard, Massachusetts, 3. viii. 1934, *Jao* (MICH, Woods Hole, No. 280 [not 274 as reported by Jao 1936, p. 240], type of *Acrochaetium microfilum* Jao). VIRGIN ISLANDS: St. Thomas (The Harbour), i. 1906, *Boergesen* (C, type of *Acrochaetium crassipes* (Boergesen) Boergesen).

Other collections: DENMARK: Vorupor, NW coast of Jutland, 30. vii. 1929, *Lund* (C). MASSACHUSETTS: Cape Codder Point (Falmouth), 19. xi. 1969, *Woelkerling* (2292, personal collection). West Falmouth Harbor, 17. x. 1970, *Woelkering* (2826, personal collection). Woods Hole (Nobska Point), 4. ii. 1970, *Woelkerling* (2320, personal

collection). NOVA SCOTIA: Cranberry Cove, 12. ix. 1965, *Edelstein* (Nat. Res. Council. Herb., Halifax, No. 1867, as *Acrochaetium microfilum* Jao). Herring Cove, 18. i. 1966, *Edelstein* (Nat. Res. Council. Herb., Halifax, No. 2217, as *Kylinia compacta* (Jao) Papenfuss). Ketch Harbour, 7. ii. 1966, *McLachlan & Edelstein* (Nat. Res. Council. Herb., Halifax, No. 2244, as *Kylinia collopoda* (Rosenvinge) Papenfuss). Peggy's Cove, 26. viii. 1965, *Edelstein* (Nat. Res. Council. Herb., Halifax, No. 2105, as *K. collopoda*).

SUMMARY

The relationship of *Audouinella microscopica* to six closely related taxa has been investigated with particular reference to the New England and adjacent coasts. The morphology of monosporangial and sexual plants in the type collection of *A. microscopica* is discussed and illustrated. Collections from the New England region previously referred to *Acrochaetium microfilum* Jao, *Kylinia collopoda* (Rosenvinge) Kylin, *K. compacta* (Jao) Papenfuss, and *K. moniliformis* (Rosenvinge) Kylin have been found to represent specimens of *Audouinella microscopica*. A comparative study of the type collections of these five taxa as well as *Acrochaetium crassipes* Boergesen and *A. catenulatum* Howe indicates that all taxa are conspecific with *Audouinella microscopica*. *Chantransia meditierranea* Levring, *C. minutissima* Reinsch non. al., *C. trifila* Buffham, and *Kylinia scapae* Lyle are regarded as probable synonyms.

ACKNOWLEDGMENTS

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Contribution No. 242 from the Systematics-Ecology Program, Marine Biological Laboratory.

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TABLE I. MORPHOLOGICAL DATA ON POPULATIONS OF *A. MICROSCOPICA COMPLEX*[1]

No.	Name	No. of Erect Axes	Height	Cell Width	Cell Length	L/W Ratio	Spore Length	Spore Width
1	"CATENULATUM"	1	40-140μ	7-11μ	7-10μ	1	9-11μ	6-7μ
2	"COLLOPODUM"	3	20-200μ	7- 9μ	10-15μ	2-4	8-15μ	7-8μ
3	"COMPACTUM"	(2-)3(-4)	20- 50μ	5- 8μ	5-10μ	1-2	6- 8μ	5-7μ
4	"CRASSIPES"	1 (-2)	40- 60μ	5- 7μ	5- 9μ	1-2	6- 8μ	5-7μ
5	"MICROFILUM"	3-4	20- 40μ	3- 6μ	4- 7μ	1	6- 8μ	4-6μ
6	"MICROSCOPICUM"	1 (-2)	40-200μ	6-12μ	6-12μ	1-2	7-10μ	5-7μ
7	"MONILIFORMIS"	2-3	40-150μ	7-11μ	7-14μ	1-2	11-15μ	6-7μ
8	N. England Populations	1-4	20-100μ	3-10μ	3-11μ	1-2	6-15μ	4-9μ
9	Australian Populations	1-3(-4)	20-140μ	3-12μ	3-10μ	.75-2	5-10μ	4-7μ

[1]Data for the first seven populations is based on an examination of the type collections of those taxa; No. 8 represents a composite of data from all New England collections examined; No. 9 represents data from Woelkerling (1971).

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SOME ALGAL INVADERS OF THE NORTHWESTERN FRINGES OF THE SARGASSO SEA

WILLIAM J. WOELKERLING

The Sargasso Sea encompasses a wide but not sharply delimited area (biologically speaking) of the North Atlantic Ocean situated roughly between 20 and 40 degrees north latitude and 35 and 75 degrees west longitude (Marmer 1928) and owes its name to the presence of two species of brown algae: *Sargassum fluitans* Boergesen and *S. natans* (L.) J. Meyen. On a recent cruise (during May 1970), the author observed numerous plants of *Ascophyllum nodosum* (L.) LeJolis and *Fucus vesiculosus* L. adrift with *Sargassum* along the northwestern fringes of the Sargasso Sea. The area visited includes the region from 69°24′ west longitude to 69°48′ west longitude and 38°53′ north latitude to 39°11′ north latitude (ca. 375 square miles) and lies roughly 125 miles south of Nantucket Island, 150 miles south of Cape Cod, Massachusetts, 170 miles east-southeast of Montauk Point, Long Island, and 75 miles north of the Gulf Stream.

The occurrence of macroscopic algae within the region appeared to be sporadic; densities as high as one plant per square meter were encountered in some places while at others virtually no weed was observed. Entangled masses of *Aescophyllum* and *Fucus* similar to those reported for *Sargassum* (Winge 1923) were not observed.

Samples taken at several stations with the aid of a long-handled dip net revealed both epiphytized and unepiphytized plants of *Ascophyllum* and *Fucus*. In all, 14 species of algae were collected (Table 1) including 2 Chlorophyta, 10 Phaeophyta, and 2 Rhodophyta. None of the epiphytic species has been recorded from the Sargasso Sea previously although isolated plants of *Ascophyllum* and *Fucus* have been reported (Collins 1917, Collins and Hervey 1917, Winge 1923). Many individuals of *Ascophyllum* and *Fucus*

examined appeared fresh and may still have been growing at the time of collection, but others bore very distended receptacles and showed signs of vegetative decay. Most of the epiphytes appeared somewhat moribund and lighter in color than their mainland counterparts and probably were not actively growing. These observations suggest that at least the epiphytized plants encountered represent detached specimens which have drifted out from the east coast of the United States rather than true pelagic forms.

Both *Ascophyllum* and *Fucus,* however, are reported to propagate vegetatively in the drifting state in European waters (Levring 1940, Oltmanns 1889, Reinke 1892, Sauvageau in Collins and Hervey 1917, p. 78) and further study appears warranted to determine whether reproduction of any sort similarly occurs in the northern Sargasso Sea. The presence of apparently healthy, unepiphytized plants of *Ascophllum* and *Fucus* in the region visited certainly suggests the possibility of vegetative propagation. In fact, Collins and Hervey (1917, p. 79) have concluded (without experimental data) that *Ascophyllum* grows actively and occasionally reproduces sexually in the Sargasso Sea. Until more direct evidence comes to hand, however, it seems best to regard *Ascophyllum, Fucus* and particularly their associated epiphytes as invaders rather than permanent components of the Sargasso Sea flora.

Sincere thanks are due Gordon Volkmann of the Woods Hole Oceanographic Institution for arranging passage on the WHOI research vessel ATLANTIS II. One of the prepared sets of herbarium specimens has been retained by the author while duplicates have been deposited in the Farlow Herbarium of Harvard University and the University of California Herbarium at Berkeley. The work described here was supported by Grant GB-13250 from the National Science Foundation to the Systematics-Ecology Program. SEP Contribution No. 231.

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TABLE 1. Algae Collected Along Northwestern Fringes of Sargasso Sea, May 1970.

SPECIES	REMARKS
Chlorophyta:	
Monostroma pulchrum Farlow	On *Fucus*
Spongomorpha arcta (Dillwyn) Kuetzing	On *Fucus*
Phaeophyta:	
Ascophyllum nodosum (L.) LeJolis	Specimens up to 1.0 m long collected
Chordaria flagelliformis (Müller) C. Ag.	Immature; on *Fucus*
Elachistea lubrica Rupr.	On *Ascophyllum* and *Fucus*

Fucus vesiculosus L.	Specimens up to .5 m long collected
Isthomoplea sphaerophora (Harvey in Hooker) Kjellman	On *Polysiphonia lanosa* in turn on *Ascophyllum*
Punctaria latifolia Grev.	On *Fucus*
Punctaria plantaginea (Roth) Grev.	On *Fucus*
Pylaiella littoralis L. Kjellman	On *Fucus*
Sargassum natans L. J. Meyen	Pelagic
Scytosiphon lomentaria (Lyngbye) C. Ag.	On *Fucus*
Rhodophyta:	
Erythrotrichia carnea (Dillwyn.) J. Ag.	On *Fucus*
Polysiphonia lanosa L. Tandy	On *Ascophyllum*

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6

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THE AUDOUINELLA COMPLEX (RHODOPHYTA) IN THE WESTERN SARGASSO SEA

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The macroscopic vegetation of the western Sargasso Sea is known mainly from four accounts (Harvey 1852, Boergesen 1914, Winge 1923, Parr 1939) which deal almost exclusively with the genus *Sargassum*. Except for two recent papers (Carpenter 1970, Woelkerling 1972b), only isolated records of other macroscopic or epibiotic algae from this region have appeared in the literature (Collins 1917, Conover and Sieburth 1964, Farlow 1914, Hentschell 1921, Prat 1935). These reports leave a number of points to be clarified including identification to species in most cases. To date only one reference (Conover and Sieburth 1964, p. 150) to an unidentified audouinelloid alga in this region has been published.

The present study was initiated after an analysis of several samples of *Sargassum* from the western Sargasso Sea revealed the presence of numerous epiphytic audouinelloid plants. This paper incorporates data from six cruises to the Sargasso Sea by vessels of the Woods Hole Oceanographic Institution and includes a morphotaxonomic account of the audouinelloid algae found to date.

MATERIALS AND METHODS

Samples of *Sargassum* were gathered with the aid of a long-handled dip net, immediately preserved in 1:10 formalin in sea water, and brought back to shore for subsequent study. Vouchers of all collections have been prepared in the form of permanent microscopic slides (Woelkerling 1970) or as liquid preserved material in 10:1 70% ethanol in glycerine. Herbarium numbers designated WJW are those in the author's personal collections; other herbarium abbreviations follow Lanjouw and Stafleu (1964). Line

drawings have been made with the aid of a Leitz drawing head microscope attachment.

In all cases morphological data is based on plants found in the Sargasso Sea and represents, wherever possible, the results of analyses of populations rather than of isolated plants.

The taxonomic proposals of Woelkerling (1971) have been adopted during this study, including the use of older generic names in cases of possible synonomy in order to avoid making new and unnecessary nomenclatural combinations. In species descriptions, the designation L/D refers to the ratio of cell length to cell diameter.

GENERAL OBSERVATIONS

Of the six species found to date, *Colaconema infestans* (Howe et Hoyt) comb. nov. occurs in nearly all collections, and *Audouinella daviesii* (Dillwyn) Woelk., *A. hallandica* (Kylin) comb. nov., and *A. thuretii* (Bornet) Woelk. appear fairly frequently as well. *Audouinella microscopica* (Naegeli) Woelk. and *Calaconema scundata* (Lyngbye) comb. nov., in contrast, have been encountered on only several occasions.

Monosporangia occur in all species and tetrasporangia also have been found in *A. thuretii*; sex organs, however, are apparently wanting. The formation of reproductive bodies is in noteworthy contrast to the situation in *Sargassum fluitans* (Boergesen) Boergesen and *S. natans* (L) J. Meyen, the two most conspicuous algae of the Sargasso Sea, which apparently never become fertile (see, however, Parr 1939, p. 49).

The audouinelloid algae probably represent a permanent component of the Sargasso Sea flora rather than being a temporary invading element (see Woelkerling 1972b) since they frequently epiphytize *Sargassum fluitans* and *S. natans*, which are apparently endemic to this region. However, all species found to date in the Sargasso Sea are also reported from Bermuda, the Caribbean, or the North

American mainland (Boergeson 1915, 1924; Collins and Hervey 1917; Taylor 1960). It is likely that these land masses act as distribution centers; in fact several collections examined during the present study have been attached to hosts (e.g. the grass *Spartina*) from inshore areas.

In general, the morphotaxonomic conclusions reached by Woelkerling (1971) are supported by this investigation. Differences between species in which the prostrate system is dominant and those in which the erect system is dominant have become more apparent to the author as a result of the current investigation, and it appears that at least two distinct habits occur among species with multicllular prostrate systems: 1) a stoloniferous habit in which the prostrate filaments are more or less widely creeping and give rise to erect filaments at irregular intervals, and 2) a more or less caespitose habit in which the prostrate filaments are generally pseudoparenchymatously united into a disc or funiform mass which, in turn, gives rise to a number of erect filaments in close proximity to one another. In stoloniferous forms, the prostrate system usually predominates while in caespitose forms, the erect system usually predominates.

KEY TO SPECIES

1. Prostrate system normally absent; plants attached to substrate by a single basal cell which may rarely divide to form several accessory cells.
   2. Cells generally 5-10μ long, more or less barrel-shaped, commonly isodiametric or broader than long ..... *Audouinella microscopica.*
   2. Cells generally 10-30μ long, more or less cylindrical, L/D usually more than 2 ..... *Audouinella hallandica.*
1. Prostrate system present, filamentous or pseudoparenchymatous.
   3. Plants more or less stoloniform; prostrate system exceeding erect system in length; erect filaments rarely over 90μ long and commonly unbranched ..... *Colaconema infestans.*
   3. Plants more or less caespitose; prostrate system not exceeding erect system in length; erect filaments commonly over 200μ long and branched.

4. Sporangia, in part at least, grouped in clusters of 3-8 in axils of lateral branches ..... *Audouinella daviesii.*
4. Sporangia usually solitary or in pairs, not clustered in axils of lateral branches.
   5. Chromoplasts distinctly stellate; prostrate system at first a parenchyma-like group of cells; sporangia commonly on short (3-5 celled) lateral branches .... *Colaconema secundata.*
   5. Chromoplasts parietal lobate; prostrate system filamentous in young stages; sporangia situated on longer lateral branches ..... *Audouinella thuretii.*

Audouinella daviesii (Naegeli) Woelkerling 1971: 28, Figs. 7, 22.

Acrochaetium daviesii (Dillwyn) Naegeli 1861: 405, Figs. 26-27. Boergesen 1924: 25, Fig. 8. 1827: 25, Fig. 15. Taylor 1960: 307.

Callithamnion daviesii (Dillwyn) Lyngbye 1819: 129 (only as to binomial).

Ceramium daviesii (Dillwyn) C. Agardh 1817: XXVII.

Chantransia daviesii (Dillwyn) Thuret in Le Jolis 1863: 106. Kylin 1907: 117, Fig. 27. Rosenvinge 1909: 104, Fig. 34.

Conferva daviesii Dillwyn 1809: 73, Suppl. pl. F.

Rhodochorton daviesii (Dillwyn) Drew 1928: 172. Nakamura 1944: 106, Fig. 5.

Trentepohlia daviesii (Dillwyn) Areschoug 1847: 338.

Note: Further synonomy is given by Woelkerling (1971. p. 28).

Plants epiphytic or epizoic, caespitose, up to 5 mm. tall; original spore non-persistent. Prostrate system consisting of branched filaments more or less forming a pseudoparenchymatous disc. Erect filaments freely and irregularly branched, commonly attenuate and ending in multicellular hair-like prolongations. Cells of main axes and laterals cylindrical, 8-15μ wide and (15-) 20-60μ long, L/D (1.75-) 2-4 (-5); cells sometimes tapering to 2-8μ wide and 20-80μ long (L/D up to 35) near the apices; each cell containing a parietal lobate chromoplast with one pyrenoid.

Monosporangia ovoid, 8-13μ wide and 13-17(-22)μ long, in clusters of 3-8 on branched stalks or singly or in pairs on 1-2 celled stalks, situated on the lowermost cells of laterals or sometimes more scattered.

Other reproductive structures not observed in material examined.

Type Locality. — Bantry Bay, Ireland (Hutchens); locality for H. Davies collection not given by Dillwyn (1809).

Holotype. — NMW.

Distribution. — Nearly cosmopolitan.

Hosts. — Hydroids, *Sargassum,* and *Spartina* (Angiospermae) fragment in Sargasso Sea; a wide variety of algae, marine angiosperms, and invertebrates elsewhere.

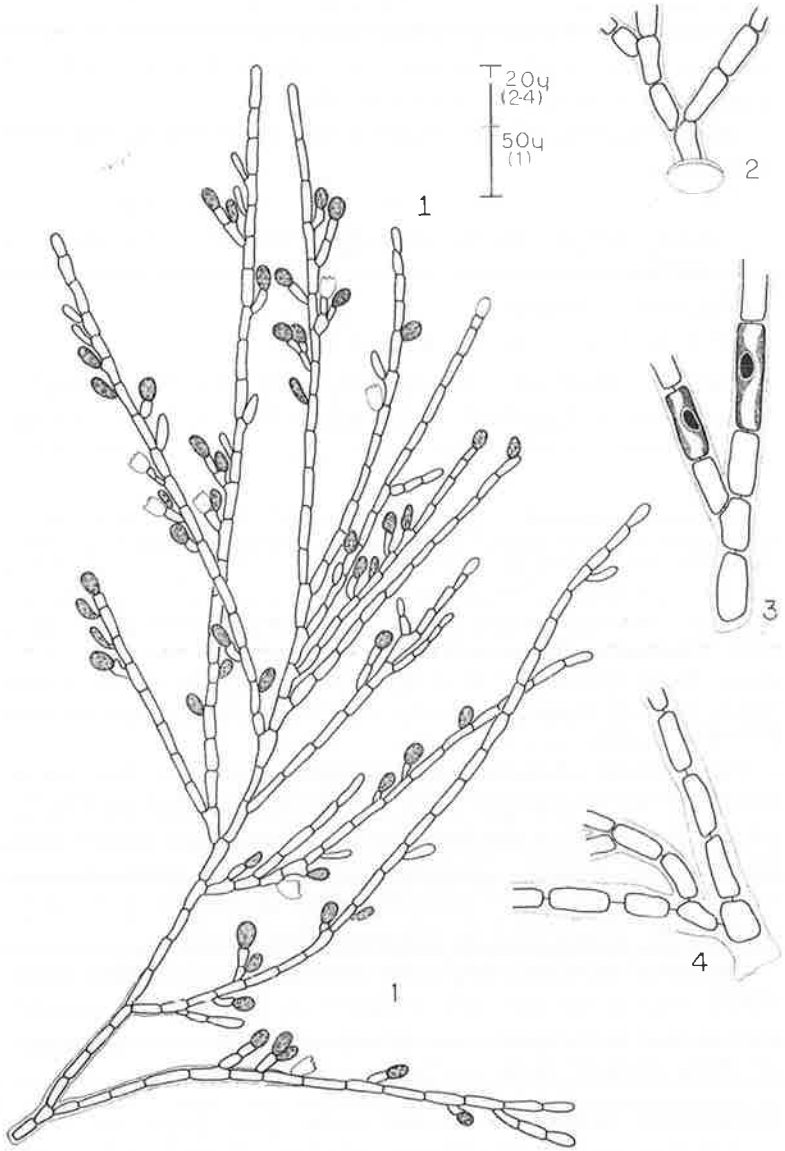
Specimens examined. — **Sargasso Sea:** 26° 57′N-72° 58′W, 26.iv. 1970, *Moore* (WJW 2648); 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2429); 31°N-69° 29′W, 3.iii.1970, *Volkman* (WJW 2380), (WJW 2364); 32° 09′N-64° 58′W, 16.V.1970, *Woelkerling* (WJW 2667); 34°N-70°W, 7.iii.1970, *Volkmann* (WJW 2396), (WJW 2409); 37°N-70°W, 12.v. 1970, *Woelkerling* (WJW 2621); 38° 22′N-70°58′W, 12.x.1970, *Volkmann* (WJW 2888); 39° 07′N-70° 35′W, 16.viii.1970, *Moore* (WJW 2930). **Ireland:** Bantry Bay, prior to 1809, *Hutchins* (NMW, Dillwyn Collection, type).

Populations of *A. daviesii* examined during this study agree in all essentials with the type material and with plants described in the accounts of Rosenvinge (1909) and Woelkerling (1971). Multicellular hair-like prolongations with poorly developed plastids often devoid of pyrenoids occur very frequently in Sargasso Sea plants.

Clustered monosporangia are common in most collections (2621 represents the only exception), but tetrasporangial and sexual individuals (see Woelkerling 1971 for accounts of these stages) have not been encountered.

Audouinella hallandica (Kylin) comb. nov. Figs. 1-4.

Acrochaetium hallandicum (Kylin) Hamel 1927: 20, Figs. 19-21; 1928: 114, Figs. 19-21.



Figs. 1-4. *Audouinella hallandica* (Kylin) comb. nov. Fig. 1. Monosporangial plant. Figs. 2-4. Variation in shape of basal cell. Note chromoplasts (Fig. 3).

Chantransia hallandica Kylin 1906: 123, Fig. 8. Rosenvinge 1909: 93, Figs. 21-23.
Chromastrum hallandicum (Kylin) Papenfuss 1945: 321.
Kylinia hallandica (Kylin) Kylin 1944: 13, 15, Fig. 7.
Rhodochorton hallandicum (Kylin) Rosenvinge 1935: 7.
Acrochaetium dufourii (Collins) Boergesen 1915: 19. Hoyt 1920: 470, Fig. 26. Collins *In* Collins, Holden, and Setchell 1909: 1594 (Nom. Nud.). Collins and Hervey 1917: 96. Taylor 1960: 305.
Chantransia dufourii Collins 1911: 187.
Kylinia dufourii (Collins) Kylin 1944: 13.
Acrochaetium sargassi Boergeson 1915: 17, Figs. 7-10. Taylor 1925: 129. 1928: 134, pl. 22, Figs. 1-5. 1960: 306.
Chantransia sargassi (Boergeson) DeToni 1924: 45.
Kylinia sargassi (Boergesen) Kylin 1944: 13.

Plants epiphytic, up to 1 mm. tall, original spore persisting as a unicellular base the same size or somewhat larger than other cells and giving rise to 1-2 main axes. Erect filaments moderately and irregularly branched, occasionally tapering towards the tips; unicellular hairs not observed. Cells cylindrical, 4-7μ wide and 10-30μ long (L/D 2-5), each containing a parietal lobate chromoplast and one pyrenoid.

Monosporangia ovoid, 6-8μ wide and 8-11 (-15)μ long, singly or in pairs, sessile or stalked, scattered over the erect filaments adaxially and occasionally abaxially as well.

Other reproductive structures not observed.

Type Locality. — Hogardsgrund, Halland, Sweden.

Holotype. — Apparently not designated by Kylin. Material on three prepared slides in LD dated 13.vii.1904 has been chosen as lectotype.

Distribution. — Sargasso Sea; Europe, Atlantic Coast of North America.

Hosts. — *Sargassum natans, Sargassum* sp., and hydroids in Sargasso Sea; elsewhere on a variety of algae.

Specimens examined. — **Sargasso Sea:** 31°N-69° 29'W, 3.iii.1970, *Volkmann* (WJW 2385); 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2210), 7.iii.1970, *Volkmann* (WJW 2401); 36°N-70° 36'W, 9.xii.1970, *Moore* (WJW 2944). **Sweden:** Hogardsgrund, Halland Coast, 13.vi.1904, *Kylin* (LD, lectotype). **United States:** Beaufort, North Carolina, 13.vii.1908, *Hoyt* (FH, Co-type of *Acrochaetium dufourii* Collins). **Virgin Islands:** St. Thomas harbour, 26.xii.1905, *Boergesen* (C, type of *Acrochaetium sargassi* Boergesen).

Specimens of *Audouinella hallandica* from the Sargasso Sea compare favorably with lectotype material from the Halland Coast of Sweden. Neither the lectotype nor any Sargasso Sea collections contain sexual plants; these, however, have been described from Denmark (Rosenvinge 1909, p. 93, Figs. 21-22), France (Hamel 1927, p. 20, Figs. 19-20), and the Virgin Islands (Boergesen 1915, p. 17, Figs. 7-10 — as *Acrochaetium sargassi*).

The taxa originally described as *Acrochaetium sargassi* Boergesen and *Chantransia dufourii* Collins are here considered conspecific with *Audouinella hallandica* after critical comparisons of type collection material. Plants in all three type collections show virtually the same range of cell and spore dimensions and also show good morphological agreement in other respects. Taylor (1960, p. 302) has attempted to distinguish *Acrochaetium sargassi* from *A. dufourii* on the basis of slight differences in cell width and basal cell size, but neither of these characters has proven reliable as a result of this study. Boergesen (1915, p. 19) also expressed some doubt about the taxonomic differences between the two taxa.

The morphotaxonomic relationships of *Audouinella hallandica* to other audouinelloid algae appear to be very complex and involve at least 15 other taxa (including *Chantransia parvula,* regarded by Rosenvinge (1909) and Hamel (1927) as conspecific with *Audouinella hallandica*). Pending critical studies of the types and other collections of all taxa involved, the relationships of *A. hallandica* to other species in the complex necessarily remain uncertain.

Audouinella microscopica (Naegeli) Woelkerling 1971: 33, Figs. 10, 23A; 1972a: 85, Figs. 1-14.

Acrochaetium microscopicum (Naegeli in Kuetzing) Naegeli 1861: 407, Figs. 24-25.

Callithamnion microscopicum Naegeli in Kuetzing 1849: 640.

Chantransia microscopica (Naegeli in Kuetzing) Batters in Schiffner 1916: 136, Figs. 13-18.

Chromastrum microscopicum (Naegeli in Kuetzing) Papenfuss 1945: 322.

Kylinia microscopica (Naegeli in Kuetzing) Kylin 1944: 13. Papenfuss 1947: 437.

Rhodochorton microscopicum (Naegeli in Kuetzing) Drew 1928: 151, 163.

Acrochaetium catenulatum Howe 1914: 84, pl. 31, Figs. 12-18.

Chantransia catenulata (Howe) DeToni 1924: 44.

Kylinia catenulata (Howe) Kylin 1944: 13.

Rhodochorton catenulatum (Howe) Nakamura 1941: 273, 280, Fig. 1.

Acrochaetium collopodum (Rosenvinge) Hamel 1927: 81.

Chantransia collopoda (Rosenvinge) Rosenvinge 1909: 81.

Chromastrum collopodum (Rosenvinge) Papenfuss 1945: 320.

Kylinia collopoda (Rosenvinge) Kylin 1944: 13, 15, Fig. 6.

Acrochaetium compactum Jao 1936: 241, pl. 10, Figs. 6-14.

Chromastrum compactum (Jao) Papenfuss 1945: 321.

Kylinia compacta Papenfuss 1947: 436.

Acrochaetium crassipes (Boergesen) Boergesen 1915: 20, Figs. 11-13. Boergesen 1927: 12, Fig. 5. Collins and Hervey 1917: 96. Howe 1918: 511. Taylor 1941: 75.

Chantransia crassipes Boergesen 1909: 1, Fig. 1. Taylor 1928: 134, pl. 28, Fig. 16.

Chromastrum crassipes (Boergesen) Papenfuss 1945: 321.

Kylinia crassipes (Boergesen) Kylin 1944: 13. Taylor 1960: 300.

Acrochaetium microfilum Jao 1936: 240, pl. 10, Figs. 1-5. (Non *A. microfilum* Levring 1945: 12, Fig. 4. = *A. Levringii* Papenfuss 1947: 436).

Acrochaetium moniliforme (Rosenvinge) Boergesen 1915: 22.

Chantransia moniliformis Rosenvinge 1909: 99, Figs. 28-29.

Chromastrum moniliforme (Rosenvinge) Papenfuss 1945: 322.

Kylinia moniliformis (Rosenvinge) Kylin 1944: 13.

Rhodochorton moniliforme (Rosenvinge) Drew 1928: 151, 164.

Plants epiphytic or epizoic, up to 75μ tall; original spore persisting as a unicellular base slightly smaller to slightly larger than other cells. Filaments of erect system 1-3, commonly acurate, simple or with a few secundly to irregularly arranged laterals. Cells barrel shaped to cylindrical, 5-9μ wide and 5-10μ long (L/D .75-2); each cell containing a parietal irregularly lobate chromoplast with one pyrenoid. Unicellular hairs up to 75μ long occur.

Monosporangia ovoid, 4-7μ wide and 5-8μ long, terminal or lateral, single or rarely in pairs, sessile or stalked, adaxially seriate or occasionally more scattered.

Other reproductive structures not observed.

Type Locality. — Torquay, England.

Holotype. — L, No. 940285 . . . 306.

Distribution. — Nearly cosmopolitan.

Hosts. — *Dictyota, Sphacelaria,* and hydroids in Sargasso Sea; a wide variety of algae elsewhere.

Specimens examined. — **Sargasso Sea:** 32° 09'N-60° 58'W, 16.v. 1970, *Woelkerling* (WJW 3232); 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2215), 7.iii.1970, *Volkmann* (WJW 2408). **England:** Torquay, 1845, *Naegeli* (L 940285 . . . 306, type).

Two of the three Sargasso Sea collections (WJW 2215, WJW 2408) contain only several plants each of *A. microscopica*. The other collection (3232) contains numerous plants on a fragment of *Dictyota* collected about 14 km. off Bermuda; it seems likely that the host had drifted out from shore. The apparent rarity of *A. microscopica* in the western Sargasso Sea suggests that it may not be a permanent component of the flora.

Woelkerling (1972a) has recently presented a detailed account of this species including descriptions of sexual stages and has reduced to synonomy of a number of allied taxa cited as references in this account.

Audouinella thuretii (Bornet) Woelkerling 1971: 36, Figs. 12, 24.

Acrochaetium thuretii (Bornet) Collins et Hervey 1917: 98. Taylor 1960: 310.

Chantransia thuretii Bornet. Collins 1900: 49 (Nom. Nud.)

Chantransia thuretii (Bornet) Kylin 1907: 119, Fig. 28.

Rhodochorton thuretii Drew 1928: 171.

Chantransia corymbifera Thuret in LeJolis 1863: 107 (in part; see Papenfuss 1945: 313 under *Acrochaetium bornetii.*

Chantrancia efflorescens var *thuretii* Bornet 1904: XVI, pl. 1. Collins 1906: 196.

Plants epiphytic, caespitose, up to 5 mm. tall; original spore nonpersistent. Prostrate system consisting of branched filaments more or less forming a pseudoparenchymatous disc. Erect filaments freely and irregularly branched and sometimes tapering towards the tips; unicellular hairs not present. Cells of main axes and laterals 8-12(-16)μ wide and 20-80μ long (L/D (2-)3-5(-8)), sometimes tapering to 4-7μ wide near the apices; each cell containing a parietal lobate chromoplast and one pyrenoid.

Monosporangia ovoid, 8-12μ wide and 16-24μ long, solitary or occasionally in pairs, sessile or sometimes stalked,

generally situated adaxially on the lower portions of lateral branches but occasionally more scattered and/or terminal. Tetrasporangia ovoid to globose, 16-24μ wide and 20-30μ long, solitary or occasionally in pairs, sessile or occasionally stalked, scattered over laterals and main axes.

Other reproductive structures not observed.

Type Locality. — Cherbourg, France.

Holotype. — PC.

Distribution. — Nearly cosmopolitan.

Hosts. — *Sargassum natans* and *Sargassum* sp. in Sargasso Sea; elsewhere on a variety of algae and marine angiosperms.

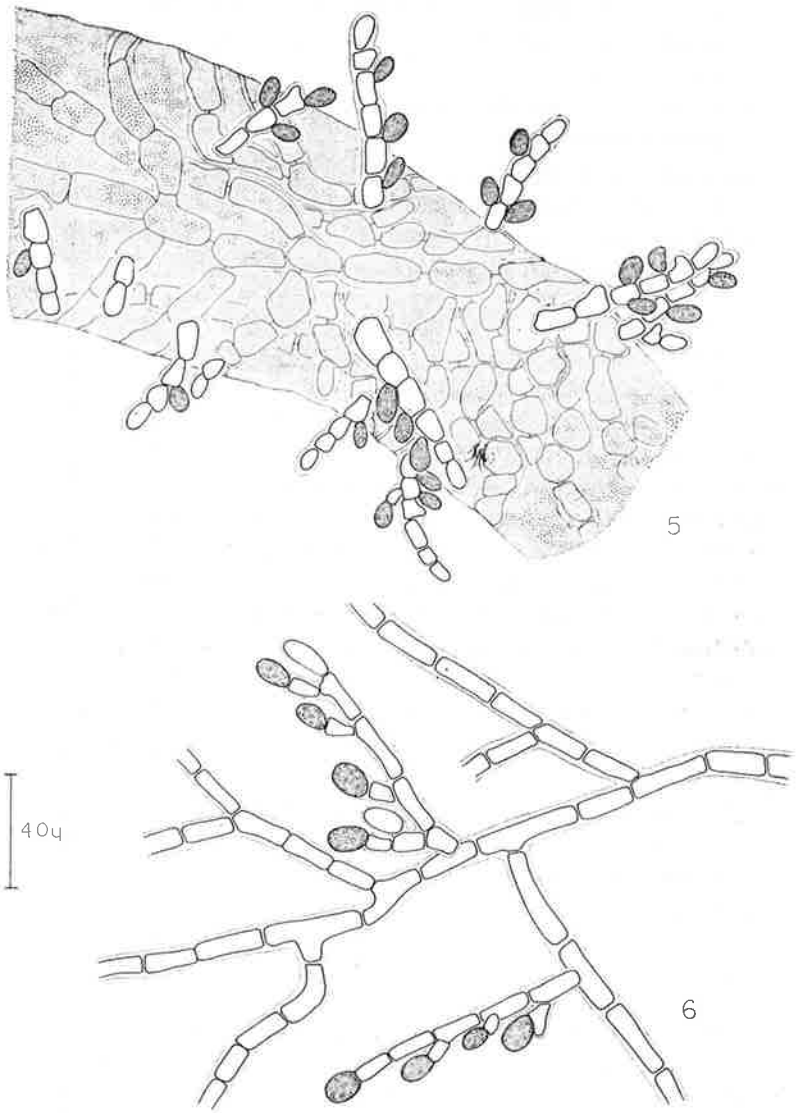
Specimens examined. — **Sargasso Sea:** 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2424); 31°N-69° 29'W, 3.iii.1970, *Volkmann* (WJW 2379); 33° 58.5'N-69° 56.5'W, 15.v.1970, *Woelkerling* (WJW 2592); 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2203); 36°N-70° 36'W, 9.xii.1970, *Moore* (WJW 2934), (WJW 2943); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 3221); 38° 22'N-70° 58'W, 12.x.1970, *Volkmann* (WJW 2889).

Specimens of *Audouinella thuretii* agree in general with descriptions of Rosenvinge (1909) and Woelkerling (1971). Sexual plants are described in detail by Kylin (1907).

The relationship of *A. thuretii* to other audouinelloid algae requires further investigation. Two similar species — *Acrochaetium avrainvillae* Boergesen (see Boergesen 1915, p. 48, Figs. 47-49) and *A. Nemalionis* (DeNotaris) Bornet (see Collins and Hervey 1917, p. 98; Taylor 1960, p. 314) — occur in the Sargasso Sea region (Virgin Is. and Bermuda, respectively), but until the types and other collections of all three taxa can be compared, they are best maintained as distinct species. The major difference between *A. Nemalionis* and the Sargasso Sea specimens of *Audouinella thuretii* is apparently the lack of a funiform prostrate system in the latter, and this difference is of doubious taxonomic value (Woelkerling 1971).

Colaconema infestans (Howe et Hoyt) comb. nov. Figs. 5-6.

Acrochaetium infestans Howe et Hoyt 1916: 116, pl. 14. Howe 1918: 511. Hoyt 1920: 473, pl. CXVIII.



Figs. 5-6. *Colaconema infestans* (Howe et Hoyt) comb. nov. Habit of monosporangial plant (Shaded portion represents host).

Chantransia infestans (Howe et Hoyt) DeToni 1924: 64.
Chromastrum infestans (Howe et Hoyt) Papenfuss 1945: 324.
Kylinia infestans (Howe et Hoyt) Papenfuss 1947: 438. Taylor 1960: 301.
Rhodochorton infestans (Howe et Hoyt) Drew 1928: 151, 187. Nakamura 1944: 118, Fig. 13.
Rhodochorton membranaceum auct. non. (Magnus) Hauck: Collins and Hervey 1917: 148.

Plants partly endozoic, more or less stoloniform, up 90μ tall, exclusive of hairs. Prostrate system consisting of branched, stoloniferous filaments creeping just beneath the surface of the host, sometimes becoming very conjested and appearing pseudoparenchymatous; cells cylindrical to irregular in shape, 4-6(-10)μ wide and 5-40μ long (L/D 1-8). Erect filaments arising more or less perpendicularly from the prostrate system, simple or sparingly and irregularly branched, occasionally bearing terminal hairs up to 125μ long. Cells cylindrical, 3-7μ wide and 6-30μ long (L/D 2-5), each bearing a single parietal lobate chromoplast with one pyrenoid.

Monosporangia ovoid, 4-6(-8)μ wide and 6-10(-15)μ long, sessile or stalked, borne singly or in pairs, scattered over the erect filaments.

Other reproductive structures not observed.

Type locality. — A reef about 37km. off of Beaufort, North Carolina.

Holotype. — NY.

Distribution. — Sargasso Sea; Bermuda, Japan, North Carolina.

Hosts. — Hydroids.

Specimens examined. — **Sargasso Sea:** 26° 50′N-71° 48′W, 5.iii.1970, *Volkmann* (WJW 2420); 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 3432); 31°N-69° 29′W, 3.iii.1970, *Volkmann* (WJW 2389); 34°N-70°W, 7.iii.1970, *Volkmann* (WJW 2403), 30.vi.1970, *Volkmann* (WJW 2725), 6.vii.1970, *Volkmann* (WJW 2749); 35° 54′-70° 30′W, 13.viii.1970, *Moore* (WJW 2902); 36°N-70° 36′W, 9.xii.1970, *Moore* (WJW 2949), (WJW 2938); 36° 28′N-70° 29′W, 15.viii.1970,

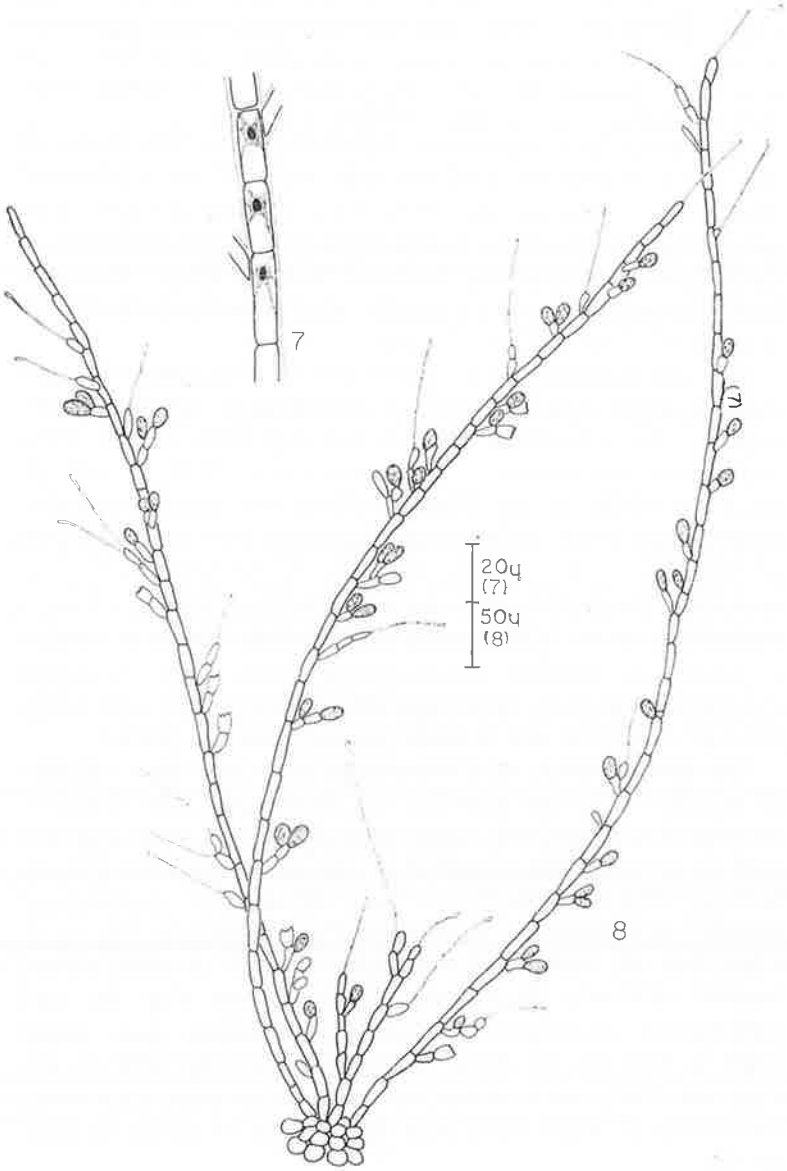
Moore (WJW 2907); 37° 30'N-70°W, 8.vii.1970, *Volkmann* (WJW 2706); 38° 22'N-70° 58'W, 12.x.1970, *Volkmann* (WJW 2887); 39° 07'N-70° 35'W, 16.viii.1970, *Moore* (WJW 2917), (WJW 2929); 39° 30'N-71°W, 6.x.1970, *Volkmann* (WJW 2810). **United States:** Beaufort, N. Carolina, 11.viii.1914, *Radcliffe* (NY, type).

Specimens of *Colaconema infestans* from the Sargasso Sea agree in general with the type material on a prepared slide in NY. This species occurs very commonly in the Sargasso Sea and has been found in nearly every collection of *Sargassum* bearing the hydroid hosts. Erect filaments rarely exceed 10 cells in length, and laterals normally do not exceed four cells in length.

The relationships of *C. infestans* to a number of other audouinelloid algae of similar morphology requires clarification. *Acrochaetium effusum* Levring 1953, p. 479, Figs. 13F-G and *Rhodochorton penetrale* Drew 1928, p. 187, pl. 44, Figs. 57-58, pl. 45, Figs. 59-60 do not appear to differ significantly from *Colaconema infestans* and a comparison of the types will probably show the three taxa to be conspecific. *Chantransia endozoica* Darbishire 1899, p. 13, pl. 1 appears to have larger cells, and further study is needed to determine whether intermediate forms occur. Pending the results of such investigation, *C. endozoica* and *Colaconema infestans* are maintained as distinct species.

The relationships of *Colaconema infestans* to a number of adouinelloid taxa growing on plant hosts also requires clarification, especially since host specificity does not appear to be a reliable criterion of specific distinction (Woelkerling 1971). Endophytic taxa of similar morphology include *Acrochaetium antillarum* Taylor 1942, p. 78, pl. 2, Figs. 3-4, *A. endophyticum* Batters 1896, p. 386, *Chantransia emergens* Rosenvinge 1909, p. 128, Fig. 55, and *Colaconema porphyrae* (Drew) Woelkerling (see Drew 1928, p. 188, pl. 46, Figs. 70-75; Woelkerling 1971, p. 50, Figs. 20, 27B), and critical studies on the types and other collections of these taxa may show some or all to be conspecific.

Further investigations are also needed to determine



Figs. 7-8. *Colaconema secundata* (Lyngbye) comb. nov. Fig. 7. Chromoplasts in vegetative cells. Fig. 8. Habit of fairly small monosporangial plant.

whether or not *Colaconema bonnemaisoniae* Batters and related taxa (see Woelkerling 1971, p. 42) possibly represent prostrate system stages of *C. infestans*.

Specimens of Collins and Hervey (1917, p. 148) from Bermuda referred to *Rhodochorton membranaceum* (Magnus) Hauck and distributed in the PBA, Vol. XLIV, No. 2194 (Collins, Holden, and Setchell 1917) have been examined and found to be plants of *Colaconema infestans*. Howe (1918, p. 511) reached the same conclusion.

Colaconema secundata (Lyngbye) comb. nov. Figs. 7-8.

Acrochaetium secundatum (Lyngbye) Naegeli 1861: 405.

Callithamnion secundatum (Lyngbye) C. Ag. 1828: 187.

Ceramium secundatum (Lyngbye) C. Agardh 1824: 132.

Chantransia secundata (Lyngbye) Thuret *In* Le Jolis 1863: 106.

Chromastrum secundatum (Lyngbye) Papenfuss 1945: 323.

Kylinia secundata (Lyngbye) Papenfuss 1947: 437.

Callithamnion daviesii var. *secundatum* Lyngbye 1819: 129, pl. 41, Fig. B4-6.

Acrochaetium luxurians (J. Agardh) Naegeli 1861: 405.

Callithamnion luxurians J. Agardh 1851: 14.

Chantransia luxurians (J. Agardh) Kylin 1907: 117, Fig. 26.

Acrochaetium virgatulum (Harvey) Bornet 1904: XXII. Boergesen 1927: 14, Figs. 7-8. Chapman 1963: 56. Hoyt 1920: 473, Figs. 29-30. Taylor 1941: 75.

Callithamnion virgatulam Harvey *In* Hooker 1833: 349.

Chantransia virgatula (Harvey) Thuret *In* LeJolis 1863: 106. Rosenvinge 1909: 109, Figs. 37-41.

Chromastrum virgatulum (Harvey) Papenfuss 1945: 323.

Kylinia virgatula (Harvey) Papenfuss 1947: 437.

Rhodochorton virgatulum (Harvey) Rosenvinge 1935: 7.

Trentepohlia virgatula (Harvey) Farlow 1881: 109.

Plants epiphytic or epizoic, more or less virgate, up to 2mm. tall; original spore non-persistent. Prostrate system at first a parenchyma-like group of cells, later forming a small, more or less circular pseudoparenchymatous disc of one to several cell layers. Erect filaments nearly simple to moderately branched, commonly bearing short laterals giving plant a virgate appearance; terminal and pseudolateral hairs common. Cells of erect filaments cylindrical (6-) 8-12μ wide and (10-) 20-70μ long (L/D 1-7), each with a distinctly stellate chromoplast and one pyrenoid.

Monosporangia ovoid, (6-) 9-13μ wide and (10-) 16-24μ long, sessile or stalked, solitary, in pairs or occasionally in threes, commonly crowded laterally or terminally on the shorter laterals or occasionally more scattered.

Other reproductive structures not observed.

Type locality. — Kvivig, Faeroes Islands (on *"Conferva rupestris"*).

Holotype. — C.

Distribution. — Sargasso Sea; Atlantic Shores of North America, Canary Islands, Europe.

Hosts. — *Sargassum fluitans, S. natans,* and hydroids in Sargasso Sea; a wide variety of algae elsewhere.

Specimens examined. — **Sargasso Sea:** 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2425); 31°N-69° 29'W, 3.iii.1970, *Volkmann* (WJW 2367); 39° 30'N-71°W, 6.x.1970, *Volkmann* (WJW 2865). **England:** Torquay, prior to 1833, *Griffiths* (TCD, type of *Acrochaetium virgatulum* (Harvey) Bornet). **Faeroes Islands:** Kvivig, 19.vi.1817, ? (C, Herb. Lyngbye, type). **Sweden:** Kattegat Channel, no date, ? (LD 35117, type of *Callithamnion luxurians* J. Agardh).

The few specimens of *Colaconema secundata* from the Sargasso Sea agree well with type material from the Faeroes Islands. Although an extremely variable species, *C. secundata* can be distinguished from other audouinelloid algae by the following combination of characters (in addition to cell and spore dimensions): 1) Spore germinating to form a distinctive parenchymatous group of cells which may later proliferate (see Kylin 1907, p. 115, Fig. 24;

Rosenvinge 1909, Figs. 37-41); 2) Cells with a distinctly stellate chromoplast with a centrally located pyrenoid, and in many cases 3) sporangia densely crowded on short lateral branches and 4) numerous terminal hairs, often terminating 1-2 celled branchlets. Tetrasporangia have not been observed but are reported by Hehre and Mathieson (1970), Kylin (1907, 1944), and Rosenvinge (1909) among others. Sexual stages remain unknown.

Unicellular hairs occur very commonly in *C. secundata* and often terminate 1-2 celled lateral branchlets, thus appearing stalked (Fig. 8).

In agreement with Hamel (1927, 1928) and Rosenvinge (1909), the taxa originally described as *Callithamnion luxurians* J. Agardh (1851, p. 14) and *C. virgatula* Harvey *In* Hooker (1833, p. 349) are considered conspecific with *Colaconema secundata*. The type collections of all three have been examined during this study and found to agree in all essential features. Since the specific epithet "secundata", first used by C. Agardh (1824, p. 132), predates the specific epithet "virgatula" (Harvey 1833) used by Hamel (1927, 1928) and Rosenvinge (1909) by nine years, it has nomenclatural priority.

Some authors (e.g. Kylin 1944, Taylor 1957) have maintained *C. secundata* and *Callithamnion* (= *Acrochaetium*, *Kylinia*) *virgatula* as distinct species on the bases of differences in the number of layers in the prostrate system or on slight differences in height, branching, or cell size, but as noted by Rosenvinge (1909), and as observed in New England collections (Woelkerling, unpublished data), considerable variation occurs in all cases, and species limits between the two taxa cannot be drawn reliably.

The taxonomy and relationships of *Colaconema secundata* to other taxa are quite involved and will be dealt with at a later date.

SUMMARY

The *Audouinella* complex is represented in the Western

Sargasso Sea by four species of *Audouinella* and two species of *Colaconema,* all newly recorded for this region. These species apparently constitute a permanent component of the Sargasso Sea flora, reproducing asexually by monospores and/or tetraspores. Species with a stoloniferous habit tend to produce more extensive prostrate systems than erect systems, whereas caespitose species usually possess better developed erect systems than prostrate systems. Critical comparisons of type and other collections indicate that *Acrochaetium dufourii* (Collins) Boergesen and *A. sargassi* Boergesen are conspecific with *Audouinella hallandica* (Kylin) comb. nov., and *Acrochaetium luxurians* (J. Agardh) Naegeli and *A. virgatula* (Harvey) Bornet are conspecific with *Colaconema secundata* (Lyngbye) comb. nov. Detailed descriptions of Sargasso Sea collections together with a taxononmic key are provided.

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THE MORPHOLOGY AND SYSTEMATICS OF THE AUDOUINELLA COMPLEX (ACROCHAETIACEAE, RHODOPHYTA) IN NORTHEASTERN UNITED STATES

BY

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WM. J. WOELKERLING

Our knowledge of the marine species of the *Audouinella* complex along the New England and adjacent coasts of North America (including New York and New Jersey) comes mainly from the papers of Collins (1906, 1908, 1911), Davis (1913), Farlow (1881), Harvey (1853), Hehre and Mathieson (1970), Jao (1936), and Woelkerling (1972). Although many of the earlier records (which leave a number of points to be clarified) are incorporated in the descriptive catalogues of Taylor (1937, 1957), a comprehensive morphotaxonomic study of New England marine audouinelloid algae has not appeared to date, and the only monographic attempt involving the New England species has been that of Collins (1906) which included all of North America and is now out of date.

The present account reviews the systematics, morphology, ecology, and distribution of New England marine audouinelloid algae and provides a taxonomic treatment of all representatives based on extensive field and herbarium studies including the examination of many of the type collections. Canadian representatives of the complex (see South and Cardinal, 1970) have not been considered in detail because of inadequate material and the questionable nature of a number of records. A brief discussion on these taxa appears at the end of this report.

The techniques employed in these studies have been detailed elsewhere (Woelkerling 1970, 1973). Abbreviations for herbaria follow Lanjouw and Stafleu (1964); collections designated by WJW refer to specimens in the author's personal herbarium, currently housed at WIS.

A comprehensive review of the taxonomic history of audouinelloid algae has appeared recently (Woelkerling

1971), and the systematic conclusions reached in that paper are supported and adopted here. D'Lacoste and Ganesan (1972), however, maintain a classification of genera based on chromoplast morphology and criticize the placement of *Rhodochorton* in synonomy with *Audouinella* on grounds that Woelkerling (op. cit.) did not examine chromoplasts in living material of *Rhodochorton purpureum*, the type species of *Rhodochorton*. Cells of living *R. purpureum* (referred here to *Audouinella*) have been examined during the present New England study and found to show the same variation in chromoplast morphology described by Drew (1928, pp. 156, 177, fig. 33).

D'LaCoste and Ganesan (1972, p. 235) also point out (citing the findings of West, 1968, p. 98) that chromoplast shape can change as a result of fixation of material and that studies on the latter (including, presumably, those of Drew, 1928) can yield misleadng results. They apparently overlooked the other comments of West (op. cit.) in the same paragraph where he indicates the ". . . . inadequacy of plastid form as a taxonomic criterion in certain instances . . .". Thus the studies of West (1968), Woelkerling (1971), and others (see Woelkerling op. cit., p. 14) clearly show that chromoplast morphology is so variable in certain taxa that any generic segregation based on differences in plastid shape would result in a situation where certain species could be placed in several genera simultaneously. As a result, the present author has abandoned the use of chromoplast morphology as a generic criterion and has referred the genus *Rhodochorton* to the synonomy of *Audouinella*. For further comments, see the discussion of *A. purpurea* below and Woelkerling 1971, p. 4.

Taylor (1937, 1957) records 27 species in 5 genera from the northeastern coast of North America, all belonging to the family Acrochaetiaceae. (G. F. Papenfuss [personal communication] and P. C. Silva [personal communication] have indicated that the family name Acrochaetiaceae can be used correctly for the *Audouinella* complex even though the genus *Acrochaetium* is considered congeneric with

Audouinella; therefore the family name Audouinellaceae [Woelkerling 1971, p. 7, 22] is superfluous.)

Taylor's list may be enlarged to include the New England records of Giard (1890) and Hehre and Mathieson (1970) and the Canadian reports summarized by South and Cardinal (1970) to yield a total of 36 taxa for the region, apparently a greater number than in any other family of Rhodophyta. Of these, 29 are reported to occur in New England waters.

This account, however, recognizes only 11 species of audouinelloid algae as definitely occurring in New England; 7 of these are referred to the genus *Audouinella* and 4 to the genus *Colaconema*. Moreover, the names and(or) taxonomic status of all 29 taxa previously reported from New England have been changed; a summary appears in Table 1.

MORPHOTAXONOMIC FEATURES

The Acrochaetiaceae is generally circumscribed to include those Florideophycidae with simple or branched monosiphonous filaments usually less than 5 (rarely to 25) mm tall, with asexual reproduction by monospores, bispores, tetraspores, and/or multipartite spores, with carpogonia sessile on cells of vegetative filaments, intercalary in vegetative filaments or terminating one to several celled stalks, with gonimoblasts, when present, forming directly from the fertilized carpogonium, and without a pericarp. *Audouinella* Bory is the type genus.

Following Woelkerling (1971), the presence (*Audouinella*) or absence (*Colaconema*) of sexual reproduction is considered to provide a useful separation of the New England taxa into genera, with *Colaconema* regarded as a form genus similar to those of the Fungi Imperfecti. Taxa referrable to *Kylinia* Rosenvinge (in its *original* sense) and *Liagorophila* apparently do not occur in New England, and the systematic status of these genera remains in doubt (see Woelkerling 1971, p. 6).

Within the genera *Audouinella* and *Colaconema*, species have been grouped into three sections based on the absence of, the presence of one, or the presence of more than one pyrenoid per chromoplast. Species possessing more than one pyrenoid per chromoplast have not been collected in New England waters to date.

Additional features which appear to be of value in defining species limits include cell and spore dimensions, and in some cases chromoplast morphology, prostrate system morphology, and spore arrangement. Certain other characteristics (e.g. height of erect filaments, degree of branching, habitat preferences) sometimes are useful features for purposes of taxon recognition and in keys, but are too variable to be of value in defining species limits.

Considerable confusion has hitherto surrounded the identification of species in New England waters, and a number of records based on incorrect determinations have crept into and subsequently have been perpetuated in the literature. Thus, for example, collections originally identified by Collins (1906, 1911) as *Acrochaetium* (= *Chantransia*) *flexuosum* Vickers and subsequently recorded by Taylor (1937, 1957) have been re-examined during this study and found to belong unmistakably to *Colaconema secundata*. Likewise collections hitherto referred to *Acrochaetium sagraeanum* involve at least three different audouinelloid taxa, and the type specimen itself is here excluded from the Rhodophyta (see "Species Excludendae").

To help minimize confusion of a similar nature in the future, the distinguishing features of each taxon known to occur in New England waters have been outlined at the onset of the discussion section of each species in the taxonomic accounts. Available distributional and ecological data are also included. While each species recognized here possesses a distinctive set of morphological features, most taxa exhibit considerable variation, and numerous plants of a collection should, therefore, be examined to build a composite picture of the population before identification is attempted. Collections of single specimens whose status is in doubt are best left unidentified.

KEY TO SPECIES OF NEW ENGLAND AUDOUINELLOID ALGAE

This key includes only species definitely known to occur in New England waters. Records of questionable occurrence, of taxa whose systematic status is uncertain, etc. are discussed in a separate section at the end of this report. Characters relating to chromoplasts and pyrenoids often are not preserved in dried or spirit material, and in these cases supplementary criteria are given in the key.

1. Multicellular prostrate system present; filamentous, parenchymatous, or pseudoparenchymatous. ..... 2.
1. Multicellular prostrate system absent; plants attached to substrate by a single cell which may rarely give rise to one or several accessory cells. ..... 7.
2. Cells with a single chromoplast containing a single pyrenoid; plants generally (but not invariably) epiphytic or endophytic. ..... 3.
2. Cells with one to a number of chromoplasts without pyrenoids; plants generally (but not invariably) saxicolous or endozoic. ..... 10.
3. Erect filaments generally over 500 μm long and usually exceeding the prostrate filaments in length; monosporangia commonly over 15 μm long. ..... 4.
3. Erect filaments generally under 250 μm long or absent, usually shorter than or equal to the prostrate filaments; monosporangia under 15 μm long. ..... 11.
4. Chromoplasts distinctly stellate; prostrate system developing from an orbicular, parenchymatous group of cells which forms a small disc that may later proliferate and become obscured; lateral branches commonly but not always virgate or secundate. ..... 11. *Colaconema secundata.*
4. Chromoplasts parietal lobate curved plates; prostrate system filamentous or pseudoparenchymatous, not developing from a distinctive parenchymatous disc; lateral branches not virgate. 5.
5. Monosporangia borne, at least in part, in clusters of 3 or more on branched stalks. 4. *Audouinella daviesii.*

5. Monosporangia borne singly or in pairs but not in clusters. ..... 6.
   6. Prostrate system composed of an enlarged, central, more or less panduriform to pyriform cell and accessory cells or filaments which arise from it. ..... 3. *Audouinella dasyae.*
   6. Prostrate system filamentous or pseudoparenchymatous, without an enlarged, central panduriform or pyriform cell. ..... 6. *Audouinella saviana.*
7. Cells commonly over 20 μm long; plants commonly over 500 μm tall. ..... 8.
7. Cells under 20 μm long; plants rarely over 100 μm tall. ..... 9.
   8. Basal cell elongate, panduriform to pyriform; usually bearing accessory cells or filaments. ..... 3. *Audouinella dasyae.*
   8. Basal cell globose or subglobose; lacking accessory cells or filaments. ..... 2. *Audouinella alariae.*
9. Cells commonly over 10 μm long; filament(s) of erect system procumbent; protoplast of basal cell hemispherical and distinctly flattened on side in contact with substrate. ..... 7. *Audouinella unifila.*
9. Cells generally 10 μm or less long; filament(s) of erect system upright to arcuate; protoplast of basal cell more or less globose. ..... 5. *Audouinella microscopica.*
   10. Sporangia (i.e. carpotetrasporangia) borne mostly in clusters on branched stalk-like gonimoblast filaments; plants commonly but not invariably saxicolous. ..... 1. *Audouinella purpurea.*
   10. Sporangia (i.e. tetrasporangia) solitary, sessile or on unbranched stalks; plants commonly but not invariably endozoic. ..... 8. *Colaconema membranacea.*
11. Cells commonly over 2 diameters long; prostrate filaments widely creeping, commonly over 1 mm long. ..... 10. *Colaconema minima.*
11. Cells rarely over 2 diameters long; prostrate filaments rarely over 500μm long. ..... 9. *Colaconema humilis.*

AUDOUINELLA Bory

Audouinella Bory 1823: 340 (as *Auduinella*). Woelkerling 1971: 22. *Acrochaetium* Naegeli 1861: 402. *Balbiania* Sirodot 1876: 149. *Chromastrum* Papenfuss 1945: 320. *Grania* Kylin 1944: 26. *Rhodochorton* Naegeli 1861: 355. *Thamnidium* Thuret In Le Jolis 1863: 110. *Trentepohlia* Pringsheim 1862: 29.

Note: Species now referrable to *Audouinella* have also been placed in the past in *Byssus, Callithammion, Ceramium, Chantransia, Conferva, Kylinia,* and *Trentepohlia* Martius (1817). In addition, some species hitherto placed in *Acrochaetium, Audouinella, Callithamnion, Cermium, Chantransia, Chromastrum, Kylinia, Rhodochorton,* and *Trentepohlia* are referable here to the form genus *Colaconema.*

Plants epibiotic, endobiotic, or saxicolous; attached to or suspended in the substrate by a single basal cell, by a prostrate system of simple or branched filaments which may or may not become pseudoparenchymatous, or by a parenchymatous disc. Erect filaments simple or branched, up to 25 mm long; cells containing one to many variously shaped chromoplasts with or without pyrenoids.

Asexual reproduction by monosporangia, bisporangia, tetrasporangia, and/or multipartite sporangia; sporangia sessile or stalked and borne on erect or prostrate filaments.

Plants monoecious or dioecious. Spermatangia in clusters or occasionlly single or in pairs, terminal or lateral on simple or branched stalks or sessile on ordinary vegetative cells. Carpogonia intercalary or more commonly sessile or terminating 1-2 celled stalks on vegetative cells, solitary or rarely in groups of 2-3; remaining undivided or dividing transversely after fertilization and giving rise directly to gonimoblast filaments bearing carposporangia or carpotetrasporangia.

Type Species: Audouinella hermanni (Roth) Duby.

Section I

Species in this section are not known to contain pyre-

noids in their chromoplasts. Within each section species are discussed in alphabetical order by specific epithet. Cell and spore dimensions are based only on the New England populations studied and may not reflect the total range of variation found in populations elsewhere. The ratio of greatest cell length to greatest cell diameter (width) is denoted by L/D in all species accounts.

1. **Audouinella purpurea** (Lightfoot) comb. nov. Figs. 52-55.

Byssus purpurea Lightfoot 1777: 1000.

Callithamnion purpureum (Lightfoot) Harvey 1841: 116, 1849: 183.

Conferva purpurea (Lightfoot) Dillwyn 1806: 56, pl. 43. C. Agardh 1817: XXIX.

Rhodochorton purpureum (Lightfoot) Rosenvinge 1900: 75. Collins, Holden, and Setchell 1895: 49. Conway and Knaggs 1966: 195 et. seq., Figs. 1-3. DeToni 1903: 1510. Edelstein and McLachlan 1966a: 1041, 1052. Edelstein et al. 1970: 626. Hamel 1927: 57, 108; 1928: 201; 1928a: 151. Hehre and Mathieson 1970: 207. Knaggs 1965: 499 et seq., 1966b: 521 et seq., pl. 102-107; 1967: 139 et seq.; 1967a: 549 et seq., pl. 134-139; 1968: 449 et seq., pl. 170-174. Mathieson et al. 1969: 132. Papenfuss 1945: 327. South 1970: 1. South and Cardinal 1970: 2079. Stone et al. 1970: 325. Taylor 1957: 226, pl. 45, Figs. 1-2. West 1967: 11; 1969: 12 et seq., Figs. 1-22; 1970: 368 et seq., Figs. 1-8.

Trentepohlia purpurea (Lightfoot) C. Agardh 1824: 36. Harvey 1833: 382. Harvey and MacKay 1836: 218.

Rhodochorton islandicum Rosenvinge 1900: 75, Figs. 1-4. Papenfuss 1945: 327.

Rhodochorton intermedium (Kjellman) Kjellman 1883: 184, pl. 15, Fig 8. DeToni 1903: 1509. Hamel 1927: 107: 1928: 200.

Thamnidium intermedium Kjellman 1875: 28, Fig. 10.

Rhodochorton parasiticum Batters 1896: 389. Collins 1900: 51; 1900a: 12; 1911: 281. Collins, Holden and Setchell 1901: 848.

Callithamnion rothii (Turton) Lyngbye 1819: 129, pl. 41a. J. Agardh 1851: 17. Bailey 1847: 85. Collins 1880: 162. Eaton 1873: 348. Farlow 1875: 376; 1876: 704; 1879: 169; 1881: 121. Harvey 1846: pl. 120B; 1853: 243. Hay 1887: 66. Hay and MacKay 1888: 173. Jelliffe 1899: 15. Jordan 1874a: 488. Klugh 1917: 83. Kuetzing 1861: XI, pl. 621. Olney 1871: 8; 1872: 132. Pike 1886: 110.

Rhodochorton rothii (Turton) Naegeli 1861: 356, pl. 1, Figs. 1, 3. Bell and McFarlane 1933: 270. Boergesen 1902: 390, Figs. 61-64. Collins 1894: 230; 1900: 51; 1905: 234; 1911: 280; 1914:4. Davis 1913: 818. DeToni 1903: 1507. Drew 1928: 177. Gibson 1891: 201, Fig. 38. Hamel 1927: 54, 106, Fig. 38; 1928: 199; 1928a: 147, Fig. 38. Hylander 1928: 169. Kjellman 1883: 185. Kuckuck 1897: 345, Fig. 5. Kylin 1944: 28, Fig. 25. Nakamura 1941: 282, Figs. 8-9. Rosenvinge 1923-24: 390, Figs. 328-330. Taylor 1937: 239, pl. 45, Figs. 1-2. Whelden 1947: 119.

Thamnidium rothii (Turton) Thuret In LeJolis 1863: 111, pl. 5.

Rhodochorton tenue Kylin 1925: 44, Figs. 25 b-e. Drew 1928: 177, pl. 40, Fig. 33. Papenfuss 1945: 328. West 1969: 12 et seq., Figs. 1-22.

Conferva violacea Roth 1797: 190, pl. 4, Fig. 1. Non *Conferva violacea* Hudson 1778: 592, nec *Ceramium violaceum* Roth 1797: 150, nec *Conferva rothii* Turton 1806: 1809.

Plants saxicolous or occasionally epibiotic, caespitose or forming conspicuous matted expanses with erect filaments up to 25 mm tall; original spore non-persistent. Prostrate system composed of branched, creeping filaments which may be loosely entangled or more compactly pseudoparenchymatous, but not forming distinct discoid holdfasts. Erect filaments moderately to freely and irregularly branched and usually tapering towards the tips. Cells cylindrical, 10-20 μm wide and 15-75 μm long, L/D (1-)2.5; tapering to 7-12 μm wide and 40-175 μm long (L/D up to 15) near and at the tips of branches; each cell containing

one to a number of irregularly lobate to reticulate to discoid chromoplasts without pyrenoids.

Monosporangia, bisporangia, parasporangia, and sex organs not observed. Carposporphytes consisting of short (up to 10 cells long), simple or usually branched gonimoblast filaments bearing terminal or occasionally lateral, ovoid, solitary or paired carpotetrasporangia 15-25 μm wide and 25-40 μm long. Other reproductive structures not observed.

Type Locality: Ruined Abbey, Island of Iona, Scotland.

Type: Possibly destroyed (see Conway and Knaggs 1966).

Distribution: Nearly cosmopolitan in temperate and polar marine waters; also known from terrestrial and freshwater sites.

Hosts: Most common on rocks but also on algae and invertebrates.

Specimens examined:

CONNECTICUT: Bridgeport (Harbor) 4. IX. 1893, *Johnson* (NY); 8. III. 1891, *Holden* (NY).

MAINE: Appledore Island (Isles of Shoals), 28. VII. 1938, *Croasdale* (NHA). Haley's Cove (Smuttynose Is., Isles of Shoals), 16. VI. 1966, *Shipman* (NHA). Harpswell, 6. VII. 1905, *Collins* (NY). Inner Mark Island, 29. VIII. 1903, *Collins* (NY). Lubec (Bailey's Mistake) 22 V. 1966, *Femino* (NHA). Lubec (West Quoddy Head), 21. V. 1966, *Ball* and *Lavise* (NHA). Peaks Island, VII. 1881, *Collins* (NY); 22. V. 1904, *Collins* (NY). Penobscot Bay, prior to 1853, *Hooper* (TCD). Popham, 7. VIII. 1900, *Chernington* (NY). South Harpswell, 17. VII. 1902, Collins (NY); 8. VII. 1903, *Collins* (NY). York (Nubble Light), 19. V. 1966, *Pollock* (NHA).

MASSACHUSETTS: Magnolia, 24. VI. 1896, *Collins* (NY). Nahant, 18. IV. 1879, *Collins* (?) (NY); 9. VI. 1889, *Collins* (NY); 30. III. 1890. *Collins*, (NY); 22. II. 1891, *Collins* (NY, = Collins, Holden, and Setchell 1895, No. 49); 30. V. 1900, *Collins* (NY, = Collins, Holden, and Setchell 1901, No. 848); 13. IV. 1907, Collins (NY). Penikese Island, 9. VII. 1926, *Taylor* (NY). Sandwich (jetty), 7. IV. 1968, *Kastelowitz* (NHA); 22. I. 1971, *Woelkerling* (WJW 3297). Scusset Beach, 7. IV. 1968, *Bosworth* (NHA); 29. III. 1969, *Mills* (NHA).

NEW HAMPSHIRE: Hampton, VIII. 1884, *Collins* (NY). North Wallis Sands, 16. VII. 1967, *Hehre* (NHA). Rye Ledge, 18. VIII. 1966, *Conway* and *Shipman* (NHA); 15. X. 1966, *Hehre* (NHA); 23. XII. 1966,

Conway and *Hehre* (NHA); 10. I. 1967, *Conway* and *Hehre* (NHA); 26. II. 1967, *Conway* and *Hehre* (NHA); 25. IV. 1967, *Hehre* (NHA); 25. V. 1967, *Hehre* (NHA); 22. VI. 1967, *Hehre* (NHA); 24. VII. 1967, *Hehre* (NHA); 12. VIII. 1967, *Mathieson* (NHA), 15. III. 1969, *Hutchinson* (NHA).

NEW JERSEY: Bay Ridge, 17. III. 1893, *Collins* (NY).

NEW YORK: Fort Hamilton (Long Island), 16. V. 1866, *Pike* (NY).

RHODE ISLAND: Newport, prior to 1853, *Bailey* (TCD).

Audouinella purpurea is distinguished from other New England audouinelloid algae in having a diphasic life cycle involving the production of carpotetraspores (Fig. 52) and in having erect filaments commonly over 10 mm long with cells containing 1 to a number of irregularly shaped to discoid chromoplasts without pyrenoids (Figs. 53-55). It is the only known New England species of audouinelloid algae which commonly develops on rocks and forms matlike expanses.

A. purpurea grows throughout the year in New England and has been collected as far south as New Jersey. Most commonly it occurs in shaded habitats in the midlittoral, especially underneath *Ascophyllum* or *Fucus*, but it has been found throughout the intertidal and in the sublittoral zones. In sublittoral communities it apparently grows primarily as an epiphyte on kelp stipes. This species is widely distributed throughout the cooler regions of the northern hemisphere, and because it sometimes becomes an ecological dominant in the intertidal zone, it has been reported more frequently from northern regions than any other audouinelloid species.

Its vegetative morphology can vary considerably, depending upon the particular ecological niche it occupies, and this morphological variation has been the subject of intensive studies (Conway and Knaggs 1966; Knaggs 1965, 1966, 1966a, 1967, 1967a, 1968). In general, plants growing under stressed conditions tend to have shorter and less branched erect filaments. Knaggs (1965, 1966, 1966a) and Conway and Knaggs (1966) have recorded this species from freshwater and terrestrial habitats as well as intertidal and sublittoral habitats and have

recognized a number of distinct taxonomic forms. These forms, however, appear to have little taxonomic value in so far as New England populations are concerned and consequently are not recognized here as distinct systematic entities.

Reproductive structures have been found only in the winter and early spring; sterile plants, however, occur throughout the year. The latter bear some superficial resemblance to *Spermothamnion* but can easily be distinguished from that genus by the possession of a true heterotrichous habit. Sex organs have not been found in New England populations and to the author's knowledge have never been found in field collected samples. West (1969, 1970) has given an excellent account of these and other stages in the life history based on culture studies; Knaggs (1968) also reported sexual stages in cultural material. Mature carposporphytes are somewhat more loosely organized in comparison with other New England species and often greatly resemble ordinary vegetative branches bearing sporangia. Only carpotetrasporangia have been seen during this study, but bisporangia and parasporangia are reported from elsewhere (Conway and Knaggs, 1966; Knaggs, 1967).

Audouinella purpurea was the first described member of the *Audouinella* complex (Lightfoot, 1777), and because of its distinctiveness as a species (primarily in terms of habit and chromoplast morphology), it traditionally has been referred (as the type species) to a separate genus — *Rhodochorton* Naegeli (1861, p. 355). While recognizing its distinctness *as a species,* no reliable characteristics of generic significance (see Woelkerling 1971, p. 4) are apparent at present; consequently *Rhodochorton* is considered congeneric with *Audouinella,* and the type species, *R. purpureum,* is also referred to *Audouinella.*

Following Papenfuss (1945) and West (1969), the taxa originally described as *Rhodochorton parasticum* Batters (1869), *R. rothii* (Turton) Naegeli (1861), *R. tenue* Kylin (1925), and *Thamnidium intermedium* Kjellman (1875)

are here considered conspecific with *Audouinella purpurea*. In agreement with Conway and Knaggs (1966), *Rhodochorton islandicum* Rosenvinge is also regarded as conspecific with *Audouinella purpurea*.

Section II

Species in this section have chromoplasts with only one pyrenoid each.

2. **Audouinella alariae** (Jonsson) comb. nov. Figs. 1-9.

Acrochaetium alariae (Jonsson) Bornet 1904: XIX. Collins 1906: 192. Croasdale 1941: 214. Erskine 1955: 151. Hamel 1927: 84; 1928: 177. South 1970: 1. South and Cardinal 1970: 2079. Taylor 1937: 229.

Chantransia alariae Jonsson 1901: 132, Fig. 1. Adams 1904: 351. Boergesen 1902: 356. Boergesen and Jonsson 1905: Appendix, p. III. Collins 1911: 276. Cotton 1912: 98, 133. DeToni 1924: 45. Levring 1937: 86, Fig. 12.

Chromastrum alariae (Jonsson) Papenfuss 1945: 320.

Kylinia alariae (Johnsson) Kylin 1944: 13. Hehre and Mathieson 1970: 206. Mathieson et al. 1969: 132. Papenfuss 1947: 436. Taylor 1957: 213.

Acrochaetium rhipidandra (Rosenvinge) Hamel 1927: 25, 82, Fig. 23; 1928: 176; 1928a: 119, Fig. 23.

Chantransia rhipidandra Rosenvinge 1909: 91, Figs. 19-20. DeToni 1924: 37. Kylin 1928: 5, Figs. 1-2. Levring 1937: 83.

Chromastrum rhipidandra (Rosenvinge) Papenfuss 1945: 322.

Kylinia rhipidandra (Rosenvinge) Kylin 1944: 13. Papenfuss 1947: 437.

Rhodochorton rhipidandra (Rosenvinge) Drew 1928: 151.

Chantransia secundata auct. non. (Lyngbye) Thuret: Collins, Holden, and Setchell 1896a: 236. Collins 1900: 49 (pro parte).

Chantransia virgatula auct. non. (Harvey) Thuret: Collins 1894: 233 (Holden collection).

Plants epiphytic, up to 1.0 mm tall; original spore persisting as a globose to subglobose unicellular base up to 25 μm in diameter and usually larger than other cells. Basal cell bearing 1-2 (-3) erect filaments which are almost always branched; laterals irregularly arranged, few in number and nearly simple to numerous and frequently further subdivided; laterals generally tapering towards the tips. Cells cylindrical or occasionally somewhat barrel-shaped near the base, 12-18 μm wide and 15-60 μm long near the base, L/D (1-) 1.5-4; (4-) 7-10 (-15) μm wide and 15-65 μm long in the laterals, L/D 2-6 (-9); tapering to 4-9 μm wide near the tips; each cell containing a single chromoplast and one pyrenoid. Unicellular hairs not observed.

Monosporangia ovoid, 8-12 μm wide and 12-20 μm long, solitary or in pairs (occasionally in groups of 3), sessile or stalked, scattered to secundate along lateral branches or occasionally opposite or terminal on the branchlets.

Other reproductive structures not observed in New England collections.

Type Locality: The Maelstrom, Hvammsfjördur, Iceland.

Type: c (Jonsson 597).

Distribution: Northern Massachusetts northward; Denmark, Faeroes Islands, France, Great Britain, Iceland, Norway.

Hosts: *Alaria* in New England; *Alaria* and *Porphyra* in Europe.

Specimens examined:

MAINE: Bald Head Cliffs (Ogunquit), 17. VIII. 1966, *Shipman* and *Conway* (NHA); 7. XI. 1967, *Stone* and *Hehre* (NHA). Boon Island, 26. VII. 1938, *Croasdale* (NHA). Burnt Island (Cushing), 17. VII. 1888, *Collins* (NY). Cushing, no date, *Collins* (NY, Collins 446A). Casco Bay, VII. 1939, *Weatherhill* (FH). Hardhead Island (Penobscot Bay), VII. 1894, *Collins* (NY, loose duplicate of P.B.A. No. 236; FH, P.B.A. No. 236; WIS, P.B.A. No. 236). Mt. Desert Island, 12. VIII. 1890, *Holden* (NY, Holden 134). Nubble Light, 19. VIII. 1969, *Hehre* (WJW 2275). Pemaquid Point, 18. VII. 1901, *Collins* (NY). South Harpswell, 8. VII. 1903, *Collins* (NY).

MASSACHUSETTS: Pigeon Cove (Cape Ann), 25. IX. 1966, *Hehre* (NHA).
NEW HAMPSHIRE: Hampton, VII. 1894, *Collins* (NY); VIII. 1894, *Collins* (NY). Star Island (Isles of Shoals), 22. VII. 1966, *Conway* and *Shipman* (NHA).
CANADA: Ferryland, Avalon Penn., Newfoundland, 4. XII. 1968, *South* (CANA 7583). Ketch Harbor, Nova Scotia, 7. II. 1966, *Edelstein* (?) (Edelstein 2239, Herb. Nat. Res. Council, Halifax). Mulholland's Bend, Campebello Island, New Brunswick, 15. VI. 1967, *Hehre* and *Stone* (NHA).
DENMARK: Frederikshavn, Kattegat, 25. VIII. 1891, *Rosenvinge* (C, type of *Chantransia rhipidandra*).
ICELAND: The Maelstrom, Hvammsfjördur, 28. VI. 1897, *Jonsson* (C, Jonsson 597, type of *Audouinella alariae*).

Audouinella alariae is distinguished from other New England audouinelloid algae by the presence of a unicellular, more or less globose base (Figs. 1-3) bearing erect filaments whose cells are commonly over 2 diameters and 20 μm long. It has been collected in New England from July through November on *Alaria esculenta* (L.) Greville, but also has been collected along the Canadian coast in February, June, and December. Further investigation may show that *Audouinella alariae* not only develops at other times of the year, but also grows on other substrates.

New England populations of *A. alariae* exhibit considerable morphological variation. Some mature plants reach heights of 1 mm while others never exceed 500 μm. A few plants consisting of a single, nearly simple erect filament have been observed (Fig. 7), but in most cases lateral branches develop. The laterals themselves may be little further branched, long, and bear a few, scattered sporangia (Figs. 8-9), or they may be more densely subdivided, relatively short, and bear numerous, rather crowded sporangia (Figs. 4-5). All intermediate situations can occur within a single population.

Although pyrenoids have been observed during this investigation, the chromoplast shape could not be definitely determined. Jonsson (1901, p. 133) and Levring (1937, p. 87) both report a stellate chromoplast, but further study is needed to determine to what extent, if any, the plastid

shape might vary in this species. Collins (1906, p. 192) and Taylor (1937, p. 229; 1957, p. 213) report unicellular hairs, but such hairs have not been observed during this study and have not been recorded by other authors.

Collins (1906), Jonsson (1901), and Taylor (1937, 1957) report the monosporangia to be sessile and opposite; Adams (1904) records mostly alternate sporangia; and Levring (1937) states that the sporangia are often scattered. Plants in New England populations show a combination of all such arrangements on the same individual (Figs. 4, 5, 7-9), with oppositely arranged sporangia occurring only occasionally. They may be either sessile or on 1-2 celled stalks and sometimes terminate short lateral branches.

Critical comparisons (Table 2) of type collection material of *Audouinella alariae* and *Chantransia rhipidandra* Rosenvinge strongly indicate that the two taxa are conspecific. Rosenvinge (1909, p. 91) stated that *C. rhipidandra* differed from *Audouinella alariae* in ". . . having much thicker and more branched filaments, and further by the branches being often opposite . . ."; he also noted the presence of sex organs in the former and their absence in the latter.

However, plants examined during this study, including the types of both taxa, indicate considerable overlap in filament diameters (Table 2), and the degree of branching and branch arrangement (Figs. 4, 5, 7-9) vary considerably. Thus these criteria do not appear reliable for separating the two taxa. The presence or absence of sex organs alone also appears unreliable as a criterion of species separation (Woelkerling 1971), and since there appear to be no other criteria by which the two taxa can be reliably separated, they are regarded here as conspecific.

Hamel (1927, 1928), Kylin (1928), and Rosenvinge (1909) have described and illustrated sexual and carposporophyte stages of this species (all using the specific epithet "rhipidandra").

Chantransia unilateralis Kjellman (1906, p. 11, Taf. II, Figs. 1-4) is almost certainly conspecific with *Audouinella*

alariae, but the type collection of Kjellman's species apparently is not at UPS (personal communication), and final judgement must, therefore, be deferred until the type can be located and examined.

The relationships of *A. alariae* to at least 15 other taxa of similiar morphology await clarification. Once critical examinations of all the types and other populations of these taxa are completed, it appears likely that a number will prove to be conspecific with *A. alariae.*

Specimens referred to *Chantransia secundata* by Collins (1900) and Collins et al. (1896a) and to *Chantransia virgatula* by Collins (1894) have been examined and found to contain only plants of *Audouinella alariae.* In the case of the former specimens, this confirms the opinions of Jonsson (1901) and Collins (1906).

Young plants of *Audouinella dasyae* bear many resemblances to *A. alariae* but usually can be recognized by the presence of a panduriform or pyriform basal cell rather than a globose one.

3. **Audouinella dasyae** (Collins) comb. nov. Figs. 10-31.

Acrochaetium dasyae Collins 1906: 191. Aziz 1967: 408. Davis 1913: 813. Edelstein et al. 1967: 195, Fig. 9. Hamel 1927: 77, 95, Figs. 47b-g; 1928: 171, 189, Figs. 47b-g. Papenfuss 1945: 308. Taylor 1937: 231; 1957: 217.

Chantransia dasyae (Collins) Collins 1911a: 186. DeToni 1924: 40.

Acrochaetium intermedium Jao 1936: 242, pl. 11, Figs. 1-4. Papenfuss 1945: 314. Taylor 1937: 231, pl. 33, Figs. 1-4; 1957: 218, pl. 33, Figs. 1-4.

Acrochaetium subseriatum Jao 1936: 243, pl. 11, Figs. 5-7 (Non *Acrochaetium subseriatum* Boergesen 1932: 118, Figs. 6-7). Taylor 1937: 232, pl. 33, Figs. 5-7.

Acrochaetium zosterae Papenfuss 1945: 307. Taylor 1957: 218, pl. 33, Figs. 5-7.

Callithamnion virgatulum auct non Harvey: Harvey 1853: 243.

Plants epiphytic, caespitose, up to 3 mm tall. Prostrate

system usually consisting of an enlarged, central, more or less panduriform to pyriform cell — the original spore — bearing several smaller accessory cells or short filaments; central cells becoming obscured by accessory filaments in robust plants or rarely remaining unicellular in young or small plants. Erect filament(s) arising from the central cell, moderately to freely and irregularly branched; sometimes tapering towards the tips. Cells cylindrical, 25-70 (-90) μm long and 7-12 (-16) μm wide [L/D 2-6 (-10)] in main axes, 15-60 μm long and 6-10 μm wide (L/D 2-7) in the laterals; each containing a single parietal chromoplast with one pyrenoid. Unicellular hairs not observed.

Monosporangia ovoid, 16-24 μm long and 9-12 (-16) μm wide, solitary or occasionally in pairs, sessile or occasionally stalked, in secundate series along the laterals or more scattered. Bisporangia and tetrasporangia not observed.

Spermatangia globose to ovoid, up to 3μm wide and 5 μm long, borne terminally or laterally on vegetative cells or unicellular stalks, or usually in clusters of varying size on multicellular simple or branched stalks. Carpogonia sessile or stalked, scattered over the lateral filaments; fertilized carpogonium dividing transversely and eventually giving rise to a branched gonimoblast bearing terminal carposporangia 16-24 μm wide and 9-12 μm long.

Type locality: Woods Hole, Massachusetts.

Type: FH (accompanied by a card in Collins script and numbered 5370). Isotypes have been distributed as No. 1342 in Phycotheca Boreali Americana (Collins, et al. 1906).

Distribution: Atlantic Coast of North America.

Hosts: Dasya (Rhodophyta) and *Zostera* (Angiospermae).

Specimens examined:

MASSACHUSETTS: Edgartown (Martha's Vineyard), 19. XII. 1969, *Woelkerling* (WJW 2245). Great Rip (1.25 km E. of Great Point, Nantucket Is.), 14. IV. 1970, *Woelkerling* (WJW 2500). North Eastham, 9. VIII. 1959, *Lamb* (FH, filed under the host, *Dasya pedicel-*

lata). Old Silver Beach, 31. X. 1970, *Woelkerling* (WJW 2853); 15. XI. 1970, *Woelkerling* (WJW 2856); 30. XII. 1970, *Woelkerling* (WJW 2977). Waquoit Bay (Falmouth), 16. X. 1969, *Conway* (WJW 2293); 27. IV. 1970, *Woelkerling* (WJW 2534). West Falmouth Harbor, 6. I. 1970, *Woelkerling* (WJW 2284); 18. VII. 1970, *Woelkerling* (WJW 2751). West Yarmouth, 17. IX. 1969, *Woelkerling* (WJW 2252); 3. X. 1969, *Woelkerling* (WJW 1852), (WJW 2255); 16. XI. 1969, *Woelkerling* (WJW 2249), (WJW 2250); 12. XII. 1969, *Woelkerling* (WJW 2260). Woods Hole, 12. VIII. 1894, *Holden* (FH, filed under the host, *Dasya pedicellata*); 2. IX. 1905, *Collins* (FH, type); 29. VIII. 1944, *Taylor* (FH, filed under the host, *Dasya pedicellata*); 4. II. 1970, *Woelkerling* (WJW 2330); 5. VII. 1970, *Wilce* (WJW 2690); 17. VII. 1970, *Woelkerling* (WJW 2716); 13. X. 1970, *Woelkerling* (WJW 2820); 29. I. 1971, *Woelkerling* (WJW 3298); 16. II. 1971, *Woelkerling* (WJW 3311); 25. VIII. 1933, *Jao* (MICH, Woods Hole No. 278, type of *Acrochaetium zosterae* Papenfuss). Pine Island (Woods Hole), 7. VIII. 1934, *Jao* [MICH, Woods Hole No. 277, type of *Acrochaetium intermedium* Jao, non *Thamnidium intermedium* Kjellman = *Audouinella purpurea* (Lightf.) comb. nov.].
NEW JERSEY: *Great Bay* (.4 km SSW of Wells Is.), 17. VII. 1963, *Moeller* (RUT, filed under the host, *Dasya pedicellata*).
NEW YORK: Hell Gate (Long Island), 29. IX. 1850, *Walters* (TCD).
CANADA: Malpeque Bay (Prince Edward Island), 5. VIII. 1966, *Edelstein* (Nat. Res. Coun. Herb., Halifax).

Audouinella dasyae is distinguished from other New England audouinelloid algae by the presence of an enlarged, central, more or less panduriform to pyriform cell in the prostrate system (Figs. 12-17) which bears accessory prostrate cells or filaments and which gives rise to the erect filaments. *A. dasyae* appears to be confined to the sublittoral and has been collected in New England all months except March, May, and June. It undoubtedly occurs throughout the year. Sexual plants have been found from July through November; tetrasporangial plants have not been observed but probably occur and are to be expected in deeper waters in late spring and early summer.

Like many audouinelloid algae, *A. dasyae* exhibits considerable variation [more than indicated by Collins (1906) or Taylor (1957)] in cell width, height, spore size, and other features. On *Dasya* for example, it is not uncommon to find mature plants under 500 μm tall anchored to the monosiphonous filaments of the host and plants up to

3 mm attached to the more robust multilayered primary axes of the the host. Likewise branching of *A. dasyae* may be dense or relatively sparse (Figs. 20, 21), depending upon the "growing room" available. In all cases the enlarged central cell representing the original spore was panduriform or pyriform; globose cells described by Taylor (1957) and illustrated by Hamel (1927, Fig. 47b; 1928, Fig. 47b) have not been observed except in sporelings (Figs. 10-11). In addition, the range of cell and spore dimensions recorded during this study are considerably greater than those reported by Collins (1906) or Taylor (1937, 1957).

Sexual plants have been reported before only by Aziz (1967). Spermatangial clusters vary considerably in size both within and between populations. In some cases the cluster is densely branched and bears numerous spermatangia, while in others it remains small, and in some cases spermatangia are even borne directly on vegetative cells or on unicellular stalks (Figs. 29-31).

It appears that the trichogynes of unfertilized carpogonia continue to elongate until a spermatium lands on the tips (Fig. 22). Only several fertilized carpogonia with clear transverse divisions have been observed (Fig. 25), and further study is needed to determine whether gonimoblast cells are cut off without such a division first occurring.

Critical comparisons of the type and other collections of *Audouinella dasyae*, *Acrochaetium intermedium* Jao (1936, p. 242, pl. 11, Figs. 1-4), and *Acrochaetium zosterae* Papenfuss (1945, p. 307 = *A. subseriatum* Jao 1936, p. 243, pl. 11, Figs. 5-7, non *A. subseriatum* Boergesen 1932, p. 118) indicates that all three taxa are conspecific (Table 3).

Jao (1936, p. 243) distinguished *A. intermedium* from *Audouinella dasyae* on the bases of an elongate rather than globose central cell, the presence of endophytic prostrate filaments, longer cells, more extensive branching, and the presence of bisporangia. However, all collections of *A. dasyae* examined, including the type, have panduriform or pyriform central cells at maturity, may or may not

produce accessory prostrate filaments, have cells of similar dimensions (Table 3), and contain plants with varying degrees of branching. Bisporangia have not been observed in the type collection material of *A. intermedium* examined during this study; however, the presence or absence of bisporangia (possibly incompletely divided tetrasporangia) alone does not warrant specific distinction (Woelkerling 1971). Since no other reliable distinguishing criteria could be found, the two taxa are considered conspecific. Aziz (1967) previously proposed that the two entities belonged to the same species.

Acrochaetium zosterae reportedly (data from Jao 1936, p. 244) differs from *Audouinella dasyae* in the shape of the central cell and in the larger size of monosporangia. Central cell shape of the two taxa is essentially the same (see above), and an examination of type material of *Acrochaetium zosterae* indicates that most monospores are 18-24 μm long and 8-11 μm wide rather than 22-31 μm long and 6.5-9.5 μm wide as reported by Jao (1936). The first set of dimensions falls within the range found for other New England populations of *Audouinella dasyae*. Since differences in host (*Dasya* vs. *Zostera*) are not taxonomically reliable (Woelkerling 1971) and since no other reliable criteria could be found to distinguish the two taxa, they are also considered conspecific.

Acrochaetium opetigenum Boergesen (1915, p. 38, Figs. 35-37), *A. robustum* Boergesen (1915, p. 40, Figs. 38-40), and *A. unipes* Boergesen (1915, p. 35, Figs. 31-35) are very similar to *Audouinella dasyae*, and a comparative examination of the type collections will probably show that all are conspecific. Boergesen (1915) separated all of these taxa on slight differences in prostrate system structure, but none appears to be taxonomically reliable (see Woelkerling 1971).

The relationships between *A. dasyae* and *Chantransia macounii* Collins (1913, p. 113) require further clarification. Collins (1913) states in the original description that the cell representing the original spore does not remain

distinct; Drew (1928, p. 184, pl. 43, Figs. 47-52, pl. 44, Fig. 53), however, describes and illustrates a distinct central cell which she says becomes obscured by other prostrate filaments. Both Drew's material and the type collection of Collins need to be re-examined and compared with *Audouinella dasyae* to determine whether any or all are conspecific.

Collins (1906, p. 192) suspected that specimens of Harvey (1853, p. 243) collected at Hell Gate, Long Island, New York in 1850 and referred to *Callithamnion virgatulum* Harvey were in reality plants of *Audouinella dasyae.* Harvey's original material from TCD has been examined and indeed contains only plants of *A. dasyae,* as suspected by Collins.

As noted previously, young plants of *A. dasyae* can under some circumstances become confused with specimens of *A. alariae.* The two can usually be distinguished on differences in basal cell shape.

4. **Audouinella daviesii** (Dillwyn) Woelkerling 1971: 28, Figs. 7, 22; 1973: 81. Figs. 32-43.

Acrochaetium daviesii (Dillwyn) Naegeli 1861: 405, Figs. 26-7. Baardseth 1941: 42, Fig. 18. Collins 1906: 194 (?); 1908: 134. Davis 1913: 813. Doty 1948: 263. Edelstein et al. 1970: 634. Hamel 1927: 39, 98, Fig. 31; 1928: 192; 1928a: 133, Fig. 31. South and Cardinal 1970: 2079. Taylor 1937: 234, pl. 31., Figs. 8-10; 1957: 221, pl. 31, Figs. 8-10.

Callithamnion daviesii (Dillwyn) Lyngbye 1819: 129 (only as to binomial). J. Agardh 1851: 11; 1876: 8. Jordan 1874: 197; 1874a: 488.

Ceramium daviesii (Dillwyn) C. Agardh 1817: XXVII.

Chantransia daviesii (Dillwyn) Thuret In LeJolis 1863: 106. Collins 1880: 162 (?); 1894: 233 (?); 1900: 49 (?); 1911: 276 (?). DeToni 1897: 67; 1924: 55. Farlow 1875: 376; 1876: 705. Kylin 1907: 117, Fig. 27. Rosenvinge 1909: 104, Fig. 34.

Conferva daviesii Dillwyn 1809: 73, Suppl. pl. F.

Rhodochorton daviesii (Dillwyn) Drew 1928: 172. Nakamura 1944: 106, Fig. 5.

Trentepohlia daviesii (Dillwyn) Areschoug 1847: 338. Farlow 1881: 109. Martindale 1889: 100.

Acrochaetium amphiroae (Drew) Papenfuss 1945: 312. Doty 1948: 263. Edelstein and McLachlan 1968: 993, Figs. 49-50 (?). Mathieson et al. 1969: 131. South 1970: 1. South and Cardinal 1970: 2079. Taylor 1957: 223.

Rhodochorton amphiroae Drew 1928: 179, pl. 40, Figs. 34-37.

Acrochaetium alcyonidii Jao 1936: 245, pl. 12, Figs. 2-4. Papenfuss 1945: 312. Taylor 1937: 234, pl. 34, Figs. 2-4; 1957: 200, pl. 34, Figs. 2-4.

Acrochaetium alcyonidii Jao var. *cylindricum* Jao 1936: 245, pl. 12, Fig. 5. Taylor 1937: 234, pl. 34, Fig. 5; 1957: 221, pl. 34, Fig. 5.

Acrochaetium sagraeanum auct. non. (Montagne) Bornet: Boergesen 1915: 35 (pro parte). Bornet 1904: XXI (pro parte). Collins 1906: 192 (pro parte). Hamel 1927: 77, 99 (pro parte); 1928: 173, 191 (pro parte). Jao 1936: 244 (pro parte). Papenfuss 1945: 311 (pro parte). Taylor 1960: 309 (pro parte). Vickers 1905: 60.

Chantransia sagraeana auct. non. (Montagne) DeToni: DeToni 1924: 51 (pro parte).

Chantransia corymbifera auct. non. Thuret In LeJolis (pro parte; see Papenfuss 1945, p. 313 under *Acrochaetium bornetii*): Collins 1896: 5. Collins, Holden, and Setchell 1896: 192.

Chantransia efflorescens var *thuretii* auct. non. Bornet: Collins 1906: 196. Davis 1913: 813.

Acrochaetium thuretii auct. non. (Bornet) Collins et Hervey: Taylor 1937: 236; 1957: 222.

Note: Additional synonomy is presented by Woelkerling (1971).

Plants partly to entirely epiphytic or epizoic, caespitose, up to 6 mm tall; original spore non-persistent. Prostrate system consisting of branched epi- or endophytic or epi- or endozoic filaments forming a pseudoparenchymatous

disc or an entangled funiform mass. Erect filaments moderately to freely and irregularly branched, sometimes tapering towards the tips or attenuate and ending in multicellular hair-like prolongations. Cells cylindrical, (6-) 9-12 (-20) μm wide and (8-) 15-50 (-70) μm long, L/D (1-) 2-4 (-6) in main axes and laterals; about 4 μm wide and up to 75 μm long in hair-like prolongations; each cell containing a single parietal lobate chromoplast with one pyrenoid.

Monosporangia ovoid, 7-13 μm wide and (8-) 12-20 μm long, in clusters of 3 or more on branched stalks or singly or in pairs on 1-2 celled stalks, situated on the lowermost cells of laterals or sometimes more scattered. Tetrasporangia ovoid, 16-22 μm wide and 24-36 μm long, borne in pairs on unicellular stalks or occasionally solitary or in groups of 3, situated on the lowermost cells of laterals or more scattered.

Spermatangia ovoid to spherical, up to 4 μm wide and 5 μm long, borne terminally or laterally in small clusters on branched stalks. Carpogonia terminal on unicellular stalks; immediate post-fertilization stages not observed. Mature carposporophyte consisting of branched gonimoblast filaments bearing terminal, ovoid carposporangia 9-18 μm wide and 18-26 μm long.

Type Locality: Bantry Bay, Ireland (Hutchens); locality for H. Davies collection not given by Dillwyn (1809).

Type: NMW.

Distribution: Nearly cosmopolitan.

Hosts: A wide variety of algae, and invertebrates.

Specimens examined:

MAINE: Eastport, 1873, *Averill* (?) (NY).

MASSACHUSETTS: Gay Head (Martha's Vineyard), VIII. 1875, *Farlow* (FH); (NY). Gloucester, IX. 1878, *Farlow* (FH). Marblehead, 16. IX. 1888, *Collins* (NY); 27. VIII. 1895, *Collins* (NY). Nantucket Center (Nantucket Is.), 14. IV. 1970, *Woelkerling* (WJW 2577). Old Silver Beach, 31. X. 1970, *Woelkerling* (WJW 2855); 30. XII. 1970, *Woelkerling* (WJW 2978), (WJW 2976). Salisbury Beach, 31. V. 1909, *Collins* (?) (NY). Waquoit (Harbor Entrance), 27. IV. 1970, *Woelk-*

erling (WJW 2536). West Falmouth Harbor, 3. X. 1970, *Woelkerling* (WJW 2769). West Yarmouth, 16. XI. 1969, *Woelkerling* (WJW 2248). Woods Hole (Butlers Point), 15-20. VII. 1895, *Nott* (FH [P.B.A. 192], NY, WIS [P.B.A. 192]). Woods Hole (Nobska Point), 4. II. 1970. *Woelkerling* (WJW 2332), (WJW 2322); 2. VII. 1970, *Woelkerling* (WJW 2678); 17. VII. 1970, *Woelkerling* (WJW 2719); 29. I. 1971, *Woelkerling* (WJW 3302); 12. II. 1971, *Fiore* (WJW 3320); 16. II. 1971, *Woelkerling* (WJW 3314). Woods Hole (Pine Island), 9. VII. 1938, *Taylor* (NY). Woods Hole (Sheep Pen Harbor), 1. IX. 1934, *Jao* (MICH, apparently a portion of type collection of *Acrochaetium alcyonidii* Jao).

NEW YORK: Montauk Point (Long Island), 20. I. 1970, *Woelkerling* (WJW 2198).

CANADA: Paddy's Head (Nova Scotia), 13. X. 1965, *Edelstein* (Herb Nat. Res. Council, Halifax, 2110).

IRELAND: Bantry Bay, prior to 1809, *Hutchins* (NMW, Dillwyn collection, type).

Audouinella daviesii is distinguished from other New England audouinelloid algae by the arrangement (at least in part) of monosporangia in clusters of 3 or more on branched stalks which are usually situated on the lowermost cells of lateral branches (Figs. 32-35). On some plants all monosporangia are borne in such clusters while on others, notably sexual and tetrasporangial plants, clustered monosporangia may not be very evident or numerous.

A. daviesii appears to be mainly a sublittoral plant although several populations have been found on *Fucus* in the lowermost littoral. It has been collected in New England in all months except March and June, but almost certainly occurs throughout the year. Sexual plants have been collected in July, August, and September (WJW 2678, FH, NY); tetrasporangial plants have appeared in January (WJW 2198).

The vegetative appearance of *Audouinella daviesii* varies considerably. When growing on *Codium,* for example, the prostrate system becomes an endophytic funiform mass of filaments lodged between the utricles of the host. When growing on *Chondria,* in contrast, the prostrate system forms an epiphytic pseudoparenchymatous disc. Similar variation has been found in Australian populations of *A. daviesii* (Woelkerling 1971). Intergrades between these

forms also occur. The ratio of cell length to cell diameter also shows considerable variation. In some populations, most plants have cells with an L/D over 3 (Fig. 32) while in other populations, the ratio of cell length to cell diameter is almost always less than 3 (Fig. 33). Intergrades always occur, and sometimes transitions from short cells to longer cells can be found along single filaments (Fig. 34).

Other vegetative features which vary include the degree of branching and the occurrence of multicellular hair-like prolongations. In some plants the degree of branching is only moderate; laterals arise at infrequent intervals and are little further divided. In other plants, however, branching is abundant and laterals often arise in groups in close proximity to one another in a more or less fasciculate manner. Hair-like prolongations occur in some populations but not in others. Often these prolongations were broken off giving the lateral branches a stubby appearance.

Several sexual and one tetrasporangial collection have been made in New England waters to date. Unfortunately, immediate post-fertlization stages have still not been observed (see Woelkerling 1971) and it is not known whether the fertilized carpogonium divides transversely, longitudinally, or gives rise directly to gonimoblast filaments. Carposporangia in the New England populations tend to be larger than those found in Australia (Woelkerling 1971).

Acrochaetium alcyonidii Jao (1936, p. 245, pl. 12, Figs. 2-4) and *A. alcyonidii* var. *cylindricum* Jao (1936, p. 245, pl. 12, Fig. 5) are here considered conspecific with *Audouinella daviesii*. Two slides labelled "alcyonidii" by Jao in MICH, which are presumably from the original collection but do not bear the number Woods Hole 279 (see Jao 1936, p. 245), have been examined and found to contain only the basal portions of several plants without any monosporangia or other reproductive structures. Thus the material is unidentifiable.

The published accounts and illustrations of Jao (1936) and Taylor (1937, 1957) leave little doubt about the con-

specificity of *Acrochaetium alcyonidii* and *Audouinella daviesii*. Jao (1936) separated the former from the latter ". . . in having a strongly marked endozoic habit and very short lateral branches." However, host differences, habit, and length of lateral branches appear to be of little taxonomic significance (Woelkerling 1971). Moreover several New England populations (Taylor, Pine Island Coll. in NY; WJW 3320) growing on *Alcyonidium* (the host of *Acrochaetium alcyonidii*) have been examined and found to agree in all essential respects with *Audouinella daviesii*. In light of these considerations, and because no other criteria of taxonomic significance are apparent (the presence of bisporangia, reported by Jao (1936) but not seen during this study, does not alone appear to be sufficient grounds for species separation), *Audouinella daviesii* and *Acrochaetium alcyonidii* are considered conspecific.

Acrochaetium amphiroae (Drew) Papenfuss has already been referred to the conspecificity of *Audouinella daviesii* (Woelkerling 1971); consequently the records of Doty (1948), Mathieson *et al.* (1969), South (1970), and Taylor (1957) are referred (at least as to name) to *A. daviesii*. None of the collections upon which these records are based, however, has been available for examination.

A number of collections of other investigators have been examined and apparently found not to contain plants of *A. daviesii*. Specimens which Harvey (1853, p. 243) referred to *Callithamnion daviesii* belong to *Colaconema secundata*. With one exception (see specimens examined listing), all the collections of Collins examined, both in FH and NY, including Phycotheca Boreali Americana Specimen No. 880, have been found not to contain plants of *A. daviesii* but rather plants referable to *Colaconema secundata*. Since there is a slight possibility that both taxa are present in Collins material, Collins references are listed with question marks in this account. The uncertainty over Collins material leads to uncertainty over the reported distribution of *A. daviesii* in the New England region; in addition to a number of stations in Massachu-

setts, *A. daviesii* is also definitely known from only one locality in Maine and one in New York as a result of the present study.

Plants from Nova Scotia referred to *Acrochaetium alcyonidii* (Edelstein *et al.* 1967) and *A. amphiroae* (Edelstein and McLachlan 1968) should be checked; one collection sent from Dr. Edelstein and identified as *A. alcyonidii* has been examined and found to contain only plants of *Colaconema membranacea* (Magnus) comb. nov. Likewise, the illustrations (Edelstein and McLachlan 1968, Figs. 49-50) of plants referred to *Acrochaetium amphiroae* leave considerable doubt as to their true relationship to *Audouinella daviesii.*

A number of specimens hitherto referred to *Acrochaetium sagraeanum* (Montagne) Bornet have been examined and found to be *Audouinella daviesii;* citations are appended. The type of *Acrochaetium sagraeanum* has been excluded from the Rhodophyta (see "Species Excludendae").

Massachusetts specimens collected by Collins in 1888 and 1895 from Marblehead, by Farlow in 1875 from Gay Head (Martha's Vineyard; host is *Cystoclonium*), and by Nott in 1895 from Butler's Point (Woods Hole) in FH and NY have been examined during this study and found to contain sexual plants of *Audouinella daviesii* and, in several instances, a plant or two of *Colaconema secundata.* In the literature, these collections have been referred erronously to *Chantransia corymbifera* (Collins 1896; Collins, Holden, and Setchell 1896, No. 192), *C. efflorescens* var. *thuretii* (Collins 1906, Davis 1913), and/or *Acrochaetium thuretii* (Taylor 1937, 1957). The vast majority of plants examined in the above populations contained numerous carposporophytes and very few monosporangia. In each case, however, the few monosporangia found tended to be arranged in axial clusters of 3-4 on branched stalks, and this is the characteristic arrangement found in *Audouinella daviesii.* In other respects these populations agree well with sexual plants collected during this study. For

additional information, see comments below under *Audouinella efflorescens*.

5. **Audouinella microscopica** (Naegeli In Kuetzing) Woelkerling 1971: 33, Figs. 10, 23A. 1972: 85 et seq., Figs. 1-14; 1973: 86. Figs. 46-51.

Acrochaetium microscopicum (Naegeli In Kuetzing) Naegeli 1861: 407, Figs. 24-25.

Callithamnion microscopicum Naegeli In Kuetzing 1849: 640.

Chantransia microscopica (Naegeli In Kuetzing) Batters In Schiffner 1916: 136, Figs. 13-18.

Chromastrum microscopicum (Naegeli In Kuetzing) Papenfuss 1945: 322.

Kylinia microscopica (Naegeli In Kuetzing) Kylin 1944: 13. Papenfuss 1947: 437.

Rhodochorton microscopicum (Naegeli In Kuetzing) Drew 1928: 151, 163.

Acrochaetium catenulatum Howe 1914: 84, pl. 31, Figs. 12-18.

Chantransia catenulata (Howe) DeToni 1924: 44.

Kylinia catenulata (Howe) Kylin 1944: 13.

Rhodochorton catenulatum (Howe) Nakamura 1941: 273, 280, Fig. 1.

Acrochaetium collopodum (Rosenvinge) Hamel 1927: 81; 1928: 175.

Chantransia collopoda (Rosenvinge) Rosenvinge 1909: 81.

Chromastrum collopodum (Rosenvinge) Papenfuss 1945: 320.

Kylinia collopoda (Rosenvinge) Kylin 1944: 13, 15, Fig. 6.

Acrochaetium compactum Jao 1936: 241, pl. 10, Figs. 6-14. Taylor 1937: 228, pl. 32, figs. 6-14.

Chromastrum compactum (Jao) Papenfuss 1945: 321.

Kylinia compacta Papenfuss 1947: 436. South 1970: 1. Taylor 1957: 212, pl. 32, Figs. 6-14.

Acrochaetium crassipes (Boergesen) Boergesen 1915: 20, Figs. 11-13. Boergesen 1927: 12, Fig. 5. Collins and

Hervey 1917: 96. Howe 1918: 511. Taylor 1941: 75.

Chantransia crassipes Boergesen 1909: 1, Fig. 1. Taylor 1928: 134, pl. 28, Fig. 16.

Chromastrum crassipes (Boergesen) Papenfuss 1945: 321.

Kylinia crassipes (Boergesen) Kylin 1944: 13. Taylor 1960: 300.

Acrochaetium microfilum Jao 1936: 240, pl. 10, Figs. 1-5. (Non *A. microfilum* Levring 1945: 12, Fig. 4. = *A. levringii* Papenfuss 1947: 436). Taylor 1937: 232, pl. 32, Figs. 1-5; 1957: 219, pl. 32, Figs. 1-5.

Acrochaetium moniliforme (Rosenvinge) Boergesen 1915: 22. Jao 1936: 241, pl. 10, Figs. 15-17. Taylor 1937: 227, pl. 32, Figs. 15-17.

Chantransia moniliformis Rosenvinge 1909: 99, Figs. 28-29.

Chromastrum moniliforme (Rosenvinge) Papenfuss 1945: 322.

Kylinia moniliformis (Rosenvinge) Kylin 1944: 13. South 1970: 1. Taylor 1957: 211, pl. 32, Figs. 15-17.

Rhodochorton moniliforme (Rosenvinge) Drew 1928: 151, 164.

Chantransia secundata auct. non. (Lyngbye) Thuret: Hauck and Richter 1892: 454.

Plants epiphytic, up to 100 μm tall exclusive of hairs; original spore persisting as a unicellular base slightly smaller to slightly larger than other cells. Filaments of erect system 1-4, commonly arcuate, simple or with a few secundly to irregularly arranged lateral branches. Cells barrel-shaped to cylindrical, 3-10 μm wide and 3-11 μm long, L/D 0.75-2; each cell containing a single parietal lobate to stellate chromoplast with one pyrenoid. Terminal hairs up to 40 μm long occur occasionally.

Monosporangia ovoid, 4-9 μm wide and 6-15 μm long, terminal or lateral, single or rarely in pairs, sessile or stalked, adaxially seriate or occasionally more scattered.

Other reproductive structures not observed in New England populations.

Type locality: Torquay, England.
Type: L, No. 940285 . . . 306.
Distribution: Nearly cosmopolitan.
Hosts: Chaetomorpha, Chordaria, Cladophora, Enteromorpha, Polysiphonia, and *Sphaerotrichia* in New England; a wide variety of algae and bryozoans elsewhere.

Specimens examined:
MASSACHUSETTS: Black Rock, Sconticut Neck, New Bedford, 25. VII. 1934, *Jao* (MICH, Woods Hole, No. 275, type of *Acrochaetium compactum* Jao). Cape Codder Point, Falmouth 19. XI. 1969, *Woelkerling* (WJW 2292). Norton Point, Martha's Vineyard, 3. VIII. 1934, *Jao* (MICH, Woods Hole, No. 280 [not 274 as reported by Jao 1936, p. 240], type of *Acrochaetium microfilum* Jao). West Falmouth Harbor, 17. X. 1970, *Woelkerling* (WJW 2826). Woods Hole (Nobska Point), 4. II. 1970, *Woelkerling* (WJW 2320).
ENGLAND: Torquay, 1845, Naegeli (L 940285 . . . 306, type of *Audouinella microscopica* (Naegeli) Woelkerling). Torquay, 1845, *Naegeli* (FH = Hauck and Richter 1892, No. 454, isotype of *A. microscopica,* which is labeled *Chantransia secundata*). Torquay, 1845, Naegeli (NY = Hauck and Richter 1892, No. 454, isotype of *A. microscopica,* which is labeled *Chantransia secundata*).

Audouinella microscopica is distinguished from other New England audouinelloid algae with a unicellular base 1) in commonly having cells isodiametric or broader than long; 2) in having a more or less globose basal cell protoplast that is not markedly flattened on the side in contact with the substrate; and 3) in having erect or ascending rather than procumbent filaments.

A detailed morphotaxonomic account of this species in New England and adjacent regions has recently appeared in the literature (Woelkerling 1972). To date this species has been collected only from Massachusetts along the New England coast, but it is known from Nova Scotia (Edelstein and McLachlan 1966, 1968; Edelstein et al. 1967; South and Cardinal 1970) and, therefore, is to be expected at intermediate points. Although collection data is incomplete, *A. microscopica* probably is present throughout the year and is to be sought on any older, epiphytized algae. Its microscopic size may account for its being generally overlooked.

6. **Audouinella saviana** (Meneghini) comb. nov. Figs. 56-60.

Acrochactium savianum (Meneghini) Naegeli 1861: 405. Feldmann 1942: 218. Hamel 1927: 41, 98, Fig. 32; 1928: 192; 1928a: 135, Fig. 32. Papenfuss 1945: 311; 1947: 435.

Callithamnion savianum Meneghini 1840: 511. J. Agardh 1851: 14; 1876: 6. Kuetzing 1849: 641.

Chantransia saviana (Meneghini) Ardissone 1883: 276 (pro parte). DeToni 1897: 68.

Chantransia efflorescens var. *thuretii* Bornet 1904: XVI, pl. 1.

Acrochaetium thuretii (Bornet) Collins et Hervey 1917: 98. Doty 1948: 263. Hamel 1927: 37, 97, Fig. 30. 1928: 191; 1928a: 131, Fig. 30. Kylin 1944: 21, Fig. 14. Papenfuss 1945: 311.

Audouinella thuretii (Bornet) Woelkerling 1971: 36, Figs. 12, 24; 1973: 88.

Chantransia thuretii Bornet. Collins 1900: 49 (nom. nud.).

Chantransia thuretii (Bornet) Kylin 1907: 119, Fig. 28. Rosenvinge 1909: 100, Figs. 30-33.

Rhodochorton thuretii (Bornet) Drew 1928: 171.

Acrochaetium sagraeaum auct. non. (Montagne) Bornet: Boergesen 1915: 35 (pro parte). Bornet 1904: XXI (pro parte). Collins 1905: 231 (pro parte); 1906: 192 (pro parte). Collins and Hervey 1917: 97. Collins, Holden, et Setchell 1917: 2181. Hamel 1927: 77, 99 (pro parte); 1928: 173, 191 (pro parte). Hylander 1928: 159 (pro parte) Jao 1936: 244 (pro parte). Papenfuss 1945: 311 (pro parte). Taylor 1937: 233 (pro parte); 1957: 220 (pro parte); 1960: 309 (pro parte).

Chantransia sagraeana auct. non. (Montagne) DeToni: DeToni 1924: 51 (pro parte).

Chantransia virgatula auct. non. (Harvey) Thuret In LeJolis: Collins 1900: 49 (pro parte). Collins, Holden, et Setchell 1895: 39. Hylander 1928: 158.

Plants partly to entirely epipytic, caespitose, up to 4 mm

tall; original spore non-persistent. Prostrate system composed of short, simple or branched filaments free from one another or united into an irregularly shaped pseudoparenchymateous disc. Erect filaments moderately to freely and irregularly branched. Cells cylindrical, (7-) 8-12 (-14) μm wide and 20-60 μm long [L/D 2-6(-8)] in main axes and laterals, sometimes tapering to 4-6 μm wide near the tips; each cell containing a single parietal lobate chromoplast and one pyrenoid. Unicellular hairs unknown.

Monosporangia ovoid, 10-15 μm wide and 18-27 μm long, sessile or stalked, single or in pairs, in a secund series along the laterals or more scattered. Tetrasporangia ovoid, 17-24 μm wide and 26-34 μm long, sessile or stalked, single or in pairs, scattered on the erect filaments.

Other reproductive structures not observed.

Type locality: Genoa, Italy.
Type: FL.
Distribution: Nearly cosmopolitan.
Hosts: A variety of algae and marine angiosperms.

Specimens examined:
MASSACHUSETTS: Sandwich Jetty (Cape Cod Canal), 13. X. 1970, *Woelkerling* (WJW 2818). West Yarmouth, 17. IX. 1969, *Woelkerling* (WJW 2253); 3. X. 1969, *Woelkerling* (WJW 2256). Waquoit Bay (Falmouth), 30. VI. 1969, *Conway* (WJW 1839); 15. IX. 1969, *Conway* (WJW 1840). Woods Hole (Eel Pond), 21. VII. 1970, *Wilce* (WJW 2753). Woods Hole (Nobska) 17. VII. 1970, *Woelkerling* (WJW 2722). Woods Hole, 1876, *Dudley* (WJW 3284).
FRANCE: Cherbourg, 1. IX. 1856, *Bornet* [PC, possibly the type of *Acrochaetium thuretti* (Bornet) Collins et Hervey].
ITALY: Genoa, (8. VI ?). 1839, *Meneghini* (FI, type of *Callithamnion savianum* Meneghini).

Audouinella saviana is distinguished from other New England audouinelloid algae of similar morphology in having a filamentous to pseudoparenchymatous prostrate system without an enlarged panduriform or pyriform cell and having the monosporangia solitary or in pairs on simple stalks rather than in clusters on branched stalks.

Audouinella saviana appears to be confined to the sublittoral and lowermost littoral in New England waters and

has been collected in June, July, September and October as an epiphyte on various algae including *Champia, Chondria,* and *Stilophora.* Tetrasporangial plants have been collected in October; sexual plants have not been found in New England waters, but are described in detail by Kylin (1907) and Rosenvinge (1909) [both as *Chantransia thuretii*]. Additional study may reveal that the species is present in New England during all or most of the year.

The vegetative system shows considerable variation in New England populations. In some cases, the prostrate system is quite reduced while in others it is comparatively robust. The L/D ratio of cells also varies considerably. In some plants, most cells are 4-8 diameters long; in others they are mostly 2-4 diameters long; and in still others they show a combination of both of the above (Figs. 57, 59-60).

Acrochaetium thuretii (Bornet) Collins et Hervey is here considered conspecific with *Audouinella saviana* after comparing specimens from the type collections of the two taxa. Material from FI and PC agree in all essential respects with one another and with New England populations (Table 4; also see Addendum).

Plants referable to *Audouinella saviana* appear to be widely distributed, but have usually been reported under the specific epithet "thuretti" while the epiphet "saviana" has persisted in relative obscurity. Hamel (1927, 1928a) attempted to distinguish the two taxa on the bases of presence or absence of sexual structures and on the relative L/D ratio of cells, but neither of these criteria appears systematically reliable.

A number of specimens hitherto referred to *Acrochaetium sagraeanum* (Montagne) Bornet have been examined and found to be *Audouinella saviana;* citations have been appended. The type specimen of *Acrochaetium sagraeanum* has been excluded from the Rhodophyta (see "Species Exludendae").

The literature references of Collins (1896, 1906), Collins, Holden, and Setchell (1896), Davis (1913), and Taylor (1937, 1957) to specimens under the names of *Chan-*

transia corymbifera, C. efforescenes var. *thuretii,* and/or *Acrochaetium thuretii* are based on misidentifications. These collections have been re-examined and found to contain plants of *Audouinella daviesii;* for further discussion, see the account of that species.

The relationships of *A. saviana* to a number of taxa of similar morphology await clarification. These include *Acrochaetium avrainvillae* Boergesen (1915, p. 48, Figs. 47-49), *A. hypneae* Boergesen (1909), and *A. pallens* (Zanardini) Naegeli (See Hamel 1927, p. 48). All of these taxa appear to be very similar to *Audouinella saviana* and a comparison of type collections may show some or all to be conspecific.

The precise publication date of Meneghini's original diagnosis of *Callithamnion savianum* requires further comment. The issue of Flora (Regensburg) containing the diagnosis is dated 28 August 1840; however reference is made on p. 511 of that issue to prior publication of diagnosis on 23 May 1840 in a Pisa "Giornale" (= journal?, newspaper?).

Copies of a three page type-set document dated 23 May 1840 which resemble a journal reprint and are entitled "Lettera del Prof. Giuseppe Meneghini at Dott. Jacob Corinaldi a Pisa" are located at FI and PC (Dr. Paul Silva, personal communication) ; Prof. Peter S. Dixon has kindly sent me a photocopy of the PC document. Hamel (1927, 1928) also has made reference to this document. The PC copy unfortunately provides no clues as to the original place of publication other than three words — "Pisa Tipografia Prosperi" — written in longhand at the bottom of the first page, and until further light can be shed on the matter of its original place of publication (if, indeed, there was one), it seems wise to continue to refer to the "Flora" article when citing Meneghini's original diagnosis of *Callithamnion savianum* since the wording of the diagnosis in "Flora" is identical to that in the PC document.

7. **Audouinella unifila** (Jao) comb. nov. Figs. 44-45.
Acrochaetium unifilum Jao 1936: 239, pl. 10, Figs. 26-32.

Taylor 1937: 228, pl. 32, Figs. 26-32. Non. *A. unifilum* Levring 1953: 472, Fig. 9 (= *Colaconema nakamurai* Woelkerling 1971: 46, Fig. 16).

Chromastrum unifilum (Jao) Papenfuss 1945: 322.

Kylinia unifila (Jao) Papenfuss 1947: 437. Taylor 1957: 212, pl. 32, Figs. 26-32.

Audouinella australis (Levring) Woelkerling 1971: 25, Figs. 4-5.

Kylinia australis Levring 1953: 487, Figs. 21A-C. Boney and White 1967: 595.

Plants epiphytic, up to 150 μm tall; original spore persisting as a hemispherical unicellular base appressed to the substrate and usually giving rise to a single erect filament. Erect filament(s) procumbent to semi-upright, simple or rarely with 1-2 celled laterals. Cells cylindrical, 6-8 μm wide and 8-20 μm long, L/D 1-3, each cell containing a single parietal lobate to stellate (Jao 1936) chromoplast and one pyrenoid. Terminal and pseudolateral hairs up to 50 μm long occur.

Monosporangia ovoid, 5-7 μm wide and 8-14 μm long, sessile or occasionally on unicellular stalks, scattered along the erect filament(s).

Other reproductive structures not observed in New England populations.

Type Locality: Norton Point, Martha's Vineyard, Massachusetts.

Type: MICH, Woods Hole No. 274.

Distribution: Massachusetts; South Australia.

Hosts: Arthrocladia villosa Duby, *Audouinella* sp.

Specimens examined:

MASSACHUSETTS: Norton Point (Martha's Vineyard), 3. VIII. 1934, *Jao* (Michigan, holotype).

AUSTRALIA: Pennington Bay (Kangaroo Island), 7. II. 1947, *Womersley* (ADU, A31373, isotype of *Kylinia australis* Levring). Note: Other Australian collections examined are cited in an earlier paper (Woelkerling, 1971, p. 26).

Audouinella unifila is distinguished from other New England audouinelloid algae with a unicellubar base by

the procumbent development of erect filaments and the characteristically flattened (compressed) hemispherical basal cell.

The one known New England collection of this taxon is the type collection, plants of which are on the permanent slides in MICH. Only monosporangial specimens occur, and the range of cell and spore dimensions of these plants is somewhat greater than reported originally by Jao (1936). Chromoplasts were not recognizable, but at least one pyrenoid was observed.

Critical comparisons of the type collections of *A. unifila* and *A. australis* strongly indicate that the two taxa are conspecific. Monosporangial plants of both taxa show virtually identical ranges of cell and spore dimensions and in general have the same habit. Apparent differences in chromoplast shape (Jao, 1936, reported stellate plastids in *A. unifila;* Levring (1953) recorded parietal plastids in *A. australis*) do not appear to be taxonomically significant (see Woelkerling 1971, p. 14). Woelkerling (1971, p. 26) previously noted similarities in the two taxa.

Although sexual plants do not occur in the type collection, this taxon is referred to *Audouinella* on the basis of the rather common occurrence of sexual plants in South Australian populations.

Some questions may be raised as to the relationships between *Audouinella unifila* and *A. microcopica.* The author's experience to date indicates that the two have quite distinct basal cells and modes of erect filament development, and no intermediates have been observed. However, the possibility exists that such intermediates do occur and they should be watched for.

COLACONEMA Batters

Colaconema Batters 1896: 8. Woelkerling 1971: 40. Non *Colaconema* Schmitz In Schmitz and Falkenberg 1897: 452.

Note: Species not referable to *Colaconema* have been placed in the past in *Acrochaetium, Audouinella, Calli-*

thamnion, Ceramium, Chantransia, Chromastrum, Kylinia, Rhodochorton, and/or *Trentepohlia.*

Plants epibiotic, endobiotic, or saxicolous; attached to or suspended in the substrate by a single-celled holdfast or more commonly by a prostrate system of simple or branched filaments, which may or may not become pseudoparenchymatous. Erect filaments, when present, simple or branched, up to 10 mm tall; cells containing one to a number of variously shaped chromoplasts with or without pyrenoids.

Asexual reproduction by sessile or stalked monosporangia, bisporangia, tetrasporangia, and/or multipartite sporangia borne on the erect and/or prostrate filaments.

Sexual reproduction unknown.

Type Species: Colaconema bonnemaisoniae Batters.

Section I

The species in this section are not known to contain pyrenoids in their chromoplasts.

8. **Colaconema membranacea** (Magnus) comb. nov. Figs. 64-65.

Audouinella membranacea (Magnus) Papenfuss 1945: 326; 1947: 438. Edelstein and McLachlan 1966a: 1052. Taylor 1957: 224, pl. 31, Figs. 11-12.

Callithamnion membranaceum Magnus 1874: 67, tab. II, Figs. 7-15. Collins 1883: 56; 1888: 10.

Rhodochorton membranaceum (Magnus) Hauck 1885: 69 (only as to binomial). Collins 1894: 230; 1900: 51, 1911: 280. Collins, Holden and Setchell 1895a: 99. Davis 1913: 818. DeToni 1903: 1513. Drew 1928: 186. Hamel 1927: 59, 109, Fig. 39A-E; 1928: 202; 1928a: 152, Fig. 39A-E. Hauck and Richter 1888: 154. Hylander 1928: 169. Kuckuck 1897: 337 et seq., Figs. 1-7. Taylor 1937: 240, pl. 31, Figs. 11-12.

Plants endozoic; original spore non-persistent. Prostrate system consisting of irregularly branched filaments of

indefinite length which may be free from one another or pseudoparenchymatously united into a sheet-like endozoic thallus. Cells of prostrate filaments cylindrical to irregular in shape, 8-60 μm long, and 5-11 μm wide, L/D 0.75-5(-8); each cell containing several to many discoid or irregularly shaped chromoplasts (sometimes becoming more or less spirally twisted) without pyrenoids. Erect filaments, when present, simple or sparingly and irregularly branched, rarely more than 25 cells long. Cells 10-45 μm long and 7-13 μm wide, L/D 1-4.

Tetrasporangia ovoid to globose, 10-15 μm wide and 16-25 μm long, solitary, sessile or occasionally stalked, terminal or rarely lateral on erect filaments or on prostrate filaments.

Type locality: Store Baelt Channel, between Sporogoe Island and Korsoer, Denmark.

Type: ?

Distribution: Europe and cooler waters of both coasts of North America.

Hosts: A variety of marine invertebrates, especially hydroids.

Specimens examined:

CONNECTICUT: Charles Island (Milford Channel), 22. IV. 1889, *Holden* (NY).

MAINE: Eagle Island, VII. 1894, *Collins* (NY).

MASSACHUSETTS: Brandt Point (Marshfield), 7. IV. 1968, *Greenwich* (NHA). Gay Head (Martha's Vineyard), 3. VIII, 1948, *Doty* (U. Hawaii). Marblehead, 30. V. 1884, *Collins* (NY). Martha's Vineyard, 16. VII. 1941, *Taylor* (FH). Nahant, 14. V. 1882. *Collins* (NY); 1. V. 1970, *Woelkerling* (WJW 2545). Revere Beach (Boston), IV. 1885, *Collins* (NY); 29. V. 1886, *Collins* (NY, FH = Hauck and Richter 1888, No. 154); 10. VI. 1894, *Collins* (NY). Sandwich Jetty (Cape Cod Canal), 13. X. 1970, *Woelkerling* (WJW 2812). Sconset Beach, 13. VIII. 1886, *Collins* (NY). Scusset Beach, 29. III. 1969, *LaPlante* (UNH). Woods Hole, 7. IV. 1968, *Logan* (NHA); 6. IV. 1968, *Kastelowitz* (NHA).

NEW HAMPSHIRE: Cedar Point (Dover), 21. XII. 1966, *Hehre* and *Conway* (NHA); 3. III. 1967 *Hehre* (NHA). Hilton Park (Dover Point), 19. III. 1967, *Hehre* and *Conway* (NHA); 27. IV. 1967, *Hehre* and *Stone* (NHA). Rye Ledge, 5. II. 1970, *Woelkerling* (WJW 2336).

NEW YORK: Montauk Point (Long Island), 20. I. 1970, *Woelkerling* (WJW 2258).

Colaconema membranacea is distinguished from other New England audouinelloid algae in having several to many irregular to discoid to spiral chromoplasts without pyrenoids and in having solitary tetrasporangia that are borne in a sessile condition or on simple stalks rather than in clusters on branched gonimoblast filaments. In addition, this species is known to occur only as an endozoophyte in hydroids and several other types of invertebrates, and while this in itself is no criterion of specific distinction, it can serve as a useful ecological guide for identification purposes.

Colaconema membranacea has been collected throughout the year in New England waters and commonly occurs on hydroids in both the intertidal zone (especially hydroids attached to *Ascophyllum* or *Fucus* in shaded habitats) and the sublittoral zone. Often the hydroids become reddish as a result of the algal infestation.

Among New England populations, the nature of the vegetative system varies considerably. In lightly infested host animals, the prostrate filaments tend to remain largely free from one another, but under more crowded conditions, the prostrate system becomes pseudoparenchymatous and all traces of a filamentous character are lost (Fig. 64). In most populations the erect system is entirely suppressed and sporangia, when present, are borne directly on the prostrate filaments. In a few instances, however, the erect systems were more highly developed and consisted of branched filaments up to 750 μm long.

The nature of the life cycle of this species awaits clarification by means of culture studies, and until such time, it is difficult to suggest definite relationships between *C. membranacea* and other audouinelloid algae. Thus, for example, *Rhodochorton concrescens* (see West 1970a) and *Audouinella purpurea* (see West 1969, 1970) share a number of morphological features with *Colaconema membranacea,* but apparently they have quite different types of life cycles.

The relationships of *C. membranacea* to *Callithamnion entozoicum* Reinsch in Giard (1890) are discussed under the latter species in the section on Species Inquirendae.

Section II

Species in this section have chromoplasts each with only one pyrenoid.

9. **Colaconema humilis** (Rosenvinge) Woelkerling 1971: 44, Figs. 15J-O. Figs. 66-73.

Acrochaetium humile (Rosenvinge) Boergesen 1915: 23. Baardseth 1941: 41. Jorde et Klavestad 1963: 76. Kylin 1944: 22, Fig. 17. Levring 1953: 478. Schiffner 1931: 143. Sundene 1953: 185.

Chantransia humilis Rosenvinge 1909: 117, Figs. 44, 45. Boergesen 1927: 21. Levring 1935: 37, Figs. 7F-S; 1937: 89; 1940: 78, Figs. 23A-B; 1942: 8.

Chromastrum humile (Rosenvinge) Papenfuss 1945: 323.

Kylinia humile (Rosenvinge) Papenfuss 1947: 437.

Rhodochorton humile (Rosenvinge) Drew 1928: 151, 169.

Acrochaetium radiatum Jao 1936: 246, pl. 10, Figs. 18-25. Edelstein et al. 1967: 196. Papenfuss 1945: 310. South and Cardinal 1970: 2079. Taylor 1937: 237, pl. 32, Figs. 18-25; 1957: 223, pl. 32, Figs. 18-25.

Plants epiphytic, up to 60 μm tall exclusive of hairs; developing from septate or occasionally aseptate spores. Prostrate system consisting of 2-6 simple or sparsely branched filaments up to 300 μm long, arising from the spore and creeping or forming an irregular, more or less pseudoparenchymatous disc. Cells of prostrate filaments cylindrical or occasionally somewhat subglobose, 6-14 μm long and 4-8 μm wide, L/D 1-2; each cell containing a single chromoplast and one pyrenoid. Erect filaments absent to numerous, simple or sparsely irregularly branched, generally less than 10 cells long; cell dimensions similar

to those of prostrate filaments. Unicellular hairs up to 100 μm long occur.

Monosporangia ovoid, 7-14 μm long and 5-8 μm wide, solitary or occasionally in pairs, sessile or stalked, scattered on prostrate or erect filaments.

Other reproductive structures unknown.

Type locality: Spodobjerg, Langeland, Denmark.

Type: C.

Distribution: Massachusetts; Nova Scotia; Australia; Atlantic and Mediterranean shores of Europe.

Hosts: Ectocarpus and *Polysiphonia* in North America; a variety of algae elsewhere.

Specimens examined:

MASSACHUSETTS: Norton Point (Martha's Vineyard), 3. VIII. 1934, *Joa* (MICH, Woods Hole No. 280, type of *Acrochaetium radiatum* Jao). West Falmouth (Harbor), 3. X. 1970, *Woelkerling* (WJW 2767). West Yarmouth, 12. XII. 1969, *Woelkerling* (WJW 2259). Woods Hole (Nobska Point), 26. VI. 1969, *Conway* (WJW 1838); 4. II. 1970, *Woelkerling* (WJW 2329).
NOVA SCOTIA: Ketch Harbor, 31. V. 1965, *Edelstein* (Herb. Nat. Res. Coun., Halifax).

Colaconema humilis can be distinguished from other New England audouinelloid algae by the following combination of features (as found in the collections examined): 1) A reduced erect system with most filaments of 10 or fewer cells; 2) Cells of erect and prostrate filaments mostly less than two diameters long; and 3) Prostrate system more or less compact; filaments rarely over 500 μm long. The first and third criteria probably do not represent very soundly based systematic characters, but until they can be re-examined in light of additional New England and other collections, they have been offered as useful guides for species recognition in this instance.

C. humilis is known in New England waters from collections made in February, June, August, October, and December. Edelstein et al. (1967) report it from May

through September in Nova Scotia, and judging from this, it seems reasonable to think that it may occur throughout the year in this region.

The erect system varies considerably and may be suppressed altogether (Fig. 67), consist of a few several celled filaments (Figs. 69-70), or of a number of short rather densely crowded filaments (Fig. 73). Likewise the extent of the prostrate system varies according to available substrate space; on the finely filamentous *Ectocapus,* it consists of a very few cells (Fig. 71) but on a larger species of *Polysiphonia* it can spread out more (Fig. 73). Most germinating spores divide into two distinct daughter cells (Fig. 68) but others do not (Fig. 66). Chromoplasts have not been observed; Jao (1936) reports a parietal plastid, Rosenvinge (1909) found a stellate plastid, and Woelkerling (1971) found a variable plastid shape.

Several investigators (e.g. Baardseth 1941, p. 41; Woelkerling 1971, p. 45) have commented upon the possible conspecificity of a number of audouinelloid algae whose morphology is similar to *Colaconema humilis.* On the basis of the examination of the type and other populations, *Acrochaetium radiatum* Jao has been referred to the synomomy of *Colaconema humilis.* Jao (1936, p. 247) separated the two taxa on the basis of the former ". . . having more than two main filaments arising from the divided germinating spore and all the filaments arranged radiately and densely from the center of a fully developed thallus." The type collection of *Acrochaetium radiatum,* however, contains plants that have 2 as well as more than two filaments emanating from the germinating spore (Fig. 68), and has plants that are not densely radiate (Fig. 69) as well as ones that are (see Jao, 1936, pl. 10, Figs. 22-25). Thus the criteria of specific distinction offered by Jao do not appear to be taxonomically reliable, and the two taxa can be considered conspecific.

The relationships of *Colaconema humilis* to a number of similar taxa (see Baardseth 1941, p. 41 and Woelkerling

1971, p. 45 for names) remains unclear, but there is increasing doubt as to whether many of these are really distinct species. In the Nova Scotia population examined during this study, plants with varying degrees of erect system development occur side by side and agree morphologically with one or several of the taxa cited by Baardseth (1941) and/or Woelkerling (1971). Similar variation occurs among the New England populations. Final clarification must await a comparison of the various type collections (which in many cases represent the only reported collections), but is seems likely that a number of these taxa will eventually be reduced to synonomy.

10. **Colaconema minima** (Collins) comb. nov. Figs. 74-76.

Acrochaetium minimum Collins 1908: 133. Collins, Holden, and Setchell 1908: 1493. Davis 1913: 813. Hamel 1927: 89; 1928: 183. Papenfuss 1945: 316. Taylor 1937: 237; 1957: 222.

Chantransia minima (Collins) Collins 1911a: 186. DeToni 1924: 62.

Acrochaetium emergens (Rosenvinge) Weber van Bosse 1921: 194. Hamel 1927: 93; 1928: 186. Jao 1936: 247, pl. 13, Figs. 7, 7B. Papenfuss 1945: 314. Taylor 1937: 235; 1957: 221.

Chantransia emergens Rosenvinge 1909: 128, Fig. 55. DeToni 1924: 67.

Rhodochorton emergens (Rosenvinge) Drew 1928: 151, 188.

Plants epi- to endophytic; sporelings not observed. Prostrate system consisting of irregularly branched filaments of indefinite length creeping on the surface or between the superficial cells of the host. Cells of prostrate filaments cylindrical to irregular in shape, 5-25 (-44) μm long and 3-8 (-14) μm wide, L/D 1-6 (-8); each cell containing a parietal chromoplast and one pyrenoid. Erect filaments 1-5 (-25) cells long, simple or with a few short, irregularly

arranged laterals; cell dimensions similar to those of prostrate filaments.

Unicellular hairs not observed.

Monosporangia ovoid to globose to hemispherical, 5-12 μm long and 4-10 μm wide, solitary or occasionally in pairs, sessile or on 1-2 celled stalks, scattered on the prostrate or erect filaments.

Other reproductive structures unknown.

Type locality: Robinson's Hole, Elizabeth Islands, Massachusetts.

Type: FH.

Distribution: Massachusetts; Denmark; Norway.

Hosts: Asparagopsis, Desmarestia, Polysiphonia.

Specimens examined:
MASSACHUSETTS: Robinson's Hole (Elizabeth Islands), VIII. 1907, *Collins* (FH, type); (WIS, isotype). [Isotypes have been distributed as No. 1493 in Collins, Holden, and Setchell (1908).] Sandwich Beach (Cape Cod Canal), 30. VI. 1970, *Wilce* (WJW 2693); 11. VII. 1970, *Woelkerling* (WJW 2699).
DENMARK: Mollegrund (Hirshals), 8. VIII. 1899, *Rosenvinge* (C, Algae Marinae Danicae No. 6574, type of *Chantransia emergens* Rosenvinge).

As circumscribed here, *Colaconema minima* can be distinguished from other New England audouinelloid algae by the following combination of features: 1) A prostrate system of indefinite length bearing no or short (1-5 (-25)) celled erect filaments, 2) Sporangia under 15 μm long and 12 μm wide; 3) Cells with single chromoplasts with one pyrenoid each; commonly over two diameters long.

Colaconema minima is known from three Cape Cod, Massachusetts collections. The type and the WIS isotype of the species consist of dried specimens that have proven difficult to work with because of the matted and rather unresponsive (to resoaking and slide making) condition. Nevertheless it has been possible to study and illustrate (Fig. 75) a portion of type material. Cells up to 15 μm long and 7 μm wide and spores up to 11 μm long and

6 μm wide have been found and thus extend the maximum limits recorded for this material by Collins (1908) and Taylor (1937, 1957). Erect filaments of more than 8 cells and cells over 6 diameters long were not encountered.

The two other collections were found growing on *Asparagopsis* and showed over all agreement with the type, although a number of cells were over 15 μm long and sporangia occurred on both prostrate and erect filaments. The relationship of these collections to *Colaconema americana* Jao is discussed under that taxon, which is regarded here as a "Species Inquirendae."

Critical comparisons of the type collections of *C. minima* and *Chantransia emergens* Rosenvinge (1909, p. 128, Fig. 55) have resulted here in regarding the two taxa as conspecific. They agree in all essential respects (Figs. 74-76; Table 5). Jao (1936, p. 247, pl. 13, Figs. 7, 7B) recorded the latter from New England waters, and Taylor (1937, p. 226; 1957, p. 217) separated it from *Colaconema minima* on the basis of slight differences in spore width. A comparison of the type collections indicates that this apparent difference is of no taxonomic significance since spores 3-5 μm wide occur in both taxa.

The relationships of *Colaconema minima* to other audouinelloid algae of similar morphology require considerable clarification. *Acrochaetium endophyticum* Batters (1896, p. 386; see also Baardseth 1941, p. 45, Figs. 19E-G) [non *Rhodochorton endophyticum* Kylin 1907, p. 188, Fig. 40 = *Acrochaetium kylinii* Hamel 1927, p. 93; 1928, p. 187 [nec *Liagorophila endophytica* Yamada 1944, p. 16, Fig. 4 (see also Abbott 1966)] appears to have a virtually identical morphology, and when the types can be compared, the two taxa will almost certainly prove to be conspecific, with the specific epithet "endophyticum" having priority. Likewise *Colaconema americana* Jao and a number of other similar taxa almost certainly will be relegated to conspecificity when critical comparisons of types can be made.

11. **Colaconema secundata** (Lyngbye) Woelkerling 1973: 94, Figs. 7-8. Figs. 77-83.[1]

Callithamnion daviesii var. *secundatum* Lyngbye 1819: 129, pl. 41, Figs. β4-6.

Acrochaetium luxurians (J. Agardh) Naegeli 1861: 405.

Callithamnion luxurians J. Agardh 1851: 14. Hall 1876: 111. Harvey 1853: 242. Jordan 1874: 197; 1874a: 488.

Chantransia luxurians (J. Agardh) Kylin 1907: 117, Fig. 26.

Acrochaetium secundatum (Lyngbye) Naegeli 1861: 405. Collins 1906: 194. Davis 1913: 813; 1913a: 477. South 1970: 1. South and Cardinal 1970: 2079. Taylor 1937: 230, pl. 31, Figs. 1-3.

Callithamnion secundatum (Lyngbye) C. Agardh 1828: 187.

Ceramium secundatum (Lyngbye) C. Agardh 1824: 132.

Chantransia secundata (Lyngbye) Thuret In LeJolis 1863: 106. Collins 1900: 49; 1911: 276. Collins, Holden, and Setchell 1903: 1088. Davis 1913a: 462, 473, 474. Farlow 1875: 376; 1876: 705. Hylander 1928: 158. Kylin 1910: 28.

Chromastrum secundatum (Lyngbye) Papenfuss 1945: 323.

Kylinia secundata (Lyngbye) Papenfuss 1947: 437. Edelstein and McLachlan 1966a: 1052, Fig. 18. Hehre and Mathieson 1970: 206, 237. Mathieson et al. 1969: 132. Taylor 1957: 214, pl. 31, Figs. 1-3.

Acrochaetium subsimplex Levring 1953: 473, Figs.

[1]According to the "Programme and Abstracts of the Twenty-first Annual Meeting of the British Phycological Society" (3-5 January 1973), W. J. Borsje, Vrije University, Amsterdam, reported sexual stages of *Acrochaetium virgatulum* in culture. If his plants are the same as New England plants (which, no doubt, will prove to be the case), *Colaconema secundata* (syn. *Acrochaetium virgatulum*) will then be transferred to the genus *Audouinella* as *A. secundata* (Lyngbye) comb. nov. Borsje's abstract also appears in *Br. phycol. J.* 8: 204-5, 1973.

10A-D, 11. Non *Rhodochorton subsimplex* (Harvey) DeToni 1897: 1515.

Acrochaetium tenuissimum (Collins) Papenfuss 1945: 319.

Chantransia tenuissima (Collins) Kylin 1941: 5, Figs. 1e, f.

Colaconema tenuissima (Collins) Woelkerling 1971: 51, Fig. 21.

Rhodochorton tenuissimum (Collins) Drew 1928: 170, pl. 38, Figs. 26, 27.

Acrochaetium virgatulum (Harvey) Bornet 1904: XXII. Collins 1906: 193. Davis 1913: 813; 1913a: 477. Doty 1948: 264. Edelstein et al. 1970: 625. South and Cardinal 1970: 2079. Taylor 1937: 230. Taylor In Lewis 1924: 214.

A. virgatulum f. *luxurians* (J. Agardh) Collins 1906: 194. Collins, Holden, and Setchell 1906: 1393. Hylander 1928: 159. Taylor 1937: 230, pl. 31, Figs. 4-7.

A. virgatulum f. *tenuissimum* (Collins) Collins 1906: 194.

Callithamnion virgatulum Harvey In Hooker 1833: 349. Jordan 1874a: 17.

Chantransia virgatula (Harvey) Thuret In LeJolis 1863: 106. Collins 1880: 162; 1894: 233; 1900: 49; 1911: 276. Davis 1913a: 462, 473, 474. Farlow 1875: 376; 1876: 705. Farlow, Anderson, and Eaton 1881: 157. Grier 1925: 296. Jelliffe 1904: 98. Hylander 1928: 158. Kylin 1910: 28. Rosenvinge 1909: 109, Figs. 37-41.

C. virgatula var. *luxurians* (J. Agardh) Rosenvinge 1909: 110. Collins 1911: 276.

C. virgatula f. *tenuissima* Collins In Collins, Holden, and Setchell 1900: 741.

Chromastrum virgatulum (Harvey) Papenfuss 1945: 323. Doty 1948: 264.

Kylinia virgatula (Harvey) Papenfuss 1947: 437. Hehre and Mathieson 1970: 206, 237. Mathieson et al. 1969: 132. Taylor 1957: 214.

K. virgatula f. *luxurians* (J. Agardh) Collins 1906: 194.

Hehre and Mathieson 1970: 206, 237. Taylor 1957: 214, pl. 31, Figs. 4-7.

Rhodochorton virgatulum (Harvey) Rosenvinge 1935: 7.

Trentepohlia virgatula (Harvey) Farlow 1881: 109, pl. X, Fig. 3. Collins 1888: 312; 1888a: 10. Martindale 1889: 100. Pike 1886: 109.

T. virgatula var. *secundata* (Lyngbye) Farlow 1881: 109. Pike 1886: 109.

Acrochaetium daviesii auct. non. (Dillwyn) Naegeli: Collins 1906: 194 (pro parte?).

Callithamnion daviesii auct. non. (Dillwyn) Lyngbye: Harvey 1853: 243.

Chantransia daviesii auct. non. (Dillwyn) Thuret In LeJolis: Collins 1880: 162 (pro parte?); 1894: 233 (pro parte?); 1900: 49 (pro parte?); 1911: 276 (pro parte?).

Trentepohlia daviesii auct. non. (Dillwyn) Pringsheim: Pringsheim 1862: 26, Taf VIII, Figs. 1-6.

Acrochaetium flexuosum auct. non. Vickers: Collins 1906: 192. Collins, Holden, and Setchell 1910: 1696. Taylor 1937: 233; 1957: 219.

Chantransia flexuosa auct. non. (Vickers) Collins: Collins 1911: 186.

Acrochaetium sagraeanum auct. non. (Montagne) Bornet: Boergesen 1915: 35 (pro parte). Bornet 1904: XXI (pro parte). Collins 1905: 231 (pro parte); 1906: 192 (pro parte). Hamel 1927: 77, 99 (pro parte); 1928: 173, 191 (pro parte). Hylander 1928: 159 (pro parte) Jao 1936: 244 (pro parte). Papenfuss 1945: 311 (pro parte). Taylor 1937: 233 (pro parte); 1957: 220 (pro parte); 1960: 309 (pro parte).

Chantransia sagraeana auct. non. (Montagne) DeToni: 1924: 51 (pro parte).

Plants epiphytic or epizoic, caespitose, up to 3 mm tall; original spore non-persistent. Prostrate system at first forming a small parenchymatous disc usually composed of a central cell and 3-4 peripheral cells; later proliferating in some plants to form a unistratose (rarely a partially bistratose) pseudoparenchymatous disc. Erect filaments sparsely

or moderately to freely and irregularly branched; laterals of variable length and some populations only 1-5 cells long. Cells cylindrical 8-15 (-20) μm wide and 15-100 μm long, L/D (1-) 2-6; each containing an axial or parietal stellate chromoplast and a central pyrenoid. Unicellular hairs up to 300 μm long abundant in some populations,, pseudolateral or terminating 1-3 celled lateral branches; sparse or absent in other populations.

Monosporangia ovoid, 10-20 μm wide and 15-26 (-32) μm long, solitary or in pairs, sessile or stalked, scattered on the erect filaments or sometimes densely crowded on short lateral branches.

Other reproductive structures not observed.

Type locality: Kvivig, Faeroes Islands (on *"Conferva rupestris"*).

Holotype: C.

Distribution: Atlantic Coast of North America, Australia, Canary Islands, Europe, Sargasso Sea.

Hosts: A wide variety of algae and on hydroids.

Specimens examined:

CONNECTICUT: Black Rock Beacon (Long Island Sound), 20. VII. 1892, *Holden* (NY, Holden 646) New Haven, prior to 1853, *Hooper* (TCD). Woodmont, 27. VII. 1893, *Holden* (NY).

MAINE: Eagle Island (Penobscot Bay), 16. VII. 1905, *Collins* (NY). Fox Island, VIII. 1880, *Collins* (NY). Inner Mark Island, 8. VII. 1903, *Collins* (NY, PBA 1088). Kennebec River Mouth, VIII. 1880, *Booth* (NY). Peak's Island, IX. 1874, *Farlow* (FH).

MASSACHUSETTS: Eastham, 10. VII. 1907, *Collins* (NY). Falmouth (Cape Codder Point), 30. X. 1966, *Conway* et al. (NHA); 19. XI. 1969, *Woelkerling* (WJW 2237); 7. I. 1970, *Conway* (WJW 2294). Falmouth (Monauhant Beach), 12. III. 1969, *Conway* (WJW 1850); (WJW 1851). Falmouth (Waquoit Bay), 21. I. 1969, *Conway* (WJW 1842); 11. III. 1969, *Conway* (WJW 2273); 30. VI. 1969, *Conway* (WJW 2274); 7. VII. 1969, *Conway* (WJW 1845); 15. IX. 1969, *Conway* (WJW 1844); 1. X. 1969, *Conway* (WJW 1841). Gloucester (Niles Beach), IX. 1875, *Farlow* (FH); no date, *Farlow* (NY, Algae Exsic. Am. Bor. — Farlow, Anderson, and Eaton, No. 157). Hingham, prior to 1853, *Brewer* (TCD). Marblehead, 17. VI. 1902, *Collins* (NY). Mattapoisett, 30. V. 1905, *Collins* (NY); 20. X. 1906, Collins (NY, PBA 1393). Nantucket (Brauts Point), 16. VIII. 1898, *Collins* (NY). Nantucket (West Jetty, Nant. Center), 14. IV. 1970, *Woelkerling* (WJW 2476). Nantucket (?), prior to 1853, Durkee (TCD). New Bedford (Scontient Point),

13. VII. 1927, *Taylor* (NY). Penikese Island, 1. X. 1970. *Woelkerling* (WJW 2808). Sandwich (Cape Cod Canal Jetty), 7. IV. 1968, *Kastelowitz* (NHA); 13. X. 1970, *Woelkerling* (WJW 2816). West Falmouth (Harbor entrance), 10. XII. 1969, *Conway* (WJW 2131); 6. I. 1970, *Woelkerling* (WJW 2276). Woods Hole, VII. 1875, *Farlow* (FH); VII. 1903, Collins (NY); 10. VIII. 1947, *Abbott* (Abbott 1638); 3. VI. 1966, *Conway* (WJW 2168); 4. II. 1970, *Woelkerling* (WJW 2316); 2. VII. 1970, *Woelkerling* (WJW 2680); 29. I. 1971, *Woelkerling* (WJW 3299); 16. II. 1971, *Woelkerling* (WJW 3315).
NEW HAMPSHIRE: Fort Constitution, 20. IX. 1966, *Conway* and *Hehre* (NHA). Fox Point, 21. VII. 1966, *Conway* and *Shipman* (NHA). Great Boar's Head, 15. X. 1966, *Hehre* and *Conway* (NHA); 11. XII. 1966, *Hehre* and *Conway* (NHA). Little Boar's Head, 14. IX. 1966, *Hehre* (NHA); 25. XI. 1966, *Conway* and *Hehre* (NHA). Rye Ledge, 29. III. 1967 *Mathieson* and *Murphy* (NHA).
NEW JERSEY: Atlantic City, 16. IV. 1892, *Morse* (NY, No. 1696 in the Phycotheca Boreali Americana); 1. IX. 1925, *Rose* (NY).
NEW YORK: Cold Spring Harbor, 21. VII. 1893, Howe (?) (NY). Little Neck Bay (Long Island), 7. IV. 1966, *Keenan* (NHA).
RHODE ISLAND: Napatree Point, 9-11. X. 1872, *Eaton* (NY); (FH).
CALIFORNIA: San Pedro, XI. 1898, *Monk* (FH, type of *Chantransia virgatula* F. *tenuissima* Collins; ADU A32706, isotype; NY, isotype; WIS, isotype).
EUROPE: England (Torquay), prior to 1833, *Griffiths* (TCD, type of *Acrochaetium virgatulum* (Harvey) Bornet). Faeroes Islands (Kvivig), 19. VI. 1817, ? (C, Herb. Lyngbye, type). Sweden (Kattegat Channel), no date, ? (LD 35117, type of *Callithamnion luxurians* J. Agardh).
AUSTRALIA: Musselroe Bay (Tasmania), 7. II. 1948, *Levring* (ADU, A19846, isotype of *Acrochaetium subsimplex* Levring).

Colaconema secundata is distinguishable from other New England audouinelloid algae in 1) having spores germinating to form a distinctive, orbicular parenchymatous group of cells (Fig. 77) which later may proliferate (Figs. 80-81), and in 2) having distinctly stellate chromoplasts (Fig. 83), each with one pyrenoid, in cells of the erect filaments. In addition, most, but not all, New England populations possess a somewhat twiggy (virgate) habit as a result of having numerous 1-3 (-5) celled lateral branches terminated by unicellular hairs (Fig. 82).

Colaconema secundata occurs throughout the year in New England on a variety of algae or invertebrates in the sublittoral, and occasionally appears in the lower littoral,

particularly on *Porphyra*. It probably is found in greater numbers than any other audouinelloid alga in New England waters and most frequently is encountered as a dense fringe on blades of the sea grass *Zostera*.

Rosenvinge (1909) has provided an excellent account of this species (as *Chantransia virgatula*) and of the variation it exhibits; his concept of this species is recognized here (see also Hamel 1927, 1928). As noted previously (Woelkerling 1973, p. 96), the specific epithet "secundata" has nomenclatural priority over the specific epithet "virgatula". The form illustrated in this study (Fig. 82) is by far the most common in New England waters, although individuals of all forms discussed by Rosenvinge (1909) have been observed.

Most previous accounts (e.g. Hamel 1927, Kylin 1907, Rosenvinge 1909) state that the germinating spore divides to form a central cell and three surrounding cells. In all New England plants examined, four cells surround the central cell (Fig. 77); this difference, however, does not appear to be of any taxonomic consequence.

Some variation in the number of cell layers in the basal disc has also been reported. Hamel (1927), Kylin (1907), and Rosenvinge (1909) all record only single layered basal discs. Boergesen (1902) separates *Chantransia secundata* from *C. virgatula* on the basis that the former always has a two layered basal disc while the latter has only a single layered disc. Collins (1906) states that the basal discs are usually two layers thick; Taylor (1937, 1957) follows Boergesen (1902) in recognizing two species in his keys (Taylor 1937, p. 227; 1957, p. 211), but states in his descriptions (Taylor 1937, p. 230; 1957, p. 214) that the base is ". . . a multicellular disc 1-2 layers or more in thickness . . . ."

During this study, several discs (Fig. 80) that are partially two layered have been seen, but the majority are single layered. None of the sort illustrated by Boergesen (1902, p. 350, Fig. 51) or Taylor (1957, pl. 31, Fig. 3) have been encountered. It also appears evident that some

variation can occur in the number of layers in the base within single populations, and therefore, this variation has little taxonomic significance. Indeed, all plants examined in the type collections of *Colaconema secundata* and the other taxa here considered conspecific have single layered basal discs.

Only monosporangial plants have been observed during the present study; tetrasporangial individuals have, however, been reported in New England by Hehre and Mathieson (1970) and Taylor (1937, 1957). Kylin (1907, 1944) and Rosenvinge (1909), among others, have recorded them from Europe. Sexual stages remain unknown.

Collins in Collins, Holden, and Setchell (1900, No. 741) described and distributed *Chantransia virgatula* f. *tenuissima* based on a collection of Monks from San Pedro, California. Later Drew (1928, p. 170, pl. 38, Figs. 26, 27) raised the taxon to specific rank (as *Rhodochorton tenuissimum* (Collins) Drew), primarily on the bases of somewhat narrower filaments, lack of hairs, and sessile and not opposite sporangia.

The type collection of this species in FH as well as several isotypes (ADU, NY, WIS) have been examined and found to agree well with the types of *Colaconema secundata* and of *Callithamnion virgatulum*. Type collection plants of all three taxa have the same characteristic development of the basal disc, which in some cases have produced proliferations. The type plants of *Chantransia* f. *virgatula tenuissima* examined also possess (in contrast to what Drew (1928) found in her material) unicellular hairs and do have *some* stalked monosporangia and *some* sporangia in an opposite arrangement. In agreement with Drew, most sporangia are sessile and scattered. Drew reported a parietal chromoplast, but this was not evident in the type material examined. Since there appear to be no other reliable criteria of separation, *Chantransia virgatula* f. *tenuissima* and *Colaconema secundata* are considered here to be conspecific as was suspected earlier (Woelkerling 1971, p. 52).

Acrochaetium subsimplex Levring (1953, p. 473, Figs. 10A-D, 11) likewise is conspecific with *Colaconema secundata* (see Woelkerling 1971, p. 51).

A number of collections referred to *Audouinella daviesii* by Collins (see discussion under that taxon) have been examined and found to contain only (?) plants of *Colaconema secundata.* If one assumes that these collections do not contain a mixture of two taxa (such a mixture was not found during the present study), Collins' material has been misidentified and has been treated accordingly.

Likewise one collection (NY, Holden collection No. 646) hitherto referred to *Acrochaetium sagraeanum* (see Collins 1905, p. 231 and discussion of that taxon under "Species Excludendae") has been found to contain only plants of *Colaconema secundata;* the literature citations have been corrected accordingly.

Two collections in NY (one from Massachusetts and one from New Jersey, the latter being distributed as specimen 1696 in the Phycotheca Boreali Americana) hitherto referred to *Acrochaetium* (= *Chantransia*) *flexuosum* by Collins (1906, 1911), Collins, Holden, and Setchell (1910), and Taylor (1937, 1957) have been examined and found to contain only young plants of *Colaconema secundata.* Parenchymatous discs typical of young plants of *C. secundata* are abundant in both collections and in the largest plants these discs have become more or less obscured by subsequent cell division in prostrate system cells. Relatively few sporangia were present, but these fell within the range of dimensions found among other New England populations.

Specimens from Rhode Island referred by Taylor (1937, 1957) to *Acrochaetium flexuosum* have not been available for examination and their status therefore remains in doubt.

OTHER NEW ENGLAND RECORDS

In addition to the species already discussed, several other audouinelloid taxa have been reported from New

England waters. As a result of the present investigation, the occurrence of four of these taxa, discussed below under "Collections Inquirendae", is surrounded by doubt. The taxonomic status of two other taxa, discussed below under "Species Inquirendae", is open to question, and the type collection of a seventh taxon, discussed below under "Species Excludendae", has been referred to the Chlorophyta.

Collections Inquirendae

Acrochaetium attenuatum (Rosenvinge) Hamel 1927: 99; 1928: 192. Edelstein et al. 1970: 625. Jao 1936: 244, pl. 12, Fig. 1. Papenfuss 1945: 308. South 1970: 1. South and Cardinal 1970: 2079. Taylor 1937: 236, pl. 34, Fig. 1; 1957: 222, pl. 34, Fig. 1.

Chantransia attenuata Rosenvinge 1909: 106, Fig. 35. DeToni 1924: 56.

Rhodochorton attenuatum (Rosenvinge) Nakamura 1944: 103, Fig. 3.

For detailed morphological accounts of this taxon, see Nakamura (1944) and Rosenvinge (1909).

Type locality: Jelstrup, Limfjord, Denmark.

Type: C (Rosenvinge 3883).

Distribution: Northern Europe, Eastern Canada, Japan.

Hosts: A variety of algae.

Specimens examined: See below.

This taxon has been recorded once in New England by Jao (1936) from Norton Point, Martha's Vineyard, Massachusetts and subsequently reported by Taylor (1937, 1957). The collection upon which this record is based is apparently represented in MICH by a prepared slide bearing the number Woods Hole 280. (This same slide contains type collection specimens of two other taxa [*Acrochaetium radiatum* Jao and *A. microfilum* Jao] which are regarded here as conspecific with *Colaconema humilis* and *Audouinella microscopia* respectively).

The MICH slide has been examined during this study and found to contain two plants somewhat similar to those

described by Jao (1936), but the material was too fragmentary and too young to make any definite identification, although the specimens showed some features similar to young plants of *Audouinella saviana*. The taxonomic status of these plants therfore remains in doubt as does the occurrence of *A. attenuatum* in New England waters.

Likewise the record of Edelstein *et al.* (1970, p. 265) requires further investigation.

Audouinella efflorescens (J. Agardh) Papenfuss 1945: 326; 1947: 438. Edelstein and McLachlan 1968: 993, Figs. 1-2. Taylor 1957: 225.

Acrochaetium efflorescens (J. Agardh) Naegeli 1861: 405. Hamel 1927: 103; 1928: 196. Taylor 1937: 236.

Callithamnion efflorescens J. Agardh 1851: 15; 1876: 10.

Chantransia efflorescens (J. Agardh) Kjellman 1875: 14; 1883: 129. Kylin 1906: 113, Figs. 1-5; 1907: 119. Rosenvinge 1909: 134, Figs. 61-64.

Grania efflorescens (J. Agardh) Kylin 1944: 26, Fig. 24.

Rhodochorton efflorescens (J. Agardh) Drew 1928: 151. Rosenvinge 1935: 7.

For detailed morphological accounts of this taxon, see Kylin (1906) and Rosenvinge (1909).

Type locality: Kattegat Channel, Sweden.

Type: LD 35129.

Distribution: Arctic, Eastern Canada, Northern Europe.

Hosts: A variety of algae and invertebrates; also on rock.

Specimens examined: Sweden: Kattegat, 13. VIII. 1833, ? (LD 35129, type of *Callithamnion efflorescens* J. Agardh).

This taxon has been recorded (as *Chantransia efflorescens*) on *Rhodymenia* from Gay Head (Martha's Vineyard) Massachusetts by Farlow (1877, p. 245), but neither he nor anyone else apparently has made further reference to this collection. Moreover, no plants of *Audouinella efflorescens* from Gay Head on *Rhodymenia* could be located in FH or NY during this investigation, and this record of

the taxon in New England must therefore remain in doubt.

Farlow (1881, p. 109) also records a *Chantransia efflorescens* Thuret from Gay Head on *Cystoclonium*. Whether this is the same specimen as the one discussed above is uncertain, but plants from the *Cystoclonium* collection, the major portion of which is in FH (a fragment cut from the sheet is in the Collins material in NY), have been examined and found to contain sexual plants of *Audouinella daviesii* rather than specimens of *A. efflorescens*. Carposporophytes of the two are easily distinguishable because carospores are only terminal in *A. daviesii* but occur in rows of 2-3 in *A. efflorescens*. The notes of Taylor (1937, p. 236; 1957, p. 225) refer to Farlow's material on *Cystoclonium,* which is regarded here to belong to*A. daviesii* (q.v. for further comments).

Audouinella efflorescens is a distinctive species with its spirally twisted chromoplasts without pyrenoids and its seriate carpospores, and future study may show it to be a component of the New England flora. It apparently has recently been found in Nova Scotia (Edelstein and McLachlan 1968).

Audouinella spetsbergense (Kjellman) comb. nov. Figs. 61-63.

Rhodochorton spetsbergense (Kjellman) Kjellman 1883: 187. DeToni 1903: 1511.

Thamnidium spetsbergense Kjellman 1875: 31, Figs. 11-12.

Rhodochorton penicilliforme (Kjellman) Rosenvinge 1894: 66, Fig. 9; 1923-24: 388, Figs. 325-327. Boergesen 1902: 389, Fig. 60. Collins 1906a: 160. Drew 1928: 176. Edelstein et al. 1967: 200, Figs. 6, 28. Kylin 1907: 188; 1925: 44, Figs. 26a-c; 1944: 28. Taylor 1937: 239; 1957: 225.

Rhodochorton mesocarpum (Carm.) Kjellman var. *penicilliformis* (Kjellman) Kjellman 1883: 187, pl. 16, Figs. 6-7. Rosenvinge 1893: 792.

Thamnidium mesocarpum (Carm.) Kleen f. *penicilliformis* Kjellman 1875: 30; 1877: 25; 1877a: 23.

Plants epiphytic, caespitose, up to 2.0 mm tall; original

spore non-persistent. Prostrate system consisting of an irregularly discoid mass of pseudoparenchymatous filaments. Erect filaments sparingly to moderately and irregularly branched. Cells cylindrical, 8-13 μm wide and (10-) 20-35 (-50) μm long, L/D (1-) 1.5-4 (4.5); each cell containing a number of discoid to irregularly shaped chromoplasts without pyrenoids. Unicellular hairs not observed.

Tetrasporangia ovoid, 25-35 μm long and 16-25 μm wide, single or occasionally in pairs (rarely in groups of 3), sessile or on stalks, scattered over the erect filaments or occasionally terminal on lateral branches.

Other reproductive structures not observed.

Type locality: Fairhavn, Spitzbergen (79° 49′ N.).

Type: UPS.

Distribution: In North America, from Washington state northwards on the Pacific coast and Rhode Island northwards (?, see discussion) on the Atlantic Coast; also reported from northern Europe.

Hosts: Various algae and hydroids.

Specimens examined: SPITZBERGEN: Fairhavn Is. (79° 49′ N.), 19. VIII. 1872, *Kjellman* (UPS, type). Fairhavn Is. (79° 41′ N.), 12. VIII. 1872, *Kjellman* (UPS, type of R. *penicilliforme* (Kjellman) Rosenvinge).

This taxon has been recorded (as *Rhodochorton penicilliforme*) from Rhode Island (Collins 1906a, p. 160) and northern Massachusetts (Taylor 1937, p. 239; 1957, p. 225). Collins material has not been found either in FH or NY and the Massachusetts material has not been available for study. (The taxonomic description given above is based on data gathered from plants in the type collection; see Rosenvinge 1923-24 for a more complete account). Moreover, no additional plants of this taxon have been collected during the present investigation and three collections in NHA examined have been found to contain only plants of other species. Thus, the occurrence of this taxon in New England waters is open to question, and further investigation appears necessary. It has recently been reported from Nova Scotia (Edelstein et al. 1967), but did

not appear in a recent survey of Campobello Island, New Brunswick (Stone et al. 1970).

Kjellman (1875) described two new taxa from collections made on Fairhavn Island, Spitzbergen: *Thamnidium spetsbergense* Kjellman and *T. mesocarpum* (Carmichael) Kjellman forma *pencilliformis* Kjellman. The latter was given species status by Rosenvinge (1894, p. 66). The type specimens of both taxa, preserved on microscope slides in UPS, have been examined during this study and found to be identical in all respects including habit, cell dimensions, spore dimensions, and chromoplast morphology. Consequently, they are here considered conspecific, with the specific epithet "spetsbergense" having nomenclatural priority. It has been referred to the genus *Audouinella* on the basis of Rosenvinge's (1923-24, p. 388, Fig. 27) record of spermatangia. Culture studies may show that *A. spetsbergense* has a diphasic life cycle similar to that of *A. purpurea* (see West. 1969).

The relationships of *A. spetsbergense* and *A. purpurea* require clarification. They differ from one another primarily in their habit (epibiotic vs. primarily saxicolous) and type of prostrate system (pseudo-parenchymatous vs. filamentous) and since none of the characters appear to be taxonomically reliable (see Woelkerling, 1971), the two entities may represent ecological variants of a single species. Because intermediate forms have not been found during this study, they are maintained as distinct taxa for the present.

Colaconema polyides (Rosenvinge) Woelkerling 1971: 49, Figs. 19, 27A.

Acrochaetium polyides (Rosenvinge) Boergesen 1915: 59. Kylin 1944: 26. Papenfuss 1945: 317.

Chantransia polyides Rosenvinge 1909: 132, Figs. 59-60. Levring 1935a: 460, Fig. 2.

For detailed morphological accounts of this taxon, see Rosenvinge (1909) and Woelkerling (1971).

Type locality: Tonneberg Banke, Denmark.

Type: C.

Distribution: Denmark, South Australia, Tasmania.
Hosts: Codium (Chlorophyta), *Polyides* (Rhodophyta).
Specimens examined: See below.

This taxon has been reported (as *Acrochaetium polyides*) from New Hampshire (Hehre and Mathieson 1970, p. 205) and Nova Scotia (Edelstein and McLachlan 1966, p. 38, Fig. 2; Edelstein et al. 1970, p. 625; South and Cardinal 1970, p. 2078), apparently in a sterile condition.

The New Hampshire collection and one Nova Scotia collection have been examined; in both cases the meagre amount of sterile Audouinella-like filaments present could not be identified to species with any certainty at all. The taxonomic affinity of these specimens and the occurrence of *A. polyides* in New England and Nova Scotia therefore remains doubtful. It seems likely that these collections have been referred to *A. polyides* solely on the basis of the type of host organism (see Edelstein and McLachlan 1969, p. 555), which, as noted above, is an unreliable criterion of systematic separation.

Species Inquirendae

Colaconema americana Jao 1936: 237, pl. 13, Fig. 8. Levring 1937: 94; 1953: 489. de Valera 1939: 3. Woelkerling 1971: 42.

Acrochaetium americanum (Jao) Papenfuss 1945: 312.

Type locality: Gay Head, Martha's Vineyard, Massachusetts.

Holotype: MICH, Woods Hole No. 272.

Distribution: Type locality; Southern Australia.

Hosts: Asparagopsis sp.

The type collection of this species has not been available for examination. Two other collections (WJW 2693, WJW 2699) of *Asparagopsis* containing an endophytic audouinelloid alga have been examined and referred to *Colaconema minima* because of overall morphological agreement with that taxon. The cell and spore dimensions of plants in these collections are somewhat smaller than those reported by Jao (1936) for the type collection of *C. americana* (Table

6), and no greatly swollen cells were found, thus placing further doubt (see Woelkerling 1971, p. 42) upon the taxonomic significance of that character. Moreover, the monospores of the collections examined may or may not rest in cup-like bases (Fig. 74), thus casting doubt upon the taxonomic validity of that character also. Upon re-examination, plants in the type collection of *C. americana* will almost certainly be found to be conspecific with *C. minima*.

The rather large number of audouinelloid taxa (including *Colaconema minima* and *C. americana*) whose thallus consists of a creeping prostrate system devoid of or bearing few celled erect filaments present more taxonomic problems and difficulties with identification than any other group within the complex. Such taxa have often been described on the basis of single collections of one or a few plants and have been distinguished on minor differences in cell or spore dimensions, spore arrangement, branching and other morphological characters whose systematic value is dubious (see Woelkerling 1971). Another whole series of such taxa are based on differences in the species of host organism (see Baardseth 1941, p. 46), and host specificity is likewise of doubtful taxonomic value (Woelkerling 1971, p. 11).

Until the type collections of all these audouinelloid algae can be critically compared and the taxa redefined (probably with considerable consolidation of present forms) on firmer morphological grounds, taxonomic procedure dictates a continued recognition of a rather large assemblage of poorly known and rather confusing entities.

Rhodochorton entozoicum (Reinsch In Giard) DeToni 1903: 1514.

Callithamnion entozoicum Reinsch In Giard 1890: 262.

Type locality: Massachusetts.

Type: BM.

Distribution: Apparently known only from the type locality.

Hosts: Marine invertebrates.

The type and only known New England collection of this

taxon has not been available for examination. Reinsch (1879) first described and illustrated material of this taxon from sponges and bryozoans, but as noted by Collins (1883), Reinsch never assigned a name to it. Giard (1890), however, formally described the taxon under the specific epithet of "entozoicum," and this was subsequently recorded by DeToni (1903).

A re-examination of the type collection will almost certainly show that *Rhodochorton entozoicum* is conspecific with *Colaconema membranaceum*. As noted by Collins (1883), DeToni (1903), and Giard (1890) himself, the two taxa are scarcely distinguishable from one another, and Hamel (1927, p. 59; 1928a, p. 152) regarded the two as conspecific. Hamel, however, gives no indication of having compared the type collections of the two taxa, and the present investigator prefers to defer final judgment until such a comparison can be made. Hamel also regards material of Giard (1890) from Wimeraux as belonging to *C. membranacea*.

Species Excludendae

Acrochaetium sagraeanum (Montagne) Bornet 1904: xxi = *Cladophora sagraena* Montagne 1856: 459.

Bornet (1904) united under the name of *Acrochaetium sagraeanum* specimens from Cuba (Montagne's type, which Bornet noted was sterile), Barbados (see Vickers 1905), California, and Connecticut (see Collins 1905). Later, Collins (1906) and Collins and Hervey (1917) referred specimens from Florida and Bermuda to this taxon.

Montagne's type has been re-examined during this study and found to belong to the Chlorophyta and probably to the genus *Cladophora* itself as originally suggested by Montagne (1856). The specimens have a distinctive green color, lack pit connections and do not possess monosporangia or other reproductive organs, all of which strongly militate against placing Montagne's plants in the *Audouinella* complex as suggested by Bornet.

New England plants referred to *Acrochaetium sagraea-*

num were originally collected by Holden (see Collins 1905, 1906) and are deposited in FH and/or NY. Four of these (Holden collection number 17,701 [= Collins, Holden and Setchell 1895: 39], 708 and 757) contain plants of *Audouinella saviana.* A fifth herbarium sheet (Holden collection number 646) contains plants of *Colaconema secundata.* The sixth collection cited by Collins (1905), Holden 750, could not be located, and its taxonomic status remains in doubt.

Plants in PC from California (which may represent fragments of UC 93071 or UC 789916 deposited at Berkeley) referred by Bornet to *Acrochaetium sagraeanum* have been examined and are referred here to *Audouinella daviesii.* Likewise plants from Barbados (Bornet 1904, Vickers 1905) are referred here to *A. daviesii.* Specimens from Bermuda (Collins and Hervey 1917); Collins, Holden and Setchell 1917, No. 2181), however, belong to *A. saviana.*

Collins (1906, p. 192) cites a collection of *Acrochaetium sagraeanum* from Florida, but no specimens could be located in FH or NY, and its status remains uncertain.

A number of literature references relating to one or more of the above collections can now be clarified. The name *Acrochaetium sagraeanum* (Montagne) Bornet as used by Boergeson (1915, p. 35), Collins (1906, p. 192), Hamel (1927, pp. 77, 99, Fig. 46; 1928, pp. 171, 193, Fig. 46), Jao (1936, p. 244), and Papenfuss (1945, p. 311) refers to the entire assemblage of collections described by Bornet (1904, p. XXI). DeToni (1924, p. 51) employed the name *Chantransia sagraeana* (Montagne) DeToni for Bornet's assemblage. The collection upon which Hamel (1927, 1928) based his illustrations has not been determined.

Vickers (1905, p. 60) relates to the Barbados collection while Collins (1905, p. 231), Collins, Holden and Setchell (1895, No. 39), Hylander (1928, pp. 158, 159), and Taylor (1937, p. 233; 1957, p. 220) pertain to the Connecticut material. The Bermuda collections are cited in Collins and Hervey (1917, p. 97) and Collins, Holden and Setchell (1917, No. 2181), Taylor (1960, p. 309) includes both the

Bermuda and Barbados collections. Corrected citations for these literature references have been listed under the synonomy of *Audouinella daviesii, A. saviana,* and *Colaconema secundata.*

EASTERN CANADIAN AND ARCTIC RECORDS

According to South and Cardinal (1970), 28 species of audouinelloid algae have been recorded from the eastern Canadian coast from Cape Chidley, Labrador southwards to the New Brunswick-Maine border.

In addition to those taxa listed from eastern Canada and the Arctic in the descriptive catalogues of Taylor (1937, 1957), seven other taxa have been reported in this region, chiefly as a result of the Nova Scotia studies of Edelstein and McLachlan (1966, 1968, 1969) and of Edelstein et al. (1967, 1970). These include *Acrochaetium bornetii* Papenfuss, *A. endozoicum* (Darbishire) Batters, *A. inclusum* (Levring) Papenfuss, *A. kylinii* Hamel, *A. ralfsiae* Boergesen, *A. subtilissimum* (Kuetzing) Hamel, and *Kylinia cytophaga* (Rosenvinge) Kylin.

A number of these records appear highly questionable. Thus, for example, Edelstein and McLachlan (1969, p. 558) record *Acrochaetium kylinii, A. ralfsiae,* and *A. subtilissimum* from Nova Scotia (the only records for this region) on the basis of some endophytic portions of sterile specimens with the comment ". . . we regard these species as preliminary records only." Other records of similar merit also occur (e.g. the Canadian record for *A. polyides* [Edelstein and McLachlan 1966, p. 38] apparently is based on sterile material), and in other cases taxa have been identified on the basis of type of host organism (Edelstein and McLachlan 1969, p. 555) or similar criteria which are of dubious taxonomic significance.

Until all of the specimens involved in publication records for the Cape Chidley, Labrador to New Brunswich-Maine border region can be critically re-examined along with other available material from the area (a task beyond the

scope of the present paper), the number and distribution of audouinelloid algae along these coasts must necessarily remain uncertain. South and Cardinal (1970, p. 2079, footnote 3) also state that many of the species require further investigation.

Only scattered records of audouinelloid algae north of Cape Chidley, Labrador have appeared in the literature and most of these are summarized in the papers of Kjellman (1883) and Lund (1959) and the catalogues of Taylor (1937, 1957). Until relevant herbarium specimens and additional field collections become available for study, the nature and distribution of audouinelloid algae in arctic regions will likewise remain uncertain.

SUMMARY

The systematics, morphology, ecology, and distribution of marine representatives of the *Audouinella* complex (Acrochaetiaceae, Rhodophyta) in New England waters (including New York and New Jersey) have been studied. These investigations support the taxonomic proposals of Woelkerling (1971) and have resulted in the recognition of two genera and eleven species to occur definitely in this region. Seven species, known to reproduce sexually are referred to *Audouinella;* the form genus *Colaconema* contains four New England representatives which are unknown in the sexual state.

A number of published records based on misidentifications have been corrected and in one instance, the type specimen of a taxon [*Acrochaetium sagraeanum* (Montague) Bornet] has been excluded from the Rhodophyta. Records of questionable occurence, taxa whose status is in doubt, and the state of knowledge of marine audouinelloid algae in eastern Canada and the Arctic are considered briefly.

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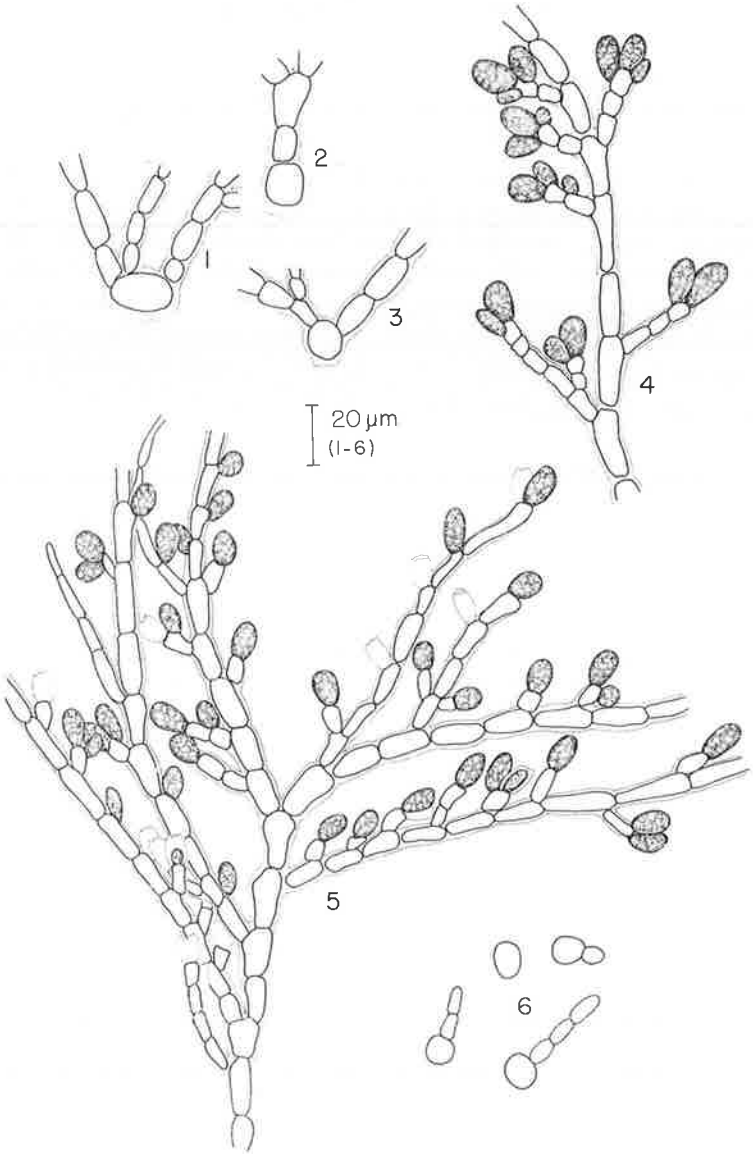
ADDENDUM

After this article had gone to press, Professor Peter S. Dixon provided me (personal communication) with some additional information about the typification of *Audouinella daviesii* and *A. thuretii*.

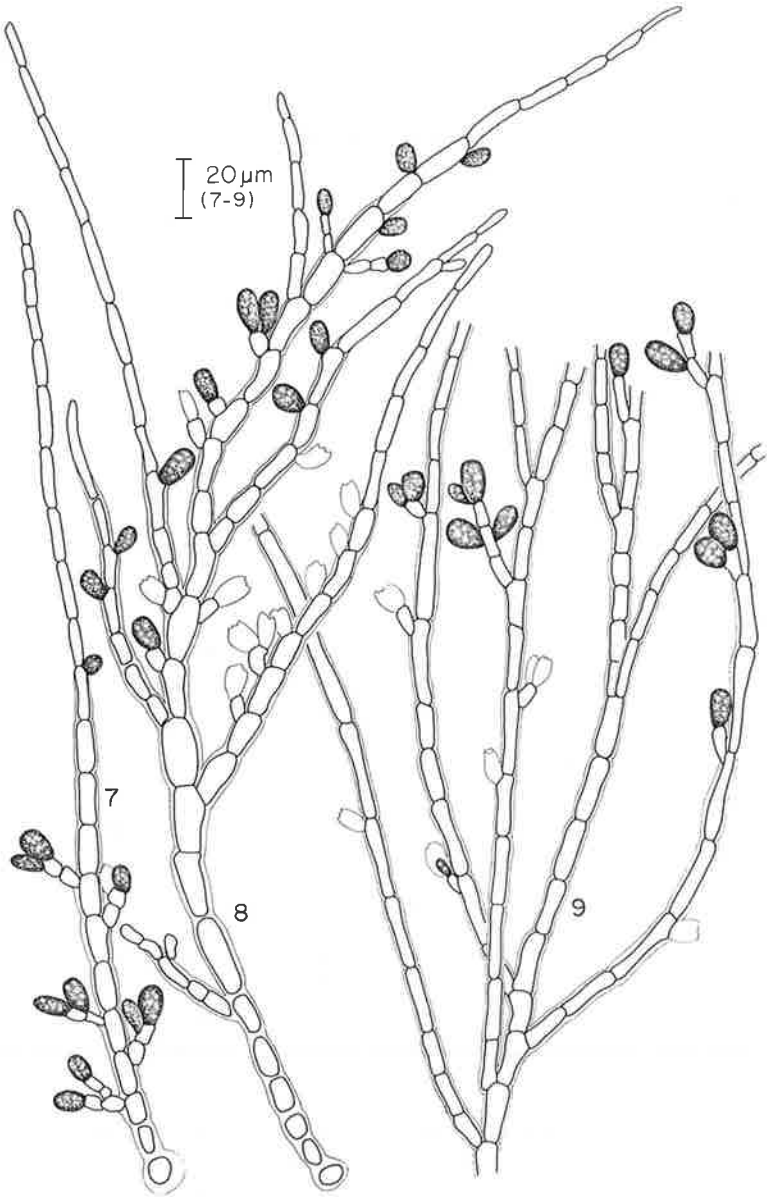
According to Professor Dixon, the only specimen of *Conferva daviesii* in the Dillwyn collections at NMW comes from Swansea rather than from Bantry Bay, the type locality given by Dillwyn. A fragment of the NMW collection was sent to me on loan, and an examination of it indicated that it was material of *C. daviesii*. However, since this specimen apparently does not come from Bantry Bay, it

can at best be regarded only as authentic material rather than type material and the statements in the body of this paper should be modified accordingly.

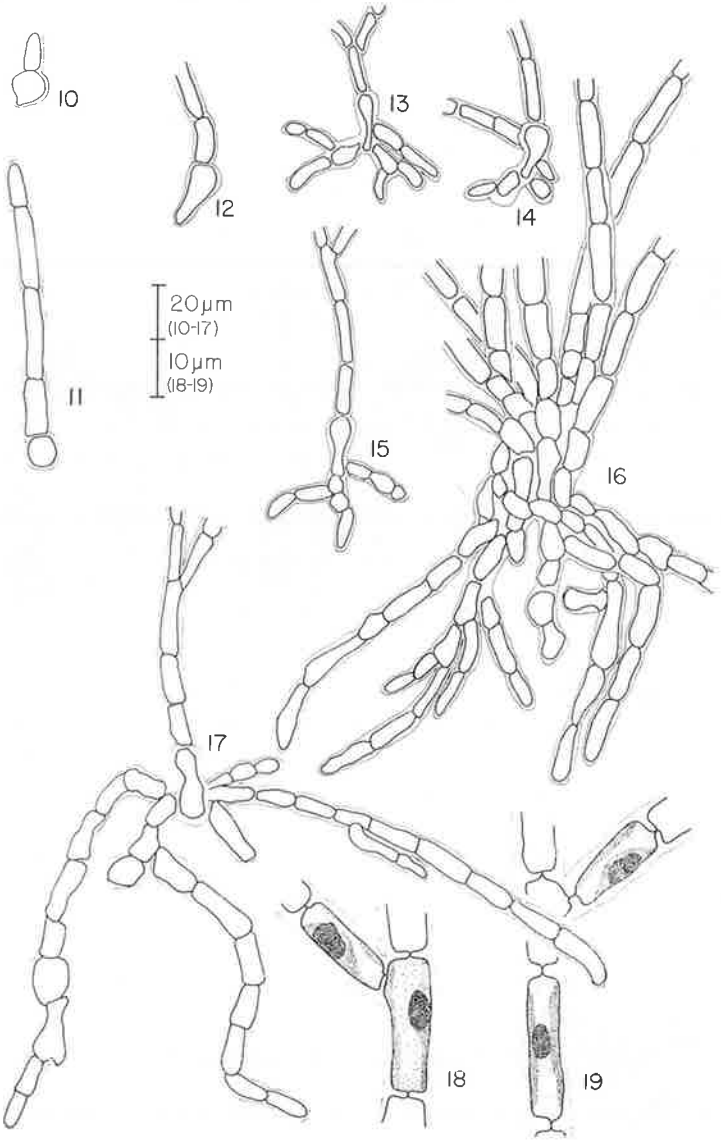
Professor Dixon also informed me that the type material of *Audouinella thuretii* should be dated 5. IX. 1853 (see Bornet 1904), but that the earliest material he could find in PC is dated 1. IX. 1856. Portions of the latter collection have been examined during this study. Until the matter of the dates is further clarified, the 1856 material should be regarded as authentic rather than type, and statements in the body of this paper should be modified accordingly.



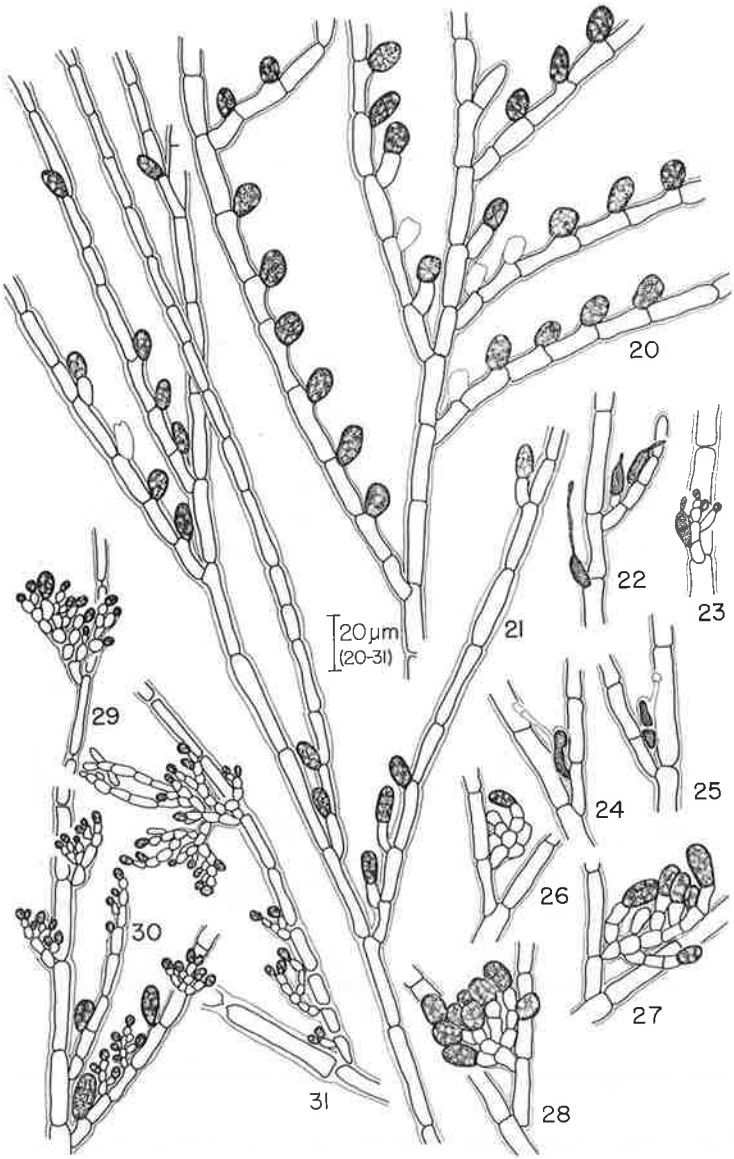
Figs. 1-6. *Audouinella alariae* (Jonsson) Woelk. Figs. 1-3. Unicellular bases bearing a variable number of erect filaments. Figs. 4-5. Portions of densely branched erect filaments with numerous monosporangia. Fig. 6. Sporelings. Figs. 1 3, 4: NY (Hardhead Island, Penobscot Bay, Maine, VII. 1894, *Collins* [= Collins, Holden, and Setchell 1896a: 236]); Fig. 2: NY (Hampton, New Hampshire, VII. 1894, *Collins*); Fig. 5: WJW 2275 (Nubble Light, Maine, 19. VIII. 1969, *Hehre*); Fig. 6: FH (Casco Bay, Maine, VII. 1939, *Weatherill*).



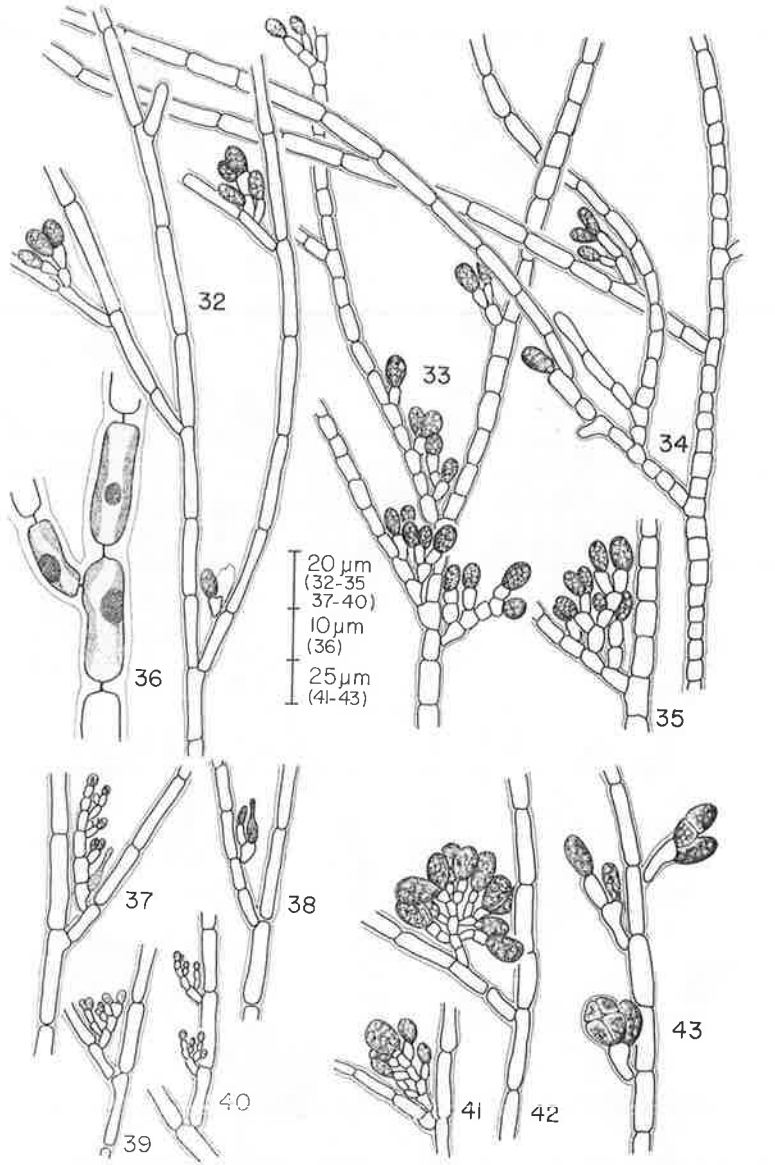
Figs. 7-9. *Audouinella alariae* (Jonsson) Woelk. Figs. 7-8. Habits of fairly small plants with mature monosporangia. Fig. 9. Portion of sparsely branched erect system with scattered monosporangia. Fig. 7: NY (Hardhead Island, Penobscot Bay, Maine, VII. 1894, *Collins* [= Collins, Holden, and Setchell 1896a: 236]); Figs. 8, 9: WJW 2275 (Nubble Light, Maine, 19. VIII. 1969, *Hehre*).



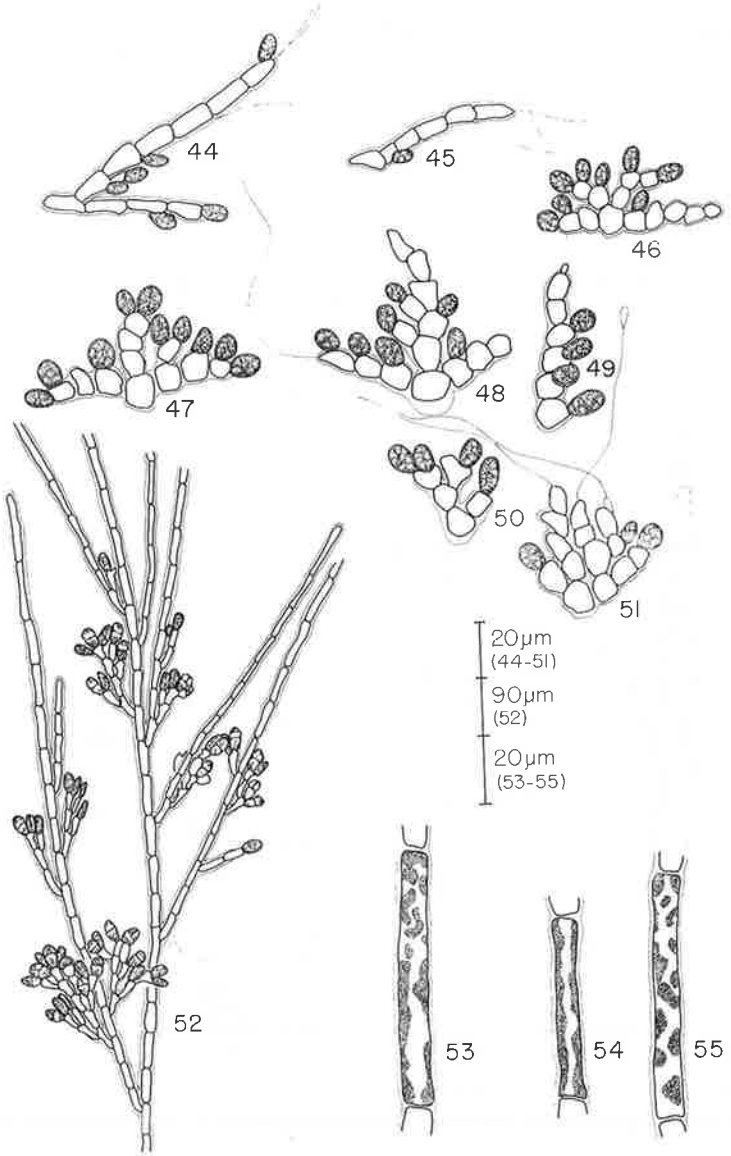
Figs. 10-19. *Audouinella dasyae* (Collins) Woelk. Figs. 10-12. Sporelings. Figs. 14-17. Variation in structure of prostrate system. Note central panduriform to pryriform cell which may become obscured in robust specimens (Fig. 16). Figs. 18-19. Chromoplasts in cells of erect filaments. Figs. 10-12: WJW 2853 (Old Silver Beach, West Falmouth, Massachusetts, 31. X. 1970, *Woelkerling*); Figs. 13, 14: Edelstein 2563 (Malpeque Bay, Prince Edward Island, 5. VIII. 1966, *Edelstein*); Figs. 15, 18, 19: WJW 3311 (Woods Hole, Massachusetts, 16. II. 1971, *Woelkerling*); Fig. 16: WJW 2977 (Old Silver Beach, West Falmouth, Massachusetts, 30. XII. 1970, *Woelkerling*); Fig. 17: WJW 2534 (Waquoit Bay [Harbor Entrance], Falmouth, Massachusetts, 27. IV. 1970, *Woelkerling*).



Figs. 20-31. *Audouinella dasyae* (Collins) Woelk. Figs. 20-21. Filaments of erect system with monosporangia. Figs. 22-23. Unfertilized carpogonia. Figs. 24-25. Fertilized carpogonia. Note transverse division (Fig. 25). Figs. 26-28. Stages in development of carposporophyte. Figs. 29-31. Spermatangia. Note varying arrangement. Fig. 20: WJW 3311 (Woods Hole, Massachusetts, 16. II. 1971, *Woelkerling*); Fig. 21: WJW 2820 (Woods Hole, Massachusetts, 13. X. 1970, *Woelkerling*); Figs. 22-23: FH (North Eastham, Massachusetts, 9. VIII. 1959, *Lamb* A-174 [filed under the host, *Dasya pedicellata*]); Figs. 24-28, 30: WJW 1852 (West Yarmouth, Massachusetts, 3. X. 1969, *Woelkerling*); Figs. 29, 31: WJW 2249 (West Yarmouth, Massachusetts, 16. XI. 1969, *Woelkerling*).



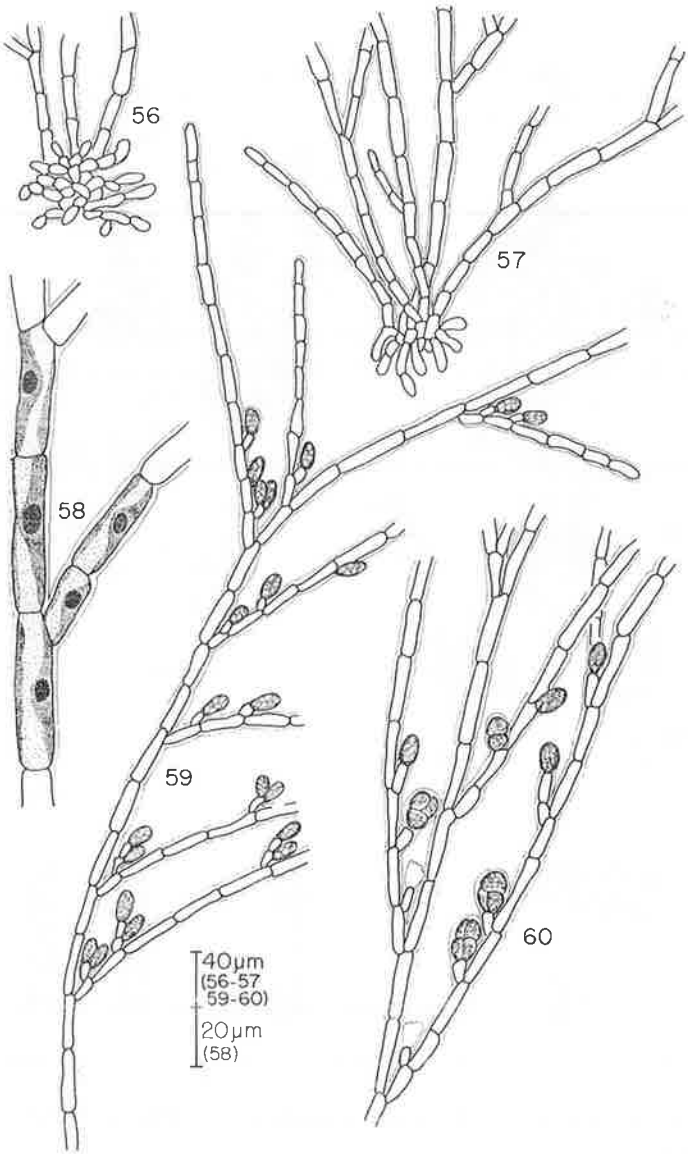
Figs. 32-43. *Audouinella daviesii* (Dillwyn) Woelk. Figs. 32-35. Filaments of erect system bearing monosporangia. Note clustered arrangement of sporangia and variation in cell size. Fig. 36. Chromoplasts in cells of erect filaments. Figs. 37-40. Spermatangia and unfertilized carpogonia. Figs. 41-42. Stages in carposporophyte development. Fig. 43. Tetrasporangia. Fig. 32: WJW 2719 (Woods Hole, Massachusetts, 17. VII. 1970, *Woelkerling*); Fig. 33: WJW 2978 (Old Silver Beach, West Falmouth, Massachusetts, 30. XII. 1970, *Woelkerling*); Fig. 34: WJW 2536 (Waquoit Harbor, Falmouth, Massachusetts, 27. IV. 1970, *Woelkerling*); Fig. 35: WJW 3302 (Woods Hole, Massachusetts, 29. I. 1971, *Woelkerling*); Fig. 36: WJW 2332 (Woods Hole, Massachusetts, 4. II. 1970, *Woelkerling*); Figs. 37-42: WJW 2678 (Woods Hole, Massachusetts, 2. VII. 1970, *Woelkerling*); Fig. 43: WJW 2198 (Montauk Point, New York, 20. I. 1970, *Woelkerling*).



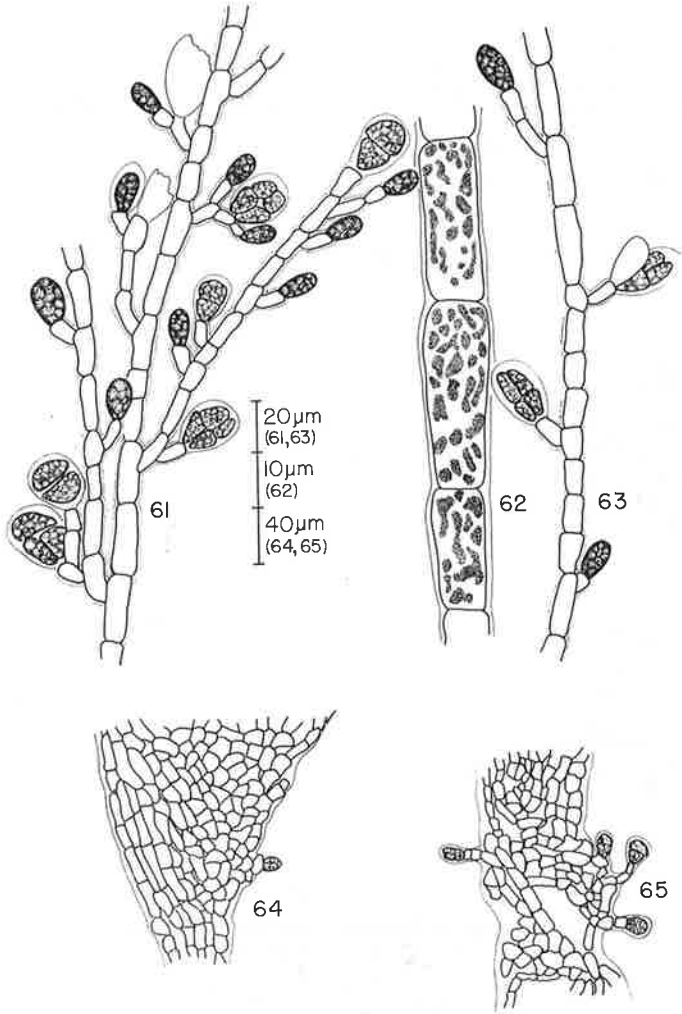
Figs. 44-45. *Audouinella unifila* (Jao) Woelk. Habit of two plants. MICH (Norton Point, Martha's Vineyard, 3. VIII. 1934, *Jao*, holotype).

Figs. 46-51. *Audouinella microscopica* (Naegeli In Kuetzing) Woelk. Habit of monosporangial plants. Figs. 46-47: MICH (Norton Point, Martha's Vineyard, 3. VIII. 1934, *Jao*, type of *Acrochaetium microfilum* Jao); Figs. 48-51: MICH (Black Rock, Sconticut Neck, New Bedford, Massachusetts, 25. VII. 1934, *Jao*, type of *Acrochaetium compactum* Jao).

Figs. 52-55: *Audouinella purpurea* (Lightfoot) Woelk. Fig. 52. Portion of erect system bearing carposporophytes. Figs. 53-55. Chromoplasts in cells of erect filaments. Figs. 52-55. WJW 3297 (Sandwich, Massachusetts, 22. I. 1971, *Woelkerling*).

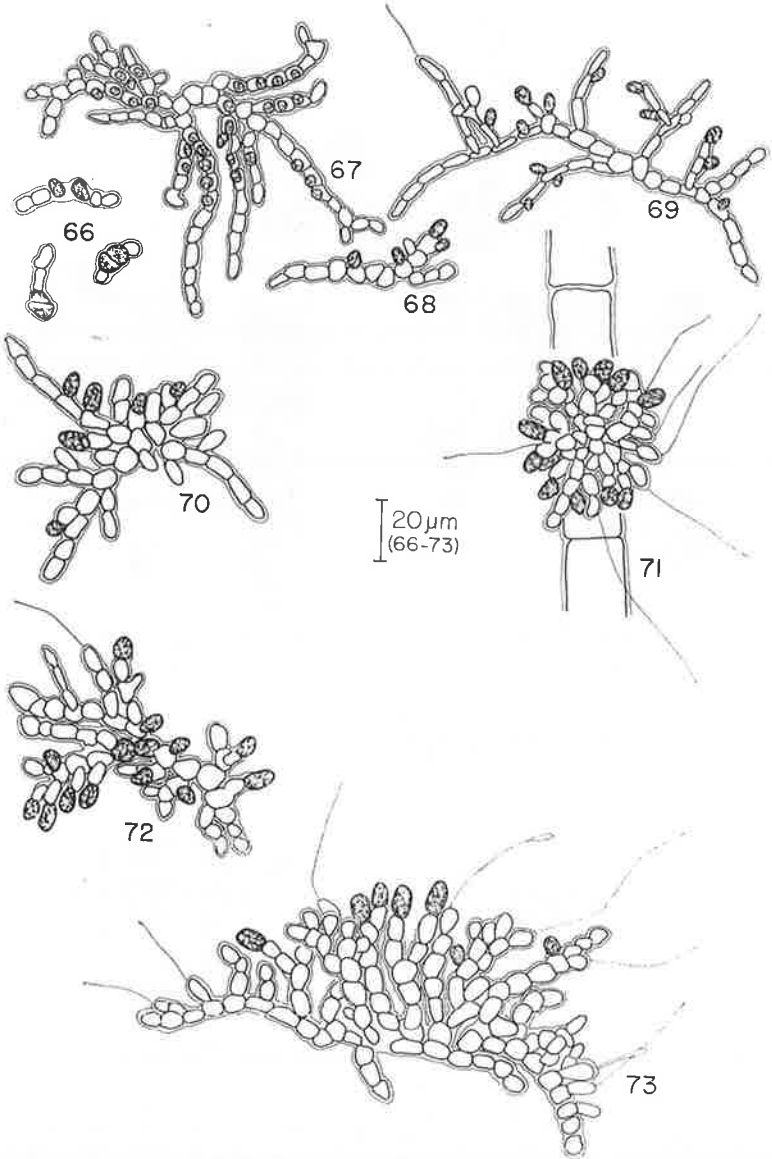


Figs. 56-60. *Audouinella saviana* (Meneghini) Woelk. Figs. 56-57. Prostrate systems. Fig. 58. Chromoplasts in cells of erect filaments. Figs. 59-60. Erect filaments bearing monosporangia (Fig. 59) and tetrasporangia (Fig. 60). Figs. 56-59: WJW 2753 (Woods Hole, Massachusetts, 21. VII. 1970, *Wilce*); Fig. 60: WJW 3818 (Sandwich, Massachusetts , 13. X. 1970, *Woelkerling*).

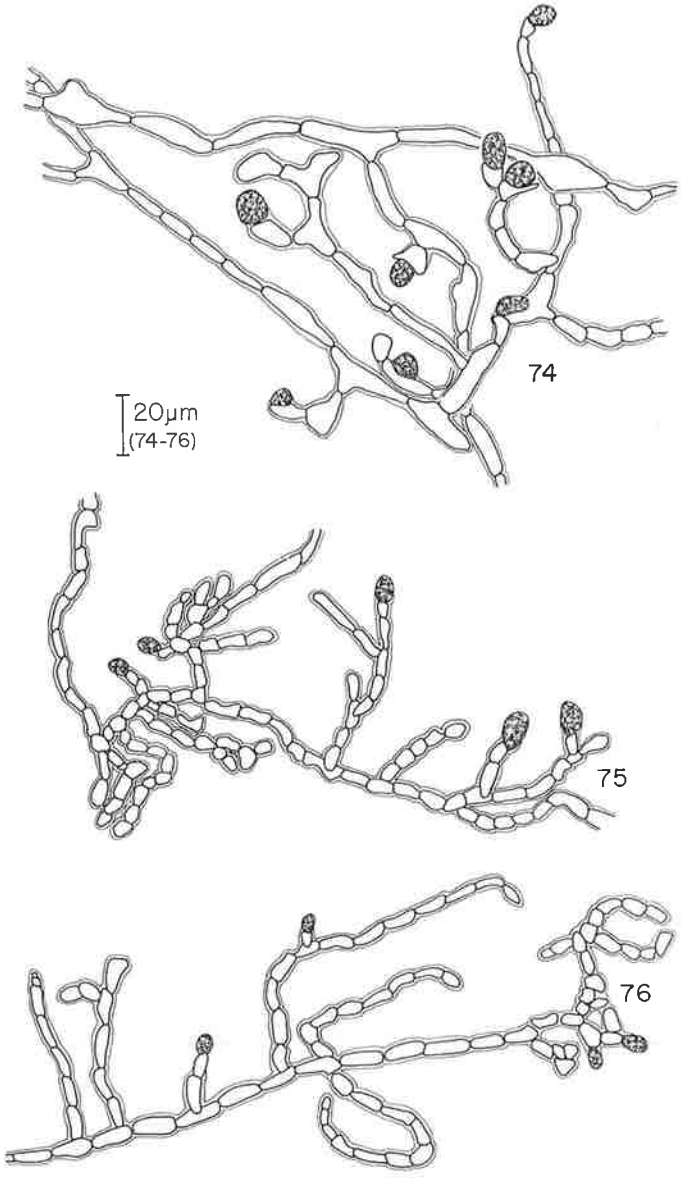


Figs. 61-63. *Audouinella spetsbergense* (Kjellman) Woelk. Figs. 61, 63. Erect filaments bearing tetrasporangia. Fig. 62. Chromoplasts in cells of erect filaments. Fig. 61: UPS (Fairhavn Island, Spitzbergen, 19. VIII. 1872, *Kjellman*, type of *A. spetsbergense*); Figs. 62, 63: UPS (Fairhavn Island, Spitzbergen, 12. VIII. 1872, *Kjellman*, type of *Rhodochorton penecilliforme*).

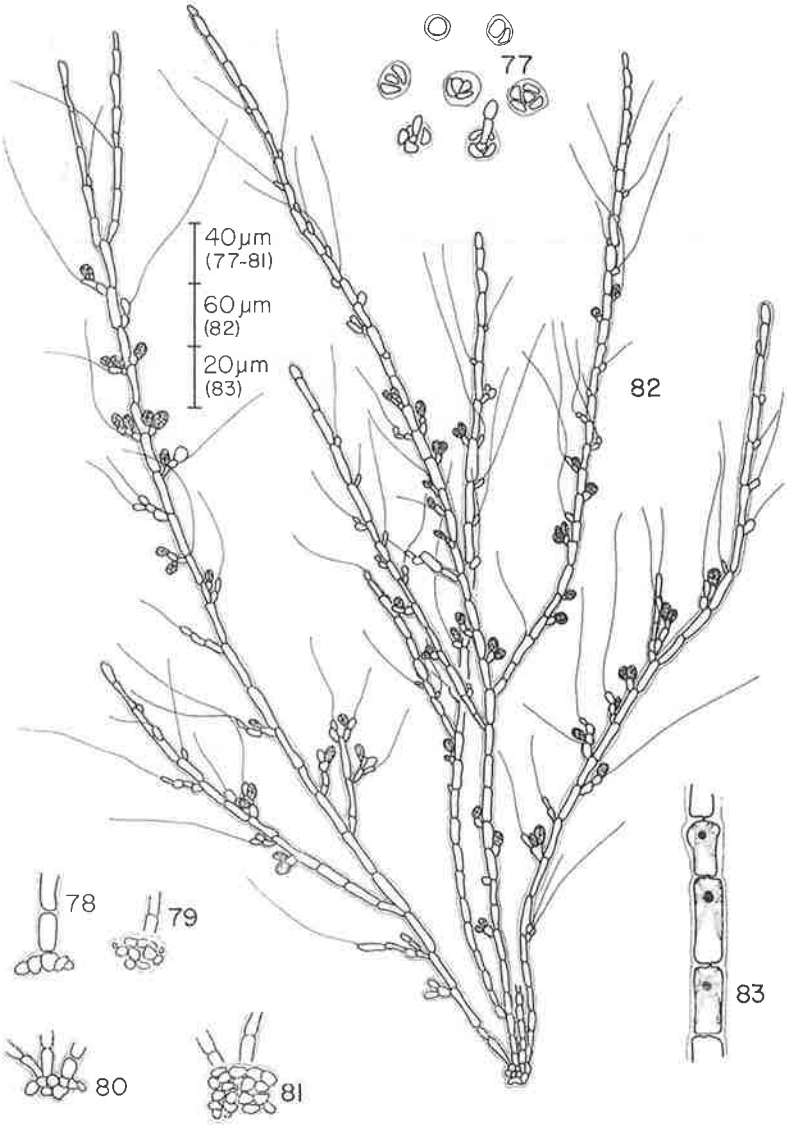
Figs. 64-65. *Caloconema membranacea* (Magnus) Woelk. Habit of portions of two plants. Note tetrasporangia (Fig. 65). Figs. 64-65: FH (Revere Beach, Massachusetts, 29. V. 1886, *Collins*, from Hauck and Richter 1888: 154).



Figs. 66-73. *Colaconema humilis* (Rosenvinge) Woelk. Fig. 66. Sporelings. Figs. 67-73. Habit of monosporangial plants. Figs. 66-69: MICH (Norton Point, Martha's Vineyard, Massachusetts, 3. VII. 1934, *Jao*, type of *Acrochaetium radiatum* Jao); Figs. 70, 72, 73: Edelstein 1382 (Ketch Harbor, Nova Scotia, 31. V. 1965, *Edelstein*); Fig. 71: WJW 1838 (Woods Hole, Massachusetts, 26. VI. 1969, *Conway*).



Figs. 74-76. *Colaconema minima* (Collins) Woelk. Habit of monosporangial plants. Note variation in shape of monosporangia and in cells subtending them. Fig. 74: WJW 2699 (Sandwich, Massachusetts, 30. VI. 1970, *Woelkerling*); Fig. 75: FH (Robinson's Hole, Elizabeth Islands, Massachusetts, VIII. 1907, *Collins*, type [= Collins, Holden, and Setchell 1908: 1493]); Fig. 76: C (Mollegrund, Denmark, 8. VIII. 1899, *Rosenvinge*, type of *Chantransia emergens* Rosenvinge).



Figs. 77-83. *Colaconema secundata* (Lyngbye) Woelk. Fig. 77. Sporelings showing characteristic parenchymatous grouping of cells. Figs. 78-81. Prostrate system of mature plants. Fig. 82. Habit of virgate plant. Fig. 83. Chromoplasts in cells of erect filaments. Fig. 77: WJW 2316 (Woods Hole, Massachusetts, 4. II. 1970, *Woelkerling*); Figs. 78-79, 82: WJW 2276 (West Falmouth, Massachusetts, 6. I. 1970, *Woelkerling*); Figs. 80-81: WJW 2476 (Nantucket Center, Massachusetts, 14. IV. 1970, *Woelkerling*); Fig. 83: WJW 2808 (Penikese Island, Massachusetts, 1. X. 1970, *Woelkerling*).

Table 1. Present status of audouinelloid taxa listed by Giard (1890), Hehre and Mathieson (1970), and Taylor (1957), (Author citations for taxa are recorded in the taxonomic treatments.)

Name of Taxon in Older Literature	*Present Status*
Acrochaetium alcyonidae	Conspecific with *Audouinella daviesii*
A. amphiroae	Conspecific with *A. daviesii*
A. attenuatum	See "Collections Inquirendae"
A. dasyae	*Audouinella dasyae*
A. daviesii	*Audouinella daviesii*
A. emergens	Conspecific with *Colaconema minima*
A. flexuosum	All New England collections referred to *Colaconema secundata*
A. intermedium	Conspecific with *Audouinella dasyae*
A. microfilum	Conspecific with *Audouinella microscopica*
A. minimum	*Colaconema minima*
A. polyides	See "Collections Inquirendae"
A. radiatum	Conspecific with *Colaconema humilis*
A. sagraeanum	See "Species Excludendae"
A. thuretii	Conspecific with *Audouinella saviana*
A. zosterae	Conspecific with *Audouinella dasyae*

Table 1 — Continued

Audouinella efflorescens	See "Collections Inquirendae"
A. membranacea	*Colaconema membranacea*
Colaconema americana	See "Species Inquirendae"
Conchocelis rosea	Referred to Bangiophycidae; not discussed in this account.
Kylinia alariae	*Audouinella alariae*
K. compacta	Conspecific with *Audouinella microscopica*
K. hallandica	Not recorded for New England and not discussed in this account
K. moniliformis	Conspecific with *Audouinella microscopica*
K. secundata	*Colaconema secundata*
K. unifila	*Audouinella unifila*
K. virgatula	Conspecific with *Colaconema secundata*
Rhodochorton entozoicum	See "Species Inquirendae"
R. penicilliforme	See "Collections Inquirendae" under *Audouinella spetsbergense*
R. purpurea	*Audouinella purpurea*

Name	No. erect Axes	Height	Cell diameter	Cell length	L/D	Spore Length	Spore Diameter
Audouinella alariae: Type, data from Jonsson 1901	1-2	500-1000 μm	11-23 μm below 7-11 μm above	24-56 μm below 20-72 μm above	2-3 below 3-6 above	17-22 μm	10-11 μm
Audouinella alariae: Type, data from present study	1-3	—	11-18 μm below 6-12 μm above	25-60 μm below 15-60 μm above	2-4 below 2-6 above	15-20 μm	10-12 μm
Chantransia rhipidandra: Type, data from Rosenvinge	2-3	350 μm	(7.5-) 9-11	—	2-3 (-4)	14-18 μm	9-10 μm
Chantransia rhipidandra: Type, data from this study	(1-) 2-3	450 μm	7-13	20-40 μm	2-4	15-18 μm	9-11 μm
Audouinella alariae: New England populations	1-2 (-3)	up to 1000 μm	12-18 μm below (4-) 7-10 (-15) μm above	15-60 μm below 15-65 μm above	(1-) 1.5-4 below 2-6 (-9) above	12-20 μm	8-12 μm

Table 2. Data on Populations of *Audoui nella alariae* and *Chantransia rhipidandra.*

	A. dasyae	*A. intermedium*	*A. zosterae*
Height	3 mm	2 mm	3 mm
Cell diameter	6-12 (-16) μm	8-10 μm [8-11 μm]	6.4-9.6 μm [6-11 μm]
Cell length	15-70 (-90) μm	(26-) 32-64 μm [15-70 μm]	32-70 μm [21-75 μm]
L/D	2-7 (-10)	—— [2-7.5]	—— [2-7]
Monospore length	16-24 μm	19-23 μm [16-20 μm]	22-31 μm [18-24 μm]
Monosopore diameter	9-12 (-16) μm	9-13 μm [9-12 (-15) μm]	6.5-9.5 μm [8-11 μm]

Table 3. Data on populations of *A. dasyae* complex. Note: Data on *A. dasyae* is a composite of all New England collections examined. Data for *A. intermedium* and *A. zosterae* in brackets is based on personal studies of the types; data not in brackets is that reported by Jao (1936).

	A. thuretii (type)	*A. saviana* (type)	*A. saviana* (New England)
Height	up to 3 mm	up to 3 mm	up to 4 mm
Cell diameter	7-10 (-13) μm	7-12 μm	(7-) 8-12 (-14) μm
Cell length	20-45 μm	20-40 μm	20-60 μm
L/D	2-5	1.5-4	2-6 (-8)
Monospore length	15-20 μm	13-21 μm	18-27 μm
Monospore diameter	9-12 μm	8-12 μm	10-15 μm

Table 4. Data on populations of the *Audouinella saviana* complex. The first two columns represent data on type collection plants; the third is a composite of data on New England populations.

Collection	Cell Length	Cell Width	L/D	Spore Length	Spore Width
Colaconema minima (Collins data)	——	2-4 μm	1-4 (-8)	7 μm	5 μm
C. minima (Woelkerling data)	4.5-15 μm	3-7 μm	1-4	6-11 μm	3-6 μm
Chantransia emergens (Rosenvinge data)	6-10.5 μm	2-3.5 μm	——	5-6.5 μm	3-4 μm
C. emergens (Woelkerling data)	7-12 μm	3-6 μm	1-4	6-10 μm	3-5 μm

Table 5. Data on Type Collections of *Colaconema minima* and *Chantransia emergens.*

Name	Cell length	Cell width	L/D	Spore length	Spore width
Colaconema americana type collection (Jao 1936)	(16-)22-38 (-55) μm	5-10 (-32) μm	?	6-13 μm	9.5-13 μm
Colaconema minima WJW 2693	8-25 μm	3-8 (-14) μm	2-5	7-10 μm	4-10 μm
Colaconema minima WJW 2699	10-25 (-44) μm	3-8 (-14) μm	2-6	5-8 μm	6-10 μm

Table 6. Data on New England populations of *Colaconema* found in *Asparagopsis.* (Cell dimensions refer to prostrate system filaments.)

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ON THE EPIBIOTIC AND PELAGIC CHLOROPHYCEAE, PHAEOPHYCEAE, AND RHODOPHYCEAE OF THE WESTERN SARGASSO SEA

WILLIAM J. WOELKERLING

This paper provides a taxonomic account of the epibiotic and pelagic Chlorophyceae, Phaeophyceae, and Rhodophyceae collected during six cruises to the Western Sargasso Sea and follows two previous studies by the author (Woelkerling, 1972; 1973) of non-planktonic algae from this region. Earlier published records (e.g. Collins, 1917; Conover & Sieburth, 1964; Farlow, 1914; Hentschell, 1921; Pratt, 1935; Winge, 1923) of green and red algae and of brown algae other than *Sargassum* from the Sargasso Sea are few and fragmentary, and, with one or two exceptions, they do not include identifications to species level.

Nearly 75 percent of the taxa encountered during this investigation have not been reported previously from the Sargasso Sea, and these new records raise the total known flora of the region to include 10 Chlorophyceae, 25 Phaeophyceae, and 33 Rhodophyceae. Epibiotic Bacillariophyceae (see Carpenter, 1970) and epibiotic Cyanophyceae (see Carpenter, 1972; Hentschell, 1921) are not treated in this paper.

Methods of sampling and processing are outlined elsewhere (Woelkerling, 1973); voucher material (with specimen numbers prefaced by WJW) has been retained in the author's personal collections, currently housed at WIS. Other herbarium abbreviations follow Lanjouw & Stafleu (1964).

Data provided for each taxon includes references to records of occurrence in adjacent regions and/or of general taxonomic value, the type locality and reported location of the type collection (in most cases, location of types has not been verified), known distribution based on published records, and collection data for all specimens examined. This information usually is followed by ecological and/or taxonomic notes. In cases where specific identification has not been possible due to fragmentary and/or very young or small plants, the available data has been summarized briefly at the generic level. The genus *Sargassum* presents special problems regarding species identification, and these are outlined in the discussion of that taxon.

Epibiotic taxa can be divided conveniently into two ecological groups, namely the permanent element and the invading element. The former includes all taxa epibiotic on *Sargassum fluitans* and/or *S. natans,* the two brown algae which comprise the vast bulk of Sargasso Sea vegetation, estimated by Parr (1939) to be in excess of 4×10^3 metric tons. These two species apparently are endemic to the Sargasso Sea. The invading element includes all other "macroscopic" taxa (*Ascophyllum, Fucus* and their associated epiphytes (Woelkerling, 1972), species of *Sargassum* other than *S. fluitans* and *S. natans,* etc.).

The permanent epibiotic element comprises both taxa which are normally of small size (less than 1 cm tall) and diminutive forms of taxa normally of larger stature. Species in both groups, however, frequently bear reproductive structures, in marked contrast to *Sargassum fluitans* and *S. natans* which never have been found with receptacles (see, however, Parr, 1939, page 49) and reproduce solely by fragmentation as far as is known.

Sincere thanks are due Mr. Gordon Volkmann of the Woods Hole Oceanographic Institution for making arrangements for the collection of samples in the Sargasso Sea and for making passage possible for the author on one of the cruises. Thanks are also due Dr. Elizabeth M. Gordon for examining collections of the Ceramiaceae.

DIVISION CHLOROPHYTA

CLASS CHLOROPHYCEAE

ORDER TETRASPORALES

Family Palmellaceae

Genus *Pseudotetraspora* Wille, 1906

Pseudotetraspora marina Wille 1906:20, Taf. 1, Figs. 32-36.

TYPE LOCALITY: Steinviksholm, Drontheimsfjord, Norway.

TYPE: not located.

DISTRIBUTION: apparently known only from the Sargasso Sea and Norway.

SPECIMENS EXAMINED: **Sargasso Sea:** 31°N-70°W, 5.vii.1970, *Volkmann* (WJW 2735); 32°09'N-64°58'W, 16.v.1970, *Woelkerling* (WJW 2670); 34°N-70°W, 30.vi.1970, *Volkmann* (WJW 2727), 6.vii.1970, *Volkmann* (WJW 2748); 35°54'N-70°30'W, 13.viii.1970, *Moore* (WJW 2901); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2625); 37°30'N-70°W, 8.vii.1970, *Volkmann* (WJW 2708); 39°07'N-70°35'W, 16.viii.1970, *Moore* (WJW 2919, 2927); 39°30'N-71°W, 6.x.1970, *Volkmann* (WJW 2871).

The small, amorphous, gelatinous thalli have been found as epiphytes on *Sargassum natans, Sargassum* sp., and *Cladophora.*

Howe (1920) described a *Pseudotetraspora antillarum* from the Bahamas and separated it from *P. marina* on the basis of apparent differences in color, shape of the gelatinous mass, and cell size. These criteria require further consideration since the Sargasso Sea specimens could conveniently be placed in either taxon. Howe (1920), for example, lists cell diameters of 3-7 μm for *P. antillarum* while Wille (1906) gives cell diameter of 4-10 μm for *P. marina.* The Sargasso Sea plants have cell diameters of 3-14 μm. A critical comparison of the types and other collections of the two taxa may well show them to be conspecific.

ORDER CHAETOPHORALES
Family Chaetopeltidaceae

Genus *Diplochaete* Collins, 1901

Diplochaete solitaria Collins 1901:242. Chapman 1961:69, Fig. 73. Collins 1909:278, Fig. 99. Collins and Hervey 1917:38. Taylor 1960:53.

TYPE LOCALITY: Kingston, Jamaica.

TYPE: NY.

DISTRIBUTION: Bermuda, Jamaica, Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 26°57′N-72°58′W, 26.iv.1970, *Moore* (WJW 2647, 2651); 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2435); 31°N-70°W, 5.vii.1970, *Volkmann* (WJW 2734); 32°09′N-64°58′W, 16.v.1970, *Woelkerling* (WJW 2664, 2668); 34°N-70°W, 30.vi.1970, *Volkmann* (WJW 2726, 2747); 35°54′N-70°30′W, 13.viii.1970, *Moore* (WJW 2900); 36°28′N-70°29′W, 15.viii.1970, *Moore* (WJW 2908); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2618); 38°22′N-70°58′W, 12.x.1970, *Volkmann* (WJW 2891); 39°07′N-70°35′W, 16.viii.1970, *Moore* (WJW 2916); 39°30′N-71°W, 6.x.1970, *Volkmann* (WJW 2860, 2885).

This species appears to be a rather common component of the Sargasso Sea flora and has been found, sometimes in considerable numbers, on both *Sargassum fluitans* and *S. natans* as well as on a variety of red algae, *Cladophora* (Chlorophyta), and on hydroids.

Cells in the collections examined bear 1-4 setae that may be oriented in any direction relative to one another but generally are directed away from the substrate. As noted by Collins (1909) the freshwater taxa often referred to the genus *Polychaetophora* West and West (1903) may be congeneric with *Diplochaete* (see also Printz, 1964; G. S. West, 1908).

ORDER ULVALES
Family Ulvaceae

Genus *Enteromorpha* Link, 1820

Enteromorpha sp.

Two collections [31°N-69°29′W, 3.iii.1970, *Volkmann* (WJW 2369) and 34°N-70°W, 7.iii.1970, *Volkmann* (WJW 2397)] of *Sargassum fluitans* contained epiphytic plants

of *Enteromorpha* which appear similar to *E. flexuosa* (Wulfen ex Roth) J. Agardh (see Bliding, 1963, for a detailed account of *E. flexuosa*). Since the Sargasso Sea plants were all stunted (under 3 cm tall), however, specific determination could not be made with certainty.

Genus *Monostroma* Thuret, 1854

Monostroma pulchrum Farlow 1881:41. Collins 1909:211. Collins, Holden, and Setchell 1900:658. Taylor 1957:72.

TYPE LOCALITY: Watch Hill, Connecticut.

TYPE: FH.

DISTRIBUTION: Connecticut to Nova Scotia, Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 39°05'N-69°48'W, 10.v.1970, *Woelkerling* (WJW 2572); 39°11'N-69°24'W, 10.v.1970, *Woelkerling* (WJW 2550).

Two small plants of *Monostroma pulchrum* were found as epiphytes on *Fucus vesiculosus* L., which had apparently drifted out into the Northwestern fringes of the Sargasso Sea (see Woelkerling, 1972). Critical studies are needed to determine whether *M. pulchrum* is really specifically distinct from the more widely distributed and better known *M. oxyspermum* (Kuetzing) Doty (see Bliding, 1968, p. 585, under *Ulvaria oxysperma*).

Genus *Percursaria* Bory, 1823

Percursaria percursa (C. Agardh) Rosenvinge 1893:963. Bliding 1963:20, Figs. 5-6. Collins 1909:197. Kylin 1949:16, Fig. 9. Taylor 1957:61; 1960:54.

Enteromorpha percursa (C. Agardh) J. Agardh Chapman 1961:66, Fig. 70.

TYPE LOCALITY: Adriatic Sea.

TYPE: LD.

DISTRIBUTION: widely distributed.

SPECIMENS EXAMINED: **Sargasso Sea:** 34°N-70°W, 13.v.1970, *Woelkerling* (WJW 2612); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2627).

In both cases the host plant was *Sargassum natans*. The main axes and laterals were pleuriseriate while the smaller laterals were uniseriate in the specimens examined.

Genus *Ulva* Linneaus, 1753

Ulva sp.

One young plant [34°N-70°W, 7.iii.1970, *Volkmann* (WJW 2412)] of *Ulva* was found as an epiphyte on a fragment of the grass *Spartina*. Specific determination was not possible. The *Spartina* fragment apparently had drifted out from the U. S. coast.

ORDER CLADOPHORALES

Family Cladophoraceae

Genus *Cladophora* Kuetzing, 1843

As noted by Taylor (1960, p. 78), the genus *Cladophora* has been difficult to cope with in the American tropics and critical studies are badly needed. The recent monographs of Soderstrom (1963) and van den Hoek (1963), which will probably provide a basis for such studies, have been used in making specific determinations during this investigation.

Cladophora dalmatica Kuetzing 1843:263. van den Hoek 1963:186, Figs. 601-35.

C. oblitterata Soderstrom 1963:47, Figs. 38-54A.

TYPE LOCALITY: Split (Spalato), Yugoslavia.

TYPE: L (No. 937/281/406).

DISTRIBUTION: probably widespread.

SPECIMENS EXAMINED: **Sargasso Sea:** 26°57′N-72°58′W, 26.iv.1970, *Moore* (WJW 2646); 31°N-69°29′W, 3.iii.1970, *Volkmann* (WJW 2374); 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2205), 13.v.1970, *Woelkerling* (WJW 2614); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2620); 37°30′N-70°W, 8.vii.1970, *Volkmann* (WJW 2704); 38°22′N-70°58′W, 12.x.1970, *Volkmann* (WJW 2886); 39°07′N-70°35′W, 16.viii.1970, *Moore* (WJW 2918).

Specimens up to 3 cm tall have been found both on *Sargassum fluitans* and *S. natans*. In all cases the apical cells were under 20 μm in diameter and the branch systems showed a distinct acropetal organization.

Cladophora laetevirens (Dillwyn) Kuetzing 1843:267. van den Hoek 1963:128, Figs. 409-429, 433, 440.

TYPE LOCALITY: England.

NEOTYPE: BM (H4351/60/6); see van den Hoek 1963; p. 128.

DISTRIBUTION: probably widespread.

SPECIMEN EXAMINED: **Sargasso Sea:** 31°N-69°29'W, 3.iii.1970, *Volkmann* (WJW 2359).

The only specimen (about 2.5 cm tall) encountered during this study occurred as an epiphyte on *Sargassum fluitans*.

Cladophora socialis Kuetzing 1849:416, 1854:15, pl. 71, Fig. 1. van den Hoek 1963:43, Figs. 79-91.

TYPE LOCALITY: Tahiti.

TYPE: L (937/253/440).

DISTRIBUTION: Europe, Tropical Oceania, Sargasso Sea.

SPECIMEN EXAMINED: **Sargasso Sea:** 26°57'N-72°58'W, 26.iv.1970, *Moore* (WJW 2650).

The plants, up to 2 cm tall, occurred as epiphytes on *Sargaassum natans*.

Genus *Spongomorpha* Kuetzing, 1843

Spongomorpha arcta (Dillwyn) Kuetzing 1849:417. Collins 1909:359. Taylor 1957:90, pl. 6, Figs. 5-6.

Cladophora arcta (Dillwyn) Kuetzing 1843:263. Collins, Holden and Setchell 1896:224; 1901:815.

TYPE LOCALITY: England.

TYPE: presumably in NMW.

DISTRIBUTION: colder waters of Europe and North America.

SPECIMENS EXAMINED: **Sargasso Sea:** 38°53'N-69°39'W, 10.v.1970, *Woelkerling* (WJW 2561, 2567); 39°05'N-69°48'W, 10.v.1970, *Woelkerling* (WJW 2571).

Specimens up to 2 cm tall were found attached to plants of *Ascophyllum nodosum* and *Fucus vesiculosus* which had drifted out to the Northwestern fringes of the Sargasso Sea (see Woelkerling 1972). *Spongomorpha arcta* is probably not a permanent component of the Sargasso Sea flora.

DIVISION CHROMOPHYTA
CLASS PHAEOPHYCEAE
ORDER ECTOCARPALES
Family Ectocarpaceae

Genus *Ectocarpus* Lyngbye, 1819

Ectocarpus elachistaeformis Heydrich 1892:470, pl. XXV, Fig. 14. Boergesen 1914:18, Fig. 11; 1920:435. Collins and Hervey 1917:70. Earle 1969:132, Fig. 28. Taylor 1928:107, pl. 14, Fig. 12; 1960:202, pl. 29, Fig. 9.

TYPE LOCALITY: New Guinea.

TYPE: probably destroyed.

DISTRIBUTION: Caribbean Islands, Gulf of Mexico, New Guinea, Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 31°N-69°29'W, 3.iii.1970, *Volkmann* (WJW 2382, 2384); 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2211).

Plants up to 5 mm tall occurred as epiphytes on *Sargassum natans* and on an unidentified *Sargassum* sp. Plurilocular organs are relatively abundant but are not as elongate-lanceolate as described by Boergesen (1914).

Genus *Feldmannia,* Hamel, 1939

Feldmannia irregularis (Kuetzing) Hamel 1931-1939:XVII, Fig. 61F. Cardinal 1964:54, Fig. 29. Kuckuck 1963:371, Fig. 6.

Ectocarpus irregularis Kuetzing. Boergesen 1926:25, Figs. 12-14. Chapman 1963:11. Rosenvinge et Lund 1941:50, Figs. 23-24. Sauvageau 1933:101, Figs. 24-27.

TYPE LOCALITY: Adriatic Sea.

TYPE: L.

DISTRIBUTION: northern Europe, Canary Islands, Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2431); 31°N-60°29'W, 3.iii.1970, *Volkmann* (WJW 2366); 34°N-70°W, 7.iii.1970, *Volkmann* (WJW 2413).

The Sargasso Sea specimens occur as epiphytes on *Sargassum fluitans* and *S. natans* and agree well with the account of *Feldmannia irregularis* given by Cardinal (1964). Plurilocular sporangia are common. Chapman (1963) records this taxon (as *Ectocarpus irregularis*) from Jamaica and, following Boergesen (1941), regards *E. rallsiae* (= *Giffordia rallsiae* (Vickers) Taylor (1960, p. 208), a widely distributed taxon in the American tropics) as conspecific. Earle (1969), however, maintains *G. rallsiae* as a distinct species. The precise relationships of *G. rallsiae* and *Feldmannia irregularis* thus remain uncertain and further critical studies of the type and other collections of the two taxa are needed.

Genus *Giffordia* Batters, 1893

Giffordia conifera (Boergesen) Taylor 1960:207. Earle 1969:135, Fig. 21.

Ectocarpus coniferus Boergesen 1914:8, Figs. 5, 6. Collins and Hervey 1917:69.

TYPE LOCALITY: U. S. Virgin Islands.

TYPE: C.

DISTRIBUTION: Sargasso Sea and tropical western Atlantic.

SPECIMENS EXAMINED: **Sargasso Sea:** 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2430); 34°N-70°W, 7.iii.1970, *Volkmann* (WJW 2416).

The Sargasso Sea specimens occur epiphytically on *Sargassum fluitans* and *S. natans* and agree with the original account of Boergesen (1914). Only plurilocular sporangia are present. Hamel (1931-39) considers this taxon to be conspecific with *Feldmannia irregularis*, but Earle (1969) maintains it as a distinct species. The status of the taxon will remain questionable until a critical study of all the ectocarpoid algae of the western tropical Atlantic is undertaken.

Giffordia mitchelliae (Harvey) Hamel 1939:XIV, Fig. 61c, d. Cardinal 1964:45, Fig. 23. Earle 1969:138, Fig. 24. Taylor 1960:206, pl. 29. Figs. 1-2.

Ectocarpus mitchelliae Harvey 1852, p. 142, pl. 12 g. Boergesen 1914:6, Figs. 3-4. 1941:7, Figs. 1-5. Collins and Hervey 1917:69.

TYPE LOCALITY: Nantucket Island, Massachusetts.

TYPE: TCD.

DISTRIBUTION: widespread in tropical and temperate seas.

SPECIMENS EXAMINED: **Sargasso Sea:** 31°N-69°29'W, 3.iii.1970, *Volkmann* (WJW 2361, 2381, 2383); 32°09'N-64°58'W, 16.v.1970, *Woelkerling* (WJW 2666); 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2206, 2218); 39°07'N-70°35'W, 16.viii.1970, *Moore* (WJW 2925).

Specimens up to 5 cm tall occur as epiphytes on *Sargassum fluitans, S. natans,* and on an unidentified species of *Sargassum.* In all cases plurilocular sporangia are abundant.

Giffordia sandriana (Zanardini in Kuetzing) Hamel 1939: XIV. Cardinal 1964:37, Fig. 18. Kylin 1947:10, Fig. 3. Taylor 1960:207.

Ectocarpus sandrianus Zanardini in Kuetzing 1849:451. Rosenvinge et Lund 1941:44, Fig. 18.

TYPE LOCALITY: Adriatic Sea.

TYPE: L.

DISTRIBUTION: Bermuda, Europe, Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 34°N-70°W, 7.iii.1970, *Volkmann* (WJW 2414).

Plants up to 5 cm tall occurred as epiphytes on *Sargassum fluitans* and bore plurilocular sporangia.

Genus *Pylaiella* Bory, 1823

Pylaiella littoralis (L.) Kjellman. Cardinal 1964:11, Fig. 1. Rosenvinge et Lund 1941:5. Taylor 1957:102, pl. 9, Figs. 1-3. Woelkerling 1972:298.

TYPE LOCALITY: Europe.

TYPE: LINN.

DISTRIBUTION: widespread.

SPECIMENS EXAMINED: **Sargasso Sea:** 38°53'N-69°39'W, 10.v.1970, *Woelkerling* (WJW 2559); 39°11'N-69°24'W, 10.v.1970, *Woelkerling* (WJW 2555).

The plants were found as epiphytes on *Fucus vesiculosus* along the northwest fringes of the Sargasso Sea and probably should not be considered as a permanent component of the Sargasso Sea flora (Woelkerling, 1972).

ORDER SPHACELARIALES
Family Sphacelariaceae

Genus *Sphacelaria* Lyngbye, 1819

Sphacelaria fucigera Kuetzing. Sauvageau 1901:145, Fig. 35. Taylor 1960:210, pl. 29, Fig. 5. Womersley 1967:199.

TYPE LOCALITY: Karak Island, Persian Gulf.

TYPE: L (937/71/472).

DISTRIBUTION: cosmopolitan in tropical and temperate waters.

SPECIMENS EXAMINED: **Sargasso Sea:** 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2202); 38°22'N-70°58'W, 12.x.1970, *Volkmann* (WJW 2896); 39°07'N-70°35'W, 16.viii.1970, *Moore* (WJW 2921).

The plants were epiphytic on *Sargassum natans* and an unidentified *Sargassum* and bore numerous propagula. One collection (WJW 2921) also had numerous multicellular hairs.

ORDER DICTYOTALES
Family Dictyotaceae

Genus *Dictyota* Lamouroux, 1809

Dictyota sp.

Two collections [32°09'N-64°58'W, 16.v.1970, *Woelkerling* (WJW 2658) and 39°30'N-71°W, 6.x.1970, *Volkmann* (WJW 2877)] of small plants referrable to *Dictyota* have been made during this study. The former, which contained both male and female reproductive structures and was about 5 cm tall, was found growing on a fragment of *Colpomenia,* which probably became detached and drifted out from the shores of Bermuda. It apparently shares a number of features with *D. dichotoma,* but definite specific determination was not considered possible.

The latter plants were attached to a fertile piece of *Sargassum* (origin uncertain) and were very young (less than 2 cm tall); specific determination likewise could not be made. It seems more probable that *Dictyota* is an invader rather than a permanent component of the Sargasso Sea flora considering that both host plants themselves appear to be invaders.

Prat (1935, p. 128) makes mention of a *Dictyota cervicornis* from this region, but no specimens referrable to that species have been encountered during the present study.

Genus *Padina* Adanson, 1763

Padina sp.

A very young *Padina* plant [32°09′N-64°58′W, 16.v.1970, *Woelkerling* (WJW 2657)] occurred on a piece of *Colpomenia* which apparently had drifted out from Bermuda. Specific determination was not possible and it seems probable that *Padina* is an invader rather than a permanent component of the Sargasso Sea flora.

ORDER CHORDARIALES
Family Elachisteaceae

Genus *Elachistea* Duby, 1830

Elachistea lubrica Ruprecht. Collins, Holden, and Setchell 1898:480. Taylor 1957:140. Woelkerling 1972:297.

TYPE LOCALITY: Okhotsk Sea.

TYPE: LE.

DISTRIBUTION: reported from eastern North America, Greenland, and the Okhotsk Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 38°53′N-69°39′W, 10.v.1970, *Woelkerling* (WJW 2564); 39°05′N-69°48′W, 10.v.1970, *Woelkerling* (WJW 2569); 39°11′N-69°24′W, 10.v.1970, *Woelkerling* (WJW 2547; 2556).

An invader species attached to drifting *Ascophyllum* and *Fucus* (see Woelkerling, 1972). The specimens have been referred to *Elachistea lubrica* because of the apparent absence of moniliform paraphyses (see Taylor, 1957, p. 139),

but critical study is needed to determine whether this is a reliable character of specific distinction. Lund (1959) and Rosenvinge (1893) have regarded *E. lubrica* as a variety of *E. fucicola.*

Family Chordariaceae

Genus *Chordaria* C. Agardh, 1817

Chordaria flagelliformis (Mueller) C. Agardh. Kylin 1947: 59, Figs. 51A, D. Lund 1959:121, Figs. 26, 27. Taylor 1957:148, pl. 12, Fig. 6; pl. 14, Fig. 4.

TYPE LOCALITY: Denmark.

TYPE: not located.

DISTRIBUTION: cooler waters of North America and Europe.

SPECIMENS EXAMINED: **Sargasso Sea:** 39°05'N-69°48'W, 10.v.1970, *Woelkerling* (WJW 2576); 39°11'N-69°24'W, 10.v.1970, *Woelkerling* (WJW 2554).

The plants were epiphytes on invading specimens of *Fucus* (see Woelkerling, 1972) and are not considered permanent components of the Sargasso Sea flora.

ORDER PUNCTARIALES

Family Punctariaceae

Genus *Colpomenia* Derbes and Solier, 1856

Colpomenia sinuosa (Roth) Derbes and Solier. Taylor 1928: 110, pl. 7, Fig. 1, pl. 19, Figs. 3-4; 1960:260, pl. 36, Fig. 1. Womersley 1967:244.

TYPE LOCALITY: Cadiz, Spain.

TYPE: probably lost.

DISTRIBUTION: widespread.

SPECIMEN EXAMINED: **Sargasso Sea:** 32°09'N-64°58'W, 16.v.1970, *Woelkerling* (WJW 2655).

The plant collected almost certainly drifted out into Sargasso Sea waters from Bermuda and does not represent a permanent component of the flora.

Genus *Petalonia* Derbes and Solier, 1850

Petalonia fascia (Mueller) Kuntze. Lund 1947:31, Fig. 10. Taylor 1957:167, pl. 14, Fig. 5; pl.15, Fig. 3.

Ilea fascia (Mueller) Fries. Kylin 1947:77, Fig. 61A.

TYPE LOCALITY: Denmark.

TYPE: not located.

DISTRIBUTION: widespread.

SPECIMEN EXAMINED: **Sargasso Sea:** 39°11'N-69°24'W, 10.v.1970, *Woelkerling* (WJW 2549).

This taxon is an invading element attached to *Fucus vesiculosus* (see Woelkerling, 1972).

Genus *Punctaria* Greville, 1830

Punctaria latifolia Greville. Collins, Holden, and Setchell 1895:82; 1901:873; 1907:1388. Taylor 1957:166, pl. 15, Fig. 5.

TYPE LOCALITY: Great Britain.

TYPE: not located.

DISTRIBUTION: widespread.

SPECIMEN EXAMINED: **Sargasso Sea:** 39°05'N-69°48'W, 10.v.1970, *Woelkerling* (WJW 2573).

A single, rather small and battered plant was found attached to an invading *Fucus* element (see Woelkerling, 1972).

Punctaria plantaginea (Roth) Greville. Rosenvinge et Lund 1947:11, Fig. 2; 1959:133, Fig. 28. Taylor 1957:166, pl. 15, Fig. 4; pl. 16, Fig. 4.

TYPE LOCALITY: Kattegat Channel between Denmark and Sweden.

TYPE: probably destroyed.

DISTRIBUTION: widespread.

SPECIMENS EXAMINED: **Sargasso Sea:** 38°53'N-69°39'W, 10.v.1970, *Woelkerling* (WJW 2560); 39°05'N-69°48'W, 10.v.1970, *Woelkerling* (WJW 2575).

Two small plants occurred as epiphytes on *Fucus;* they are not considered permanent components of the Sargasso Sea flora (see Woelkerling, 1972).

Genus *Scytosiphon* C. Agardh, 1811

Scytosiphon lomentaria (Lyngbye) C. Agardh. Rosenvinge et Lund 1947:27, Fig. 9; 1959:103, Fig. 20. Taylor 1957: 168, pl. 15, Fig. 2; pl. 16, Fig. 3.

TYPE LOCALITY: Denmark.

TYPE: C.

DISTRIBUTION: nearly cosmopolitan.

SPECIMENS EXAMINED: **Sargasso Sea:** 38°53'N-69°39'W, 10.v.1970, *Woelkerling* (WJW 2562); 39°05'N-69°48'W, 10.v.1970, *Woelkerling* (WJW 2574); 39°11'N-69°24'W, 10.v.1970, *Woelkerling* (WJW 2548).

These collections occurred as epiphytes on *Fucus* and probably do not represent permanent components of the Sargasso Sea flora. The species does, however, occur in Bermuda and along the southeastern U. S. Coast (Taylor, 1960), and may eventually be found to occur on *Sargassum fluitans* or *S. natans* in the Sargasso Sea.

Family Striariaceae

Genus *Isthmoplea* Kjellman, 1877

Isthmoplea sphaerophora (Harvey in Hooker) Kjellman. DeToni 1895:569. Kylin 1947:67, Figs. 56D-E. Taylor 1957:156, pl. 9, Figs. 4-5. Woelkerling 1972:298.

Ectocarpus sphaerophorus Carmichael. Harvey 1846: pl. CXXVI.

TYPE LOCALITY: Appin, Scotland.

TYPE: TCD.

DISTRIBUTION: cooler waters of Eastern North America and Europe.

SPECIMEN EXAMINED: **Sargasso Sea:** 38°53'N-69°39'W, 10.v.1970, *Woelkerling* (WJW 2566).

The single collection contains a number of fertile plants attached to *Polysiphonia lanosa,* in turn an epiphyte on a plant of *Ascophyllum,* which had drifted out into the Northwestern fringes of the Sargasso Sea (see Woelkerling, 1972).

ORDER FUCALES

Family Fucaceae

Genus *Ascophyllum* Stackhouse 1809

Ascophyllum nodosum (L.) Le Jolis. Kylin 1947:84. Taylor 1957:195, pl. 27, Figs. 1-2.

TYPE LOCALITY: Atlantic Ocean.

TYPE: LINN.

DISTRIBUTION: widespread in colder waters of the northern hemisphere.

SPECIMENS EXAMINED: **Sargasso Sea:** 38°53'N-69°39'W, 10.v.1970, *Woelkerling* (WJW 2558); 39°05'N-69°48'W, 10.v.1970, *Woelkerling* (WJW 2568); 39°11'N-69°24'W, 10.v.1970, *Woelkerling* (WJW 2546).

The plants were found adrift along the northwest fringes of the Sargasso Sea; there is some question as to whether they should be regarded as permanent components of the Sargasso Sea flora (see Woelkerling, 1972).

Genus *Fucus* Linneaus, 1753

Fucus vesiculosus L. Harvey 1852:71. Kylin 1947:83, Tab. 17, Figs. 53-54. Taylor 1957:192, pl. 25, Figs. 1-3.

TYPE LOCALITY: Atlantic Ocean.

TYPE: LINN.

DISTRIBUTION: widespread in colder waters of northern hemisphere.

SPECIMENS EXAMINED: **Sargasso Sea:** 38°53'N-69°39'W, 10.v.1970, *Woelkerling* (WJW 2563); 39°05'N-69°48'W, 10.v.1970. *Woelkerling* (WJW 2570); 39°11'N-69°24'W, 10.v.1970, *Woelkerling* (WJW 2557).

The plants were found adrift along the northwest fringes of the Sargasso Sea with *Ascophyllum* and *Sargassum natans* and bore a number of epiphytes (see Woelkerling, 1972).

Family Sargassaceae

Genus *Sargassum* C. Agardh, 1820

The tropical American Atlantic species of *Sargassum* are poorly known and specific limits and distinctions remain

very unclear (see Taylor, 1960, p. 268). Moreover, keys to species occurring in this region (e.g. Howe, 1920; Taylor, 1928, 1960) are based largely on vegetative features rather than on reproductive structures, which appear to be of more fundamental significance (Setchell, 1931; Womersley, 1954). The situation is further complicated by the fact that the two species of *Sargassum* most commonly found in the Sargasso Sea apparently have never been found in a fertile state (see, however, Parr, 1939).

During the course of this study, seven apparently distinct species of *Sargassum* have been found adrift in the western Sargasso Sea. Only three of these, however, have been identified with any certainty. The remaining four have not been definitely identified as yet and, following the approach of Winge (1923), are referred to here as *Sargassum* A, B, etc., to avoid further name confusion until such time as a critical monographic study of the genus is undertaken for this region.

Differences between the seven taxa are summarized as follows:

Conspectus of *Sargassum* Taxa in the Western Sargasso Sea

1. Plants sterile, pelagic, without evidence of a basal holdfast. ..... 2.
   2. Stems smooth; vesicles often apiculate; leaves linear, up to 4 mm wide. ..... *S. natans.*
   2. Stems muriculate; vesicles at most muticous; leaves lanceolate, up to 8 mm wide. ..... *S. fluitans.*
1. Plants commonly fertile, normally attached, usually showing evidence of a holdfast. ..... 3.
   3. Fruiting branches often carpophyllaceous (i.e. of mixed receptacles, leaves, and vesicles). ..... 4.
      4. Receptacles pedicellate; cryptostomata tending to be in a single row adjacent to the costa. .... "*Sargassum* D."

4. Receptacles not pedicellate; cryptostomata scattered. ..... *"Sargassum* B."
3. Fruiting branches not carpophyllaceous (i.e. composed solely of receptacles). ..... 5.
5. Receptacles pedicellate. ..... 6.
6. Receptacles commonly spiny; costa not spiny or dentate. .... *Sargassum hystrix* var. *buxifolium.*
6. Receptacles not spiny; costa prominently dentate to spiny. ..... *"Sargassum* A."
5. Receptacles sessile. ..... *"Sargassum* C."

Sargassum fluitans (Boergesen) Boergesen 1914a:6. Taylor 1928:127, pl. 18, Fig. 9; pl. 19, Fig. 5; 1960:281, pl. 39, Fig. 2, pl. 40, Fig. 7.

Sargassum hystrix J. Ag. var. *fluitans* Boergesen 1914a: 11, Fig. 8. Winge 1923:23, Fig. 6 (as *"Sargassum* III").

TYPE LOCALITY: Sargasso Sea.

TYPE: C.

DISTRIBUTION: known only from the Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 21°58'N-68°20'W, 24.iv.1970, *Moore* (WJW 2639); 26°57'N-72°58'W, 26.iv.1970, *Moore* (WJW 2649); 28°N-70°W, 4.vii.1970, *Volkmann* (WJW 2738); 31°N-69° 29'W, 3.iii.1970, *Volkmann* (WJW 2394); 31°N-70°W, 5.vii.1970, *Volkmann* (WJW 2731); 32°09'N-64°58'W, 16.v.1970, *Woelkerling* (WJW 2654); 33°58'N-69°56'W, 15.v.1970, *Woelkerling* (WJW 2602); 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2224), 7.iii.1970, *Volkmann* (WJW 2418), 6.vii.1970, *Volkmann* (WJW 2742), 14.viii.1970, *Moore* (WJW 2933); 36°N-70°36'W, 9.xii.1970, *Moore* (WJW 2947); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2616); 37°30'N-70°W, 8.vii.1970, *Volkmann* (WJW 2712); 38°34'N-69°11'W, 19.v.1970, *Woelkerling* (WJW 2606).

Sargassum fluitans is the less frequently encountered of the two species of *Sargassum* endemic to the Sargasso Sea but apparently enjoys almost as wide a distribution. The specimens examined during this study were commonly covered with bryozoans and to a lesser extent with epibiotic algae.

Sargassum hystrix J. Agardh var. *buxifolium* (Chauvin) J. Agardh 1889:91, tab VII, Fig. 1. Boergesen 1914:221. Chapman 1963:45. Earle 1969:225, Fig. 118. Grunow 1915:399. Howe 1920:594. Taylor 1928:128, pl. 18, Fig. 1, pl. 19, Fig. 9; 1960:279, pl. 38, Fig. 2, pl. 40, Fig. 6.

TYPE LOCALITY: Caribbean Area (see DeToni 1895:53).

TYPE: LD(?).

DISTRIBUTION: Florida to Brazil, Caribbean Islands, Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 36°N-70°36'W, 9.xii.1970, *Moore* (WJW 2912); 39°30'N-71°W, 6.x.1970, *Volkmann* (WJW 2873).

The specimens examined agree well with the descriptions and illustrations of Earle (1969) and Taylor (1960), and probably are the same as "*Sargassum* VI" of Winge (1923, p. 25, Fig. 10). The material was collected in the immediate vicinity of the Gulf Stream, the same region reported by Winge (1923), and apparently is known mainly from drift specimens (Earle, 1969; Taylor, 1928, 1960).

Both specimens bore non-carpophyllaceous receptacles which were simple or once funcate, terete or slightly compressed, verrucose or occasionally with odd spines, pedicellate, and more or less racemose.

Sargassum natans L. Boergesen 1914a:7, Figs. 3-7. Taylor 1928:128, pl. 18, Figs. 2-4, pl. 19, Fig. 13; 1960: pl. 37, Fig. 2, pl. 40, Figs. 3, 8. Winge 1923:24, Figs. 3-5 (as "Sargassum I & III").

TYPE LOCALITY: Sargasso Sea.

TYPE: LINN.

DISTRIBUTION: known only from the Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 20°50'N-67°15'W, 24.iv.1970, *Moore* (WJW 2645); 21°58'N-68°20'W, 24.iv.1970, *Moore* (WJW 2640); 26°50'N-71°48'W, 5.iii.1970, *Volkmann* (WJW 2422); 26°57'N-72°58'W, 26.iv.1970, *Moore* (WJW 2653); 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2437), 4.vii.1970, *Volkmann* (WJW 2739), 31°N-69°29'W, 3.iii.1970, *Volkmann* (WJW 2393); 31°N-70°W, 5.vii.1970, *Volkmann* (WJW 2732); 32°09'N-64°58'W, 16.v.1970, *Woelkerling* (WJW 2662); 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2223), 7.iii.

1970, *Volkmann* (WJW 2417), 13.v.1970, *Volkmann* (WJW 2607), 30.vi.1970, *Volkmann* (WJW 2723), 6.vii.1970, *Volkmann* (WJW 2743), 14.viii.1970, *Volkmann* (WJW 2931); 35°54′N-70°30′W, 13.viii.1970, *Moore* (WJW 2904); 36°N-70°36′W, 9.xii.1970, *Moore* (WJW 2950); 36°28′N-70°29′W, 15.viii.1970, *Moore* (WJW 2905); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2617); 37°30′N-70°W, 8.vii.1970, *Woelkerling* (WJW 2711); 38°22′N-70°58′W, 12.x.1970, *Volkmann* (WJW 2897); 38°34′N-69°11′W, 19.v.1970, *Woelkerling* (WJW 2605); 39°07′N-70°35′W, 16.viii.1970, *Moore* (WJW 2909); 39°11′N-69°24′W, 10.v.1970, *Woelkerling* (WJW 2644).

Sargassum natans plants comprise the vast bulk of the Sargasso Sea macroscopic vegetation, estimated by Parr (1939) to be up to 40 million metric tons. It also harbored the greatest variety and quantity of epibiotic algae. The considerable quantities of *S. natans* which wash up on the shores of Bermuda, in contrast, are apparently devoid of epiphytes (Woelkerling, personal observations).

"Sargassum A"

The single specimen [39°30′N-70°W, 6.x.1970, *Volkmann* (WJW 2867)] referred to this "taxon" bears a small, discoid holdfast and a sparsely branched, nearly terete main axis with a few, scattered, long laterals whose stems are muriculate. The leaves are lanceolate, up to 3 mm broad and 30 mm long, finely serrate, with a prominent dentate to spiny costa. Cryptostomata are lacking. Vesicles up to 5 mm in diameter are mostly single and pedicellate and scattered among the leaves.

The receptacles are not carpophyllaceous, and are simple or up to several times furcate, terete, verrucose, not spiny or dentate, pedicellate, racemose, and up to 10 mm long.

While these features are most closely associated with *Sargassum filipendula* var. *montagnei* as described in Taylor (1960), definite specific affiliation of the specimen in question remains uncertain.

"Sargassum B"

The single specimen [34°N-70°W, 10.i.1970, *Volkmann* (WJW 2222)] lacks a holdfast and has a smooth stem with a number of short lateral branches. The leaves are mostly

lanceolate ovate, up to 5 mm broad and 30 mm long, serrate, have costae without ridges or wings and bear scattered cryptostomata. Vesicles up to 6 mm broad are short pedicellate and are scattered among the leaves and receptacles.

The receptacles are generally carpophyllaceous and usually 2-4 times furcate, are terete, not dentate or spiny, are not pedicellate and are borne in dense cymose clusters.

Although this taxon shows many of the features of *Sargassum vulgare* C. Agardh as described in Taylor (1960), final specific identification remains uncertain.

"Sargassum C"

The single specimen [33°58.5'N-69°56.5'W, 15.v.1970, *Woelkerling* (WJW 2589)] lacks a holdfast and has muriculate stems bearing lateral branches of variable length. The leaves are linear lanceolate, up to 3 mm broad and 30 mm long, entire or finely serrate, and bear inconspicuous costae and scattered cryptostomata. Shortly pedicellate vesicles up to 5 mm in diameter are scattered along the branches.

The receptacles generally are not carpophyllaceous, are one to several times furcate, terete, verrucose, generally not pedicellate, and are racemose.

This specimen could not be linked to any of the species described by Taylor (1960). In some respects it is similar to what Taylor (1960) calls *Sargassum filipendula* var. *montagnei,* but differs in the nature of the costa and in having non-pedicellate receptacles.

"Sargassum D"

The one specimen [34°N-70°W, 10.i.1970, *Volkmann* (WJW 2225)] lacks a holdfast and has a stem that is muriculate in the younger portions and smooth in the older portions. Lateral branches vary in length and bear lanceolate leaves up to 3 mm broad and 30 mm long which are mostly entire, costate, and bear cryptostomata which tend to lie in a single row on each side of the costa. Shortly pedicellate vesicles up to 5 mm in diameter are scattered along the lateral branches.

The receptacles are carpophyllaceous, simple or once furcate, terete, not dentate or spiny, pedicellate, and generally cymose.

Of the species described by Taylor (1960), this specimen most closely approximates *Sargassum acinarium* (L.) C. Agardh, but apparent differences in receptacle morphology leaves some doubt as to the specimen's true affinities.

A second specimen [37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2673)] shares many features with "*Sargassum* D" including the linear distribution of cryptostomata, but the racemose nature of the receptacles leaves some doubt as to its exact relationships until further material becomes available for study.

CLASS RHODOPHYCEAE

SUBCLASS BANGIOPHYCIDAE

ORDER BANGIALES

Family Bangiaceae

Genus *Asterocytis* Gobi, 1879

Asterocytis ramosa (Twaites in Harvey) Gobi. Boergesen 1915:3, Fig. 1. Chapman 1963:49. Kylin 1944:6, Fig. 1d-f. Rosenvinge 1909:77, Fig. 17. Taylor 1928:132, pl. 20, Figs. 1-2; 1960:287. Wille 1900:7, Tab. 1, Figs. 8-14.

Hormospora ramosa Twaites in Harvey 1846-51:Pl. CCXII.

TYPE LOCALITY: Wareham, Dorsetshire, Great Britain.

TYPE: TCD.

DISTRIBUTION: widespread.

SPECIMENS EXAMINED: **Sargasso Sea:** 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 3957); 39°07'N-70°35'W, 16.viii.1970, *Moore* (WJW 2920).

In both cases the plants were epiphytic on *Cladophora* which, in turn, was growing on *Sargassum natans*.

Hamel (1924), Boergesen (1927), and Pham Hoang-Ho (1969), among others, have referred this species to the synonomy of *Asterocystis ornata* (C. Agardh) Hamel.

Kylin (1944) and Taylor (1957, 1960), however, prefer to separate the two taxa on grounds that *A. ramosa* is marine and *A. ornata* freshwater. The validity of such a separation requires further investigation, and until new evidence comes to light, the two taxa will be kept distinct for purposes of the present study.

Genus *Erythrocladia* Rosenvinge, 1909

Erythrocladia subintegra Rosenvinge 1909:73, Figs. 13-14. Boergesen 1915:7, Figs. 3-4. Collins and Hervey 1917:95. Pham-Hoang-Ho 1969:80, Figs. 2-12. Taylor 1960:290.

TYPE LOCALITY: Hirshals, Skagerak, Denmark.

TYPE: C.

DISTRIBUTION: Europe, western tropical Atlantic, Southeast Asia.

SPECIMENS EXAMINED: **Sargasso Sea:** 31°N-69°29'W, 3.iii.1970, *Volkmann* (WJW 2387, 2391, 2392); 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2212), 7.iii.1970, *Volkmann* (WJW 2405, 2406); 36°N-70°36'W, 9.xii.1970, *Moore* (WJW 2939, 2940).

All specimens occurred as epiphytes on hydroids which, in turn, were growing on *Sargassum fluitans, S. natans,* or *Sargassum* sp.

Erythrocladia recondita Howe et Hoyt 1916:112, pl. 12, Figs. 1-5, pl. 13, Fig. 1. Hoyt 1920:467, pl. CXVI, Fig. 1, pl. CXVII, Figs. 1-5.

TYPE LOCALITY: Beaufort, North Carolina.

TYPE: NY.

DISTRIBUTION: type locality, Sargasso Sea.

SPECIMEN EXAMINED: **Sargasso Sea:** 39°30'N-71°W, 6.x.1970, *Volkmann* (WJW 2866).

The specimens occurred epizoically on hydroids which in turn grew on an unidentified *Sargassum.*

Genus *Erythrotrichia* Areschoug, 1850

Erythrotrichia carnea (Dillwyn) J. Agardh. Boergesen 1915:7. Collins and Hervey 1917:94. Hoyt 1920:466, Fig. 24. Rosenvinge 1909:67, Fig. 8. Taylor 1957:202, pl. 28, Figs. 13-15; 1960:292. Woelkerling 1972:298.

TYPE LOCALITY: Great Britain.

TYPE: NMW.

DISTRIBUTION: widespread.

SPECIMENS EXAMINED: **Sargasso Sea:** 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2433); 31°N-69°29'W, 3.iii.1970, *Volkmann* (WJW 2360; 2390); 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2216), 7.iii.1970, *Volkmann* (WJW 2404); 39°11'N-69°24'W, 10.v.1970, *Woelkerling* (WJW 2551).

With the exception of the last cited specimen, all plants occurred epizoically on hydroids which in turn were attached to *Sargassum fluitans, S. natans,* or *Sargassum* sp. In the other collection, the plants occurred epiphytically on *Fucus* (Woelkerling, 1972).

SUBCLASS FLORIDEOPHYCIDAE

ORDER NEMALIALES

Family Acrochaetiaceae

Four species of *Audouinella* (*A. daviesii, A. hallandica, A. microscopica, A. saviana* [= *A. thuretii*]) and two species of *Colaconema* (*C. infestans, C. secundata*) occur in the western Sargasso Sea and are the subject of a recent detailed morphotaxonomic study (Woelkerling, 1973).

ORDER CRYPTONEMIALES

Family Corallinaceae

Subfamily Corallineae

Genus *Jania* Lamouroux, 1812

Jania adherens Lamouroux. Boergesen 1917:195, Figs. 184-187. Chapman 1963:86, Fig. 85. Taylor 1928:205. Howe 1920:589. 1960:413, pl. 49, Figs. 1-2.

TYPE LOCALITY: Mediterranean Sea.

TYPE: not located.

DISTRIBUTION: widespread in tropical and warm temperate waters.

SPECIMEN EXAMINED: **Sargasso Sea:** 32°09'N-65°58'W, 16.v.1970, *Woelkerling* (WJW 2656).

The single collection occurred as an epiphyte on a plant of *Colpomenia* (q.v.) which probably drifted out from the

Bermuda Islands; consequently this species of *Jania* probably does not represent a permanent component of the Sargasso Sea flora.

Jania capillacea Harvey 1853:85. Boergesen 1917:198, Fig. 188. Chapman 1963:86, Fig. 86. Collins, Holden, and Setchell 1895:150. Howe 1920:589. Taylor 1928:206, pl. 29, Figs. 2, 10. 1960:413, pl. 49, Figs. 1-2.

TYPE LOCALITY: Bahia Honda, Florida.

TYPE: TCD.

DISTRIBUTION: tropical western Atlantic.

SPECIMENS EXAMINED: **Sargasso Sea:** 31°N-69°29'W, 3.iii.1970, *Volkmann* (WJW 2217); 36°N-70°36'W, 9.xii.1970, *Moore* (WJW 2945); 39°07'N-70°35'W, 16.viii.1970, *Moore* (WJW 2926).

Jania capillacea has been found growing on *Sargassum fluitans, S. natans,* and on several unidentified *Sargassum* taxa. Prat (1935) previously reported this taxon from the Sargasso Sea.

Subfamily Melobesieae

Genus *Fosliella* Howe, 1920

Fosliella farinosa (Lamouroux) Howe 1920:587. Chapman 1963:91, Fig. 92. Dawson 1960:30, pl. 21, Fig. 1, pl. 22, Fig. 1. Taylor 1960:388. Womersley and Bailey 1970: 309.

Melobesia farinosa Lamouroux. Lemoine in Boergesen 1917:170, Fig. 165. Hoyt 1920:523, Fig. 47. Taylor 1928:211.

TYPE LOCALITY: Adriatic Sea.

TYPE: CN.

DISTRIBUTION: nearly cosmopolitan.

SPECIMENS EXAMINED: **Sargasso Sea:** 31°N-69°29'W, 3.iii.1970, *Volkmann* (WJW 2355); 34°N-70°W, 13.v.1970, *Woelkerling* (WJW 2608).

The plants occurred epiphytically on *Sargassum fluitans* and *S. natans.*

Fosiella lejolisii (Rosanoff) Howe 1920:588. Masaki 1968: 23, pls. XII, XLIX, L. Taylor 1957:253, pl. 36, Figs. 6-8.

Melobesia lejolisii Rosanoff 1866:62, pl. 1, Figs. 1-13, pl. 7, Figs. 9-11. Rosenvinge 1917:238, Figs. 156-159.

TYPE LOCALITY: Cherbourg, France.

TYPE: not located.

DISTRIBUTION: Europe, Atlantic North America, Japan, Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2436); 31°N-69°29'W, 3.iii.1970, *Volkmann* (WJW 2356, 2378); 32°09'N-64°58'W, 16.v.1970, *Woelkerling* (WJW 2659, 2672); 33°58.5'N-69°56.5'W, 15.v.1970, *Woelkerling* (WJW 2590, 2600); 34°N-70°W, 7.iii.1970, *Volkmann* (WJW 2400, 2402); 36°N-70°36'W, 9.xii.1970, *Moore* (WJW 2946, 2948); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2634); 39°07'N-70°35'W, 16.viii.1970, *Moore* (WJW 2928).

Fosliella lejolesii occurs as an epiphyte on *Sargassum fluitans, S. natans, Sargassum* sp. as well as on other algae, and in terms of numbers of individuals, is probably the most common red alga in the Sargasso Sea. Only *Ceramium gracillimum* (q.v.) approaches the same quantitative frequency.

According to Taylor (1960, p. 387) *Fosiella lejolisii* is distinguished from *L. affinis* and *L. bermudense* by having thallus cells 6-7 μm broad rather than 9-18 μm broad or 10-12 μm broad. However, cells up to 13 μm broad were found in Sargasso Sea collections, and this suggests that the relationships of the three taxa require critical reinvestigation.

ORDER CERAMIALES

Family Ceramiaceae

Genus *Antithamnion* Naegeli, 1847

Antithamnion antillarum Boergesen 1917:226, Figs. 213-216. Taylor 1960:499. Womersley and Bailey 1970:322.

TYPE LOCALITY: St. Thomas, Virgin Islands.

TYPE: C.

DISTRIBUTION: Virgin Islands, Sargasso Sea, tropical Pacific Ocean.

SPECIMENS EXAMINED: **Sargasso Sea:** 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2426); 31°N-69°29'W, 3.iii.1970, *Volkmann* (WJW 2376).

In both cases, plants occurred epiphytically on *Sargassum natans*. One (WJW 2376) bore tetrasporangia; the other was sterile. The genus *Antithamnion* in this area needs critical reinvestigation in light of recent studies of Wollaston (1968, 1971) on southern Australian and Pacific Coast species.

Genus *Ceramium* Roth, 1797

Ceramium gracillimum (Kuetzing) Griffiths and Harvey. Dawson 1962:57, pl. 20, Figs. 2-3. Feldmann-Mazoyer in Boergesen 1952:42, Fig. 21. Nakamura 1965:136, pl. 1, 5-6, Fig. 6.

Ceramium gracillimum var. *byssoideum* (Harvey) Mazoyer 1938:323. Chapman 1963:178, Fig. 186. Feldmann-Mazoyer 1940:293, Fig. 109.

Ceramium byssoideum Harvey 1853:218. Taylor 1928: 190, pl. 27, Figs. 20, 21; 1960:528, pl. 67, Figs. 1-3.

Ceramium transversale Collins and Hervey 1917:145, pl. 5, Figs. 29-31. Boergesen 1918:243.

TYPE LOCALITY: Trieste, Italy.

TYPE: C.

DISTRIBUTION: widespread in tropical and warm temperate seas; England.

SPECIMENS EXAMINED: **Sargasso Sea:** 21°58.5'N-68°20'W, 24.iv.1970, *Moore* (WJW 2642); 26°50'N-71°48'W, 5.iii.1970, *Volkmann* (WJW 2419); 26°57'N-72°58'W, 26.iv.1970, *Woelkerling* (WJW 2652); 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2428); 31°N-70°W, 5.vii.1970, *Volkmann* (WJW 2733); 32°09'N-64°58'W, 16.v.1970, *Woelkerling* (WJW 2661, 2669); 33°58.5'N-69°56.5'W, 16.v.1970, *Woelkerling* (WJW 2591); 34°N-70°W, 13.v.1970, *Woelkerling* (WJW 2609), 6.vii. 1970, *Volkmann* (WJW 2746); 35°54'N-70°30'W, 13.viii.1970, *Moore* (WJW 2903); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2619); 37°30'N-70°W, 8.vii.1970, *Volkmann* (WJW 2705); 38°22'N-70°58'W, 12.x.1970, *Volkmann* (WJW 2890).

Ceramium gracillimum is a common epiphyte on *Sargassum fluitans, S. natans,* and *Sargassum* sp. as well as on

other algae attached to *Sargassum* and often occurs in considerable numbers. One collection (WJW 2619) bore tetrasporangial individuals; the remainder were sterile.

Taylor (1960, p. 528) maintains *Ceramium byssoideum* and *C. gracillimum* as distinct taxa; however, following Feldmann-Mazoyer (1940), Nakamura (1965) and others the former is referred to the conspecificity of the latter. Likewise, *C. transversale* is regarded as conspecific in accordance with Feldmann-Mazoyer (1940).

Ceramium fastigiatum Harvey in Hooker [non *C. fastigiatum* Roth = *Polysiphonia fastigiata* (Roth) Greville]. Boergesen 1918:241, Fig. 231. Chapman 1963:177, Fig. 184a-c. Nakamura 1965:129, pl. 1(3), Fig. 4. Taylor 1928:191; 1957:309, pl. 47, Figs. 3-5, 7, pl. 48, Figs. 2-4, pl. 49, Figs. 3-4, pl. 50, Fig. 4, pl. 51, Figs. 6-7; 1960:526, pl. 67, Figs. 4-6.

TYPE LOCALITY: Great Britain.

TYPE: TCD.

DISTRIBUTION: widespread.

SPECIMENS EXAMINED: **Sargasso Sea:** 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2427); 31°N-69°29′W, 3.iii.1970, *Volkmann* (WJW 2348, 2370, 2373); 34°N-70°W, 7.iii.1970, *Volkmann* (WJW 2395); 39°07′N-70°35′W, 16.viii.1970, *Moore* (WJW 2923).

This taxon occurs as an epiphyte on *Sargassum fluitans*, *S. natans*, and *Sargassum* sp. All specimens examined were sterile. The author citations of Taylor (1960) and Boergesen (1918) (i.e. *C. fastigiatium* (Roth) Harvey) are incorrect; Roth's taxon was described from Germany and has been referred by Greville (1824) to *Polysiphonia* (see DeToni, 1903, p. 945-6) whereas Harvey's taxon was described from Great Britain (Harvey in Hooker, 1833).

Genus *Crouania* J. Agardh, 1842

Crouania attenuata (C. Agardh) J. Agardh, Boergesen 1917:230, Figs. 219-221. Chapman 1963:167, Fig. 173. Collins and Hervey 1917:142. Harvey 1853:226, Tab. XXXI, D. Taylor 1928:193, pl. 27, Figs. 7-9, pl. 32, Fig. 9.

TYPE LOCALITY: Mediterranean Sea.

TYPE: LD.

DISTRIBUTION: Mediterranean, England, tropical western Atlantic Ocean, Japan.

SPECIMENS EXAMINED: **Sargasso Sea:** 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2626); 39°30'N-71°W, 6.x.1970, *Volkmann* (WJW 2882).

Male (WJW 2626) and tetrasporangial (WJW 2882) individuals occurred as epiphytes on *Sargassum natans* and on *Sargassum* sp.

Genus *Griffithsia* C. Agardh, 1817

Griffithsia radicans Kuetzing 1862:11, tab. 33, Fig. A-C. Taylor 1960:515.

TYPE LOCALITY: Brazil.

TYPE: L.

DISTRIBUTION: Brazil, Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2629); 39°30'N-71°W, 6.x.1970, *Volkmann* (WJW 2881).

The plants occurred as epiphytes on *Sargassum natans* and *Sargassum* sp. and appeared to have some tetrasporangial initials. They are referred to this species because of their agreement with the description given by Taylor (1960).

Genus *Spermothamnion* Areschoug, 1847

Spermothamnion investiens (Crouan in Maze et Schramm) Vickers. Boergesen 1909:17, Fig. 10; 1917:200, Figs. 189-190; 1920:461, Fig. 422. Collins and Hervey 1917:132. Howe 1920:578. Taylor 1960:520.

TYPE LOCALITY: Guadeloupe.

TYPE: PC.

DISTRIBUTION: North Carolina, Caribbean Islands, Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 39°30'N-71°W, 6.x.1970, *Volkmann* (WJW 2863).

Female and tetrasporangial plants were found as epiphytes on "*Sargassum* A" and may not, therefore, be a

permanent component of the Sargasso Sea flora. Tropical and subtropical western Atlantic members of the Spermothamneae are in need of thorough reinvestigation in light of the recent study of Gordon (1972).

Genus *Wrangelia* C. Agardh, 1828

Wrangelia argus (Montagne) Montage. Boergesen 1916: 116, Figs. 125-6. Gordon 1972:40. Taylor 1928:144, pl. 20, Fig. 13, pl. 22, Fig. 6, pl. 32, Fig. 4; 1960:502, pl. 66, Figs. 7-8.

TYPE LOCALITY: unknown.

TYPE: probably C.

DISTRIBUTION: see Gordon 1972, p. 40.

SPECIMENS EXAMINED: **Sargasso Sea:** 31°N-69°29'W, 3.iii.1970, *Volkmann* (WJW 2371); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2628); 39°30'N-71°W, 6.x.1970, *Volkmann* (WJW 2880).

Male and tetrasporangial plants occurred as epiphytes on *Sargassum natans* and on *Sargassum* sp.

Family Dasyaceae

Genus *Dasya* C. Agardh, 1824

Dasya rigidula (Kuetzing) Ardissone. Howe 1920:576. Taylor 1960:558, pl. 72, Fig. 4.

TYPE LOCALITY: Spalato, Adriatic Sea.

TYPE: L.

DISTRIBUTION: Bermuda, Caribbean Islands, Mexico, Sargasso Sea, Venezuela, Adriatic and Mediterranean Seas.

SPECIMENS EXAMINED: **Sargasso Sea:** 34°N-70°W, 7.iii.1970, *Volkmann* (WJW 2398); 36°N-70°36'W, 9.xii.1970, *Moore* (WJW 2941); 39°30'N-71°W, 6.x.1970, *Volkmann* (WJW 2861, 2884).

Male, female, and tetrasporangial plants occurred epiphytically on *Sargassum fluitans* and on *Sargassum* sp.

Genus *Heterosiphonia* Montagne, 1842

Heterosiphonia wurdemanni (Bailey in Harvey) Falkenberg 1901:638, pl. 16, Fig. 11. Boergesen 1919:324, Figs. 326-328. Collins and Hervey 1917:131. Howe 1920:575. Taylor 1928:178, pl. 25, Fig. 3; 1960:565, pl. 72, Fig. 9.

Dasya wurdemanni Bailey in Harvey 1853:64, Tab. XV, C.

TYPE LOCALITY: Key West, Florida.

TYPE: TCD.

DISTRIBUTION: western tropical Atlantic; Mediterranean.

SPECIMENS EXAMINED: **Sargasso Sea:** 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2213).

A single tetrasporangial plant occurred epiphytically on "*Sargassum* B"; its status in the Sargasso Sea flora must remain in doubt until further collections come to hand.

Family Delesseriaceae

Genus *Hypoglossum* Kuetzing, 1843

Hypoglossum tenuifolium (Harvey) J. Agardh. Howe 1920: 564. Taylor 1960:545, pl. 68, Fig. 2.

Delesseria tenuifolia Harvey 1853:97, Tab. XXII, Fig. B. Boergesen 1919:344, Figs. 340-343.

TYPE LOCALITY: Key West, Florida.

TYPE: TCD.

DISTRIBUTION: western tropical Atlantic Ocean.

SPECIMENS EXAMINED: **Sargasso Sea:** 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2220).

A single plant was found epiphytically on "*Sargaassum* B", and until further collections come to hand, its status as a permanent component of the Sargasso Sea flora must remain in doubt.

Family Rhodomelaceae

Genus *Chondria* C. Agardh, 1817

Two collections — one tetrasporangial [37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2632)] and one sterile [39°07′N-70°35′W, 16.viii.1970, *Moore* (WJW 2910)] — contained very small (less than 1 cm long) plants of *Chondria* attached to *Sargassum natans*. While both plants appear to come close to the diagnosis of *Chondria dasyphila* (Woodward) C. Agardh provided by Taylor (1960, p. 616), specific affinity could not be determined with certainty on the basis of the material at hand.

Genus *Herposiphonia* Naegeli, 1846

Herposiphonia secunda (C. Agardh) Ambronn. Boergesen 1920:469, Figs. 428-429. Chapman 1963:125, Figs. 130 a-b. Collins and Hervey 1917:126. Howe 1920:574. Taylor 1928:176, pl. 25, Figs. 8-10; 1960:604, pl. 72, Figs. 10-11.

TYPE LOCALITY: LD.

TYPE: LD.

DISTRIBUTION: western tropical Atlantic Ocean, Mediterranean Sea, Adriatic Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 31°N-69°20′W, 3.iii.1970, *Volkmann* (WJW 2362); 32°09′N-64°58′W, 16.v.1970, *Woelkerling* (WJW 2660); 36°N-70°36′W, 9.xii.1970, *Moore* (WJW 2935); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2630); 39°07′N-70°35′W, 16.viii.1970, *Moore* (WJW 2911); 39°30′N-71°W, 6.x.1970, *Volkmann* (WJW 2864).

Male, female and tetrasporangial plants have been found on *Sargassum fluitans, S. natans,* and on *Sargassum* sp.

Herposiphonia tenella (C. Agardh) Naegeli. Boergesen 1918:286, Figs. 287-289; 1920:472, Fig. 430. Chapman 1963:127, Fig. 133. Collins and Hervey 1917:126. Howe 1920:573. Taylor 1928:177, pl. 25, Fig. 11; 1960:604, pl. 72, Fig. 12.

TYPE LOCALITY: Sicily.

TYPE: LD.

DISTRIBUTION: western tropical Atlantic Ocean; Mediterranean and Adriatic Seas.

SPECIMENS EXAMINED: **Sargasso Sea:** 33°58.5′N-69°56.5′W, 15.v.1970, *Woelkerling* (WJW 2596); 39°30′N-71°W, 6.x.1970, *Volkmann* (WJW 2875).

The tetrasporangial specimens (WJW 2875) grew epiphytically on *Sargassum hystrix;* the sterile material was found on *"Sargassum* C." Until specimens attached to *S. fluitans* and/or *S. natans* are collected the status of this taxon as a permanent component of the Sargasso Sea remains in doubt.

Genus *Laurencia* Lamouroux, 1813

Tropical Atlantic American species of *Laurencia* are in need of critical study in light of the recent investigations of Saito (1967, 1969). Saito (1967, p. 72-73) recognizes 5 subgenera of *Laurencia* based on the presence or absence of secondary pit connections in the cortex, shape of cortical cells, presence or absence of lenticular thickenings in medullary cell walls, and plant form (compressed or cylindrical). Taylor (1960) does not provide full information on these features, and his keys are based partly on features of questionable taxonomic significance, thus making specific identification of taxa difficult.

Seven collections of *Laurencia* have been made during the present study, but in view of their small size (mostly under 1 cm tall) and with one exception their sterile condition, species affinities have not been determined. One of these [34°N-70°W, 30.vi.1970, *Volkmann* (WJW 2729)] belongs to the subgenus *Palisadae;* the other six [31°N-69°29′W, 3.iii.1970, *Volkmann* (WJW 2361); 33°58.5′N-69°56.5′W, 15.v.1970, *Woelkerling* (WJW 2593); 34°N-70°W, 6.vii.1970. *Volkmann* (WJW 2745); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2636); 37°30′N-70°W, 8.vii.1970, *Volkmann* (WJW 2710); 39°30′N-71°W, 6.x. 1970, *Volkmann* (WJW 2874)] belong to the subgenus *Chondrophycus.* The specimens occurred as epiphytes on *Sargassum natans* and on *Sargassum* sp.

Genus *Lophosiphonia* Falkenberg, 1897

Lophosiphonia cristata Falkenberg 1901:499, Tab. 9, Figs. 7-10. Boergesen 1918:297, Figs. 295-298. Chapman 1964:125, Fig. 129. Hollenberg 1958:68. Taylor 1960: 606.

TYPE LOCALITY: Scogliera, Puntadel Posilipo, Gulf of Napal.

TYPE: not located.

DISTRIBUTION: Mediterranean, Bermuda, Bahamas, Jamaica, Virgin Islands, Sargasso Sea.

SPECIMEN EXAMINED: **Sargasso Sea:** 31°N, 69°29'W, 3.iii.1970, *Volkmann* (WJW 2363).

The single collection contained tetrasporangial plants epiphytic on *Sargassum fluitans.*

Genus *Polysiphonia* Greville, 1824

As noted by Taylor (1960, p. 572-3), much taxonomic uncertainty exists over tropical American Atlantic species of *Polysiphonia,* and a critical revision of the genus for this region is badly needed. Although several sources (including Taylor, 1960) have been consulted during this study, taxonomic identifications of Sargasso Sea collections have been made mainly from the publications of Hollenberg (1968, 1968a). The relationships of Hollenberg's Pacific taxa to the species names employed by Taylor (1960) for tropical American Atlantic taxa remain uncertain.

Polysiphonia delicatula Hollenberg 1968:62, Fig. IF.

TYPE LOCALITY: Pokai Bay, Oahu, Hawaii.

TYPE: US (D1911662).

DISTRIBUTION: Hawaiian Islands, Tuamotu Archipelago, Marshall Islands, Caroline Islands, Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2423); 33°58'N-69°56.5'W, 15.v.1970, *Woelkerling* (WJW 2595); 37°N-70°W, 12.v.1970, *Woelkerling* (WJW 2631, 3229).

Female and tetrasporangial plants occurred as epiphytes on *Sargassum natans* and *Sargassum* sp.

Polysiphonia lanosa (L.) Tandy. Taylor 1957:341, pl. 56, Fig. 4, pl. 57, Figs. 14-15, pl. 59, Fig. 4. Woelkerling 1972:298.

Polysiphonia fastigiata auct. non. (Roth) Greville: Collins, Holden, and Setchell 1895:145; 1907:1444. Farlow 1881: 175. Harvey 1853:54.

TYPE LOCALITY: unknown.

TYPE: LINN.

DISTRIBUTION: North Atlantic Ocean.

SPECIMENS EXAMINED: **Sargasso Sea:** 38°53'N-69°39'W, 10.v.1970, *Woelkerling* (WJW 2565).

Polysiphonia lanosa occurred as an epiphyte on *Ascophyllum nodosum* (see Woelkerling, 1972) and is regarded as an invader.

Polysiphonia poko Hollenberg 1968:70, Figs. 3A, 15, 22.

TYPE LOCALITY: North Island, Pacific Ocean.

TYPE: US (H65-113.1).

DISTRIBUTION: tropical Pacific Islands (see Hollenberg), Sargasso Sea.

SPECIMENS EXAMINED: **Sargasso Sea:** 34°N-70°W, 10.i.1970, *Volkmann* (WJW 2207); 37°30'N-70°W, 8.vii.1970, *Volkmann* (WJW 2703); 39°30'N-71°W, 6.x.1970, *Volkmann* (WJW 2858).

Female and tetrasporangial plants occurred as epiphytes on *Sargassum natans* and *Sargassum* sp.

SUMMARY

The epibiotic and pelagic algal flora of the western Sargasso Sea has been extended to include ten Chlorophyceae, 25 Phaeophyceae, and 33 Rhodophyceae. Nearly 75% of these taxa are newly reported for the Sargasso Sea. Pertinent references and taxonomic and ecological data are provided for each taxon, and indication is provided as to whether each species is likely to be a permanent component of the Sargasso Sea flora or merely a temporary invading element.

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OBSERVATIONS ON BATRACHOSPERMUM (RHODOPHYTA) IN SOUTHEASTERN WISCONSIN STREAMS

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Knowledge of the genus *Batrachospermum* (Rhodophyta) in Wisconsin stems mainly from the report of Prescott (1951) who records four species from lotic environments without reference to locality and with only scant ecological data. Moreover, information on seasonal periodicity and environmental conditions of the type obtained by Dillard (1966) in North Carolina, Minckley and Tindall (1963) in Kentucky, and Rider and Wagner (1972) in Pennsylvania apparently is lacking for Wisconsin. (The last reference includes a literature review of *Batrachospermum* ecology.)

The present investigation has been undertaken to gain information on 1) the occurrence of *Batrachospermum* in southeastern Wisconsin streams and 2) the environmental conditions present at localities where this taxon grows. During the course of the study 201 randomly selected stream localities have been visited; *Batrachospermum* plants occurred at 13 or 6.4% of these sites.

MATERIALS AND METHODS

At each station (Table 1) where *Batrachospermum* plants were found, chemical and physical data on alkalinity, carbon dioxide, hardness (calcium and total), nitrate nitrogen, orthophosphate, oxygen, pH, temperature, and turbidity have been gathered using a Hach Water Analysis Field Kit, model DR-EL, which employs microadaptations from the "Standard Methods" handbook (American Public Health Association 1965). In addition, some observations on the type of substrate, relative current velocity, and relative exposure to sunlight have been made.

At stations where *Batrachospermum* populations persisted for extended periods, observations were made at 4-6 week intervals for 10-11 months to note any seasonal changes.

TABLE 1

LIST OF *BATRACHOSPERMUM* LOCALITIES, DATES SAMPLED, AND LOCALITY ABBREVIATIONS USED IN TEXT DISCUSSION

Text Abbreviation	County	Locality	Dates
B	Walworth	Bluff Ck, T4N, R15E, S23 at Co. Hwy P crossing	7.VI.1972
BE	Dane	Black Earth Ck, T7N, R7E, S2 along U.S. Hwy 14	15.VII.1972, 12.XI.1972, 9.i.1973
F	Walworth	"Fontana Ck", T1N, R16E, S11 at St. Hwy 67 crossing	7.VI.1972, 11.VII.1972, 3.XII.1972, 7.I.1973, 3.II.1973, 10.III.1973, 17.IV.1973
J	Manitowoc	Jumbo Ck, T21N, R23E, S26 at unnamed town road crossing	22.VII.1972
K	Sauk	Koshwego Springs, Devils Lk. St. Pk, T11N, R6E, S23	31.V.1972, 5.VII.1972, 9.XI.1972, 6.XII.1972, 5.I.1973, 9.II.1973, 10.III.1973, 17.IV.1973
M	Dane	Merrill Springs, Lk. Mendota, Madison, T7N, R9E, S18	11.V.1972

TABLE 1 cont.

MC	Iowa	Mill Creek, T7N, R3E, S35 at Twin Valley Lks. Road	3.VII.1972
N	Sheboygan	Nichols Ck, T14N, R21E, S18, at Cedar Lane Rd Crossing	23.VII.1972
Q	Washington	Quas Ck, T11N, R19E, S25 at U.S. Hwy 45 junct with Co. Hwy. NN	15.VI.1972
SC	Waukesha	Scuppernong Ck, T6N, R17E, S36 at U.W. Field Station near Waterville	5.VI.1972, 10.VII.1972, 5.VIII.1972, 17.IX.1972, 4.XI.1972, 2.XII.1972, 6.I.1973, 4.II.1973, 3.III.1973, 16.IV.1973
SR	Waukesha	Scuppernong R., T6N, R17E, S34, near junct of St. Hwy 67 and Co. Hwy 22	5.VI.1972, 7.VII.1972, 5.VII.1972, 17.IX.1972, 2.II.1973
SS	Waukesha	Scuppernong Spring, T5N, R17E, S3 along St. Hwy 67	17.IV.1972, 10.VII.1972
T	Racine	Tichigan Ck, T4N, R19E, S15 at Ranke Road crossing	13.VI.1972, 10.VII.1972, 2.VII.1972, 17.IX.1972, 29.X.1972, 8.XII.1972, 7.I.1973, 3.II.1973, 3.III.1973, 16.IV.1973

Voucher specimens from all localities have been collected and immediately preserved in FAA (10:7:2:1 95% ethanol:water:formalin:glacial acetic acid). Dried herbarium specimens (bearing numbers prefaced by WJW) and permanent microscope slides using KARO as a mountant (Woelkerling, 1970) as well as liquid preserved material have been retained in the author's personal collections, currently housed at WIS. Species determinations have been made primarily with the aid of the taxonomic key of Israelson (1942); the papers of Kylin (1912), Prescott (1951), Sirodot (1884), and Whitford and Schumacher (1969) also have been consulted.

RESULTS AND DISCUSSION

Two taxa of *Batrachospermum* found during this study have been identified to species. *Batrachospermum boryanum* Sirodot, not recorded previously from Wisconsin, occurred at seven localities (B, F, K, SC, SR, SS, T; abbreviations explained in Table 1), and with one exception (locality B), it always grew mixed with other *Batrachospermum* taxa. Sexually mature plants ranged in size from 4-21 cm with most plants averaging about 8-10 cm tall. Sexual plants have been encountered in all months except February, March, and October; further study will probably show that sexual plants do occur throughout the year.

Batrachospermum moniliforme Roth has been found at ten localities (BE, F, J, K, MC, N, SC, SR, SS, T), and has been reported previously from Wisconsin (Prescott, 1951). Except for two stations (J, N), it grew mixed with other *Batrachospermum* taxa. Sexually mature plants occurred throughout the year and ranged in length from 3-25 cm with an average height of 6-9 cm.

In addition to the above two taxa, sterile (and thus specifically unidentifiable) plants of *Batrachospermum* have been encountered at five localities (BE, M, Q, SC, T) from January-March, May-July, and in December. They varied in length from 3 cm to 15 cm. The size of some Wisconsin

plants (up to 25 cm) greatly exceeds the 6 cm maximum recorded by Rider and Wagner (1972) and the 10 cm maximum found by Israelson (1942).

All Wisconsin populations of *Batrachospermum* observed during this investigation grew at or near the headwaters of spring-fed streams, thus agreeing with the findings of Minckley and Tindall (1963). Rider and Wagner (1972) also recorded their taxa from a spring-fed stream but without mention of the headwater areas. Current velocities at Wisconsin localities never dipped below 10 cm/sec and in most cases exceeded 25 cm/sec. In addition, all Wisconsin localities but one (BE) contained rocky or rocky-sandy bottoms and usually appeared free from heavy siltation and high turbidity levels.

Except for seasonal fluctuations in temperature and diurnal fluctuations in carbon dioxide and oxygen levels, chemical and physical conditions at any one locality tended to remain within relatively narrow limits during the study period. Conditions did vary considerably between localities, however, and the taxa of *Batrachospermum* encountered appear to tolerate a fairly wide range of environmental conditions (Table 2).

Of particular note is the variation in carbon dioxide levels. At no time did CO_2 levels exceed 24 ppm, and levels as low as 1 ppm have been encountered. These values are decidedly lower than those reported by Minckley and Tindall (1963) for *Batrachospermum* sp. and by Rider and Wagner (1972) for *B. vagum*, but they more or less agree with the range in values measured by Rider and Wagner (op. cit.) for *B. moniliforme*. Since both species found in Wisconsin (*B. moniliforme* and *B. boryanum*) apparently require free CO_2 for photosynthesis (Ruttner, 1960), data from the present study strongly suggest that these taxa can survive at very low concentrations of free CO_2, at least for short periods of time.

At six of the thirteen localities (B, J, M, MC, N, Q), *Batrachospermum* plants were encountered on only one occasion (Table 1), and data for three additional localities

TABLE 2

RANGE IN ENVIRONMENTAL CONDITIONS UNDER WHICH *BATRACHOSPERMUM* OCCURRED

	B. boryanum	*B. moniliformis*	*B.* spp.
Alkalinity	15-342 ppm	12-387 ppm	287-368 ppm
Carbon Dioxide	2-23 ppm	1-23 ppm	2-20 ppm
Hardness, Calcium	2-340 ppm	15-410 ppm	176-408 ppm
Hardness, Total	22-442 ppm	29-500 ppm	352-420 ppm
Nitrate	1.0-4.8 ppm	0.2-16.5 ppm	2.0-10.0 ppm
Oxygen	8-20 ppm	5-21 ppm	5-17 ppm
pH	6.2-8.4	6.7-8.4	7.2-8.2
Ortho-phosphate	0.007-4.0 ppm	0.02-4.9 ppm	0.02-8.1 ppm
Temperature	6°-18°C	1°-21°C	4°-22°C
Turbidity	0-7 J.U.	0-10 J.U.	0-15 J.U.

TABLE 3

RANGE IN SELECTED ENVIRONMENTAL CONDITIONS AT SCUPPERNONG CK. (SC) AND TICHIGAN CK. (T) DURING STUDY PERIOD

Environmental Factor	SC	T
Alkalinity	275-310 ppm	300-360 ppm
Carbon Dioxide	2-23	3-18 ppm
Hardness, Ca	190-225 ppm	170-250 ppm
Hardness, Total	350-400 ppm	375-425 ppm
pH	7.5-8.4	7.7-8.3
Temperature	4-15°C	5-22°C

(BE, SR, SS) are confined to three or four dates. Consequently, information on seasonal changes is restricted to limited observations at four localities (F, K, SC, T) from either May or June, 1972 through April, 1973. *Batrachospermum boryanum* and *B. moniliforme* occurred in mixed populations at all four sites; consequently, reference to *Batrachospermum* in the ensuing discussion includes both taxa.

The Fontana population (F) grew in very hard water (Ca hardness $\geqq$ 250 ppm $CaCO_3$; total hardness 410 ppm $CaCO_3$), swift flowing stream 1-2 m across whose temtures ranged from 12°C in summer to 6°C in winter. Carbon dioxide levels varied from 2-23 ppm, pH from 7.8-8.4, and alkalinity from 330-390 ppm. The stream bottom was primary gravel. During most of the day the habitat was exposed to full sunlight.

When first discovered in June, 1972, *Batrachospermum* plants occurred in considerable numbers and reached lengths of up to 18 cm. By July, 1972, however, most of the plants had disappeared or were obviously moribund. Several plants (preserved as WJW 3936) appeared heavily calcified. The population disappeared entirely by August, and new adult gametophytes did not become apparent until December, 1972, when about a dozen plants up to 6 cm tall were discovered. By January, 1973, *Batrachospermum* had become the dominant alga in the stream with most plants averaging 3-6 cm in length. Throughout the remainder of the study period (ending in April, 1973), *Batrachospermum* maintained its dominance in the stream and plants gradually increased in size to 12-15 cm on the average.

Similar seasonal fluctuation in population levels also occurred at Koshwego Springs (K), where certain chemical and physical conditions differed considerably from those at Fontana. At Koshwego, the water was very soft (Ca hardness $\leqq$ 15 ppm $CaCO_3$; total hardness $\cong$ 25-30 ppm $CaCO_3$), acid (pH varied from 6.2-7.0), and showed alkalinity readings of 12-34 ppm. Stream bottom varied from rocky to sandy to partially silty with *Batrachospermum*

confined to rocky areas. At all times, the habitat was subjected to deep shade. In other respects the two localities appear more or less similar; at Koshwego, temperature varied from 12°C in summer to 1.0°C in winter and CO_2 levels fluctuated between 1 and 11 ppm.

In May, 1972, *Batrachospermum* plants up to 8 cm tall dominated the stream vegetation, but by mid-July they had become very moribund or had disappeared. Small (i.e., less than 2.5 cm tall) plants reappeared in considerable numbers in November, 1972, and dominated the stream vegetation throughout the winter. Noticeable increase in size occurred between February (average size under 2.5 cm) and March, 1973 (average size 6 cm). Severe flooding and silting of the stream occurred in late March and early April, 1973, and the *Batrachospermum* population was almost entirely destroyed.

At the remaining two stations (SC, T) *Batrachospermum* plants occurred throughout the year and formed the dominant component of the algal vegetation during much of that time. Both stations had environments (Table 3) similar to that at Fontana except that one (SC) was largely shaded throughout the day and the other (T) was exposed to full sunlight during most of the day. In addition the latter (T) had summer temperatures of 18-22°C or 5-10°C higher than at the other hard water localities.

Immediately below the spring from which Scuppernong Creek originates, *Batrachospermum* plants constituted the dominant form of vegetation. Within 100 m, however, angiosperm vegetation became dominant and the *Batrachospermum* population consisted only of scattered plants. During winter months most plants encountered were 4-6 cm long and during summer they were 8-10 cm long; one 15 cm tall plant was encountered.

The Tichigan Creek population of *Batrachospermum* dominated the macroscopic vegetation throughout the year. Summer plants generally did not exceed 10 cm in length; winter plants all (i.e., December-April) were enormous in size and reached lengths of up to 25 cm. The very large

size of these individuals as compared to the other winter populations studied could not be accounted for on the basis of the physical or chemical parameters examined during the study.

The above observations suggest that different populations of *Batrachospermum* (at least in Wisconsin streams) may either produce mature gametophytes throughout the year (SC, T) or show seasonal variation with an absence of mature plants from mid-summer to late fall (F, K). They also suggest that maximum vegetative development can occur in spring (F, K), summer (SC), or winter (T). Previous American studies (Dillard, 1966, Minckley and Tindall, 1963, Rider and Wagner, 1972) all reported definite seasonal fluctuations in *Batrachospermum* populations with a disappearance of plants in summer and a reappearance in fall. Yoshida (1959), however, makes mention of both seasonal and year-round populations of *Batrachospermum* in Japanese streams.

Various attempts have been made to account for seasonal fluctuation in population levels in terms of temperature changes, changes in light intensity, and differences in current velocity (see Dillard, 1966, Minckley and Tindall, 1963, Rider and Wagner, 1972, Yoshida, 1959). The results of the Wisconsin study, however, indicate that mature plants and maximum vegetative development can occur under both low and high light intensities and under both summer and winter temperatures. Therefore, other factors, perhaps genetic, appear to be involved in determining why different populations of the same species either persist year round or show seasonal fluctuations. No relationship to current velocity has been observed in this investigation.

The apparently consistent occurrence of *Batrachospermum* in the headwater areas of spring-fed streams likewise requires further investigation. Minckley and Tindall (1963) suggest that the availability of unbound carbon dioxide may be a controlling factor (their stream reportedly has super-saturated CO_2 levels), but the relatively low CO_2 levels found during this study again suggest that other

factors may be involved, and additional study appears warranted.

SUMMARY

The occurrence and some ecological aspects of *Batrachospermum* in southeastern Wisconsin streams have been investigated. *Batrachospermum boryanum* (newly reported for Wisconsin), *B. moniliforme*, and *Batrachospermum* sp. occurred in 6.4% of the localities visited and were found in both alkaline, hard water and acid, soft water environments. Depending upon the population, mature plants persisted throughout the year or disappeared in summer and fall, and they showed maximum vegetative development in spring, or summer, or winter. The seasonal behavior does not appear to be correlated entirely with changes in light intensity or temperature. Likewise the apparent occurrence of *Batrachospermum* near the headwaters of spring-fed streams apparently cannot be explained solely on the basis of greater availability of unbound carbon dioxide in these habitats.

ACKNOWLEDGMENTS

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10

A Species Index (Including Subspecific Taxa) to the Algal Publications of Frank Shipley Collins

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September 1975

A Species Index (Including Subspecific Taxa) to the Algal Publications of Frank Shipley Collins

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The botanical contributions of Frank Shipley Collins (1848-1920) include 77 papers on marine and fresh water algae dealing with Alaska, the Arctic, the Bahamas, Bermuda, Canada, China, the Chincha Islands, Jamaica, and the Sargasso Sea. The greatest number of papers, however, concern New England algae, and these publications constitute an important series of references on the algal flora of the region. In most cases voucher specimens exist for the published records and are on deposit in the Farlow Herbarium of Harvard University and/or the New York Botanical Gardens.

Because of the great number of papers involved, and because Collins published in a number of outlets and frequently used relatively nondescript titles, retrieving information on particular species often becomes an arduous and time consuming task. It is apparent, then, that an index to Collins' papers would greatly facilitate systematic investigations, especially of the New England algal flora, and the present compilation is offered in the hope of helping to meet that need.

This index includes all algal species and subspecific taxa mentioned in Collins' writings from 1880 to 1927 with the exceptions of five floristic accounts (1909b, 1912a, 1917a, 1918a, 1920) which contain their own indices, one generic key (1918b), and one paper (1896b) which has not been seen. In all cases the names and author citations are those used by Collins and do not take into account any errors or subsequent nomenclatural changes. Certain entries lack author citations because Collins did not use them in those cases.

Further information on Frank S. Collins can be found in two additional sources. Setchell (1925) prepared an informative biographic sketch together with a nearly complete bibliography of Collins publications. An unpublished index to the Phycotheca Boreali Americana, the largest algal exsiccatae issued in North America (and prepared primarily under the direction of Collins), has been prepared and distributed in mimeograph form by Professor Maxwell S. Doty.

Sincere thanks are due Mr. Robert Dietrich for assistance with the initial stages of preparing this document.

SPECIES INDEX

Agardhiella coulteri (Harvey) Setchell
1913:117.
Agardhiella tenera (J. Agardh) Schmitz
1899b:123; 1900a:48; 1901b:253, 265; 1905b:231; 1913:117, 133.
Agarum fimbriatum Harvey
1913:109, 132.
Agarum turneri Postels et Ruprecht
1880a:163; 1894:236; 1900a:45; 1908a:115, 116; 1911:274.
Ahnfeldtia concinna J. Agardh
1913:116, 133.
Ahnfeldtia gigartinoides J. Agardh
1913:116.
Ahnfeldtia plicata (Hudson) Fries
1880a:160; 1888a:84; 1894:232; 1900a:48; 1901a:134; 1905b:231; 1908a:116; 1908d:160; 1911:277; 1911a:187; 1913:116, 133; 1927: 10B, 12B.
NOTE: AUTHOR VARIOUSLY REPORTED AS FRIES, (HUDSON) FRIES, AND (TURNER) FRIES.
forma furcellata Collins
1911a:187.
Alaria cordata
1913:111.
Alaria curtipes Saunders
1913:110.
Alaria esculenta (Linneaus) Greville
1880a:163; 1894:236; 1899a:69, 70; 1899b:124; 1900a:45; 1905b:242; 1906d:192; 1911:274, 276.
Alaria grandifolia J. Agardh
1913:110, 132.
Alaria lanceolata
1913:110.
Alaria laticosta
1913:110.
Alaria marginata Postels et Ruprecht
1913:110, 132.
forma nana (Schrader) Collins
1913:110.
Alaria membranacea J. Agardh
1927:B11.
Alaria nana Schrader
1913:110.
Alaria praelonga
1913:110.
Alaria pylaii (Bory) J. Agardh
1894:236; 1900a:45; 1911:274; 1913:111.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [1900a, 1911].
Alaria tenuifolia Setchell
1913:111, 132.
forma amplior Setchell et Gardner
1913:111.
Alaria valida
1913:110.

Amansia multifida Lamouroux
1901b:257, 267.
Amphiroa californica
1913:129.
Amphiroa charoides Lamouroux
1901b:260, 268.
Amphiroa cretacea (Postels et Ruprecht) Areschoug
1913:129.
Amphiroa debilis Kuetzing
1901b:261, 268.
Amphiroa epiphlegnoides
1913:130.
Amphiroa fragilissima Lamouroux
1901b:261, 268.
Amphiroa tuberculosa (Postels et Ruprecht) Endlicher
forma typica Setchell et Gardner
1913:129.
forma californica (Decaisne) Setchell et Gardner
1913:129.
forma frondescens (Postels et Ruprecht) Setchell et Gardner
1913:129.
forma planiuscula (Keutzing) Setchell et Gardner
1913:129.
Amphithrix janthina (Montagne) Bornet et Flahault
1896:2; 1900a:41; 1905b:237.
var. torulosa (Grunow) Bornet et Flahault
1900a:41.
Amphithrix violacea (Kuetzing) Bornet et Flahault
1900a:41; 1905b:223; 1908d:162; 1911:262.
NOTE: AUTHOR ALSO REPORTED AS BORNET ET FLAHAULT [1911].
Anabaena (Sphaerozyga) bornetiana Collins
1896a:120.
Anabaena catenula (Kuetzing) Bornet et Flahault
1899:10, 11.
var. americana Collins
1896:119, 120; 1899:10.
Anabaena felisii (Meneghini) Bornet et Flahault
1896:120.
Anabaena flos-aquae Kuetzing
var. circinalis Kirchner
1888a:163.
Anabaena gigantea Wood
1888a:163.
Anabaena oscillarioides Bory
1905b:236.
Anabaena torulosa (Carmichael) Lagerheim
1900a:41; 1905b:223; 1908d:162; 1911:262.
NOTE: AUTHOR ALSO REPORTED AS LAGERHEIM [1911].
Anabaena variabilis Kuetzing
1900a:41; 1905a:172; 1905b:223; 1911:262.
var. brachyspora Collins
1911:262.

Anadyomene stellata (Wulf.) C. Agardh
1901b:237, 247, 264.
Anatheca furcata Setchell et Gardner
1913:117, 133.
Androgynia huntii Wood
1908:57.
Antithamnion americanum (Harvey) Farlow
1896c:461; 1900a:48; 1900b:131; 1905b:234.
Antithamnion boreale (Gobi) Kjellman
1896c:461; 1900a:48; 1902a:177; 1908a:116; 1911:280; 1927:B9, 14B.
Antithamnion butleriae Collins
1901b:258, 267.
Antithamnion cruciatum (C. Agardh) Naegeli
1900a:48; 1905b:234; 1919:203, 204, 206.
var. radicans J. Agardh
1899b:125; 1900a:48.
Antithamnion floccosum (Mueller) Kleen
1900a:48; 1911:279; 1913:124, 135; 1914:4.
var. pacificum Harvey
1913:124.
Antithamnion plumula (Ellis) Thuret
1900a:48.
var. boreale Gobi
1927:14B.
Antithamnion pteroteon (Schousboe) Bornet
1901b:259.
Antithamnion pylaisaei (Montagne) Kjellman
1894:230; 1900a:48; 1902a:177; 1911:280; 1913:124, 135.
NOTE: AUTHOR ALSO REPORTED AS (MONTAGNE) FARLOW [1894].
Antithamnion subulatum (Harvey) J. Agardh
1913:124, 135.
Aphanochaete vermiculoides Wolle
1905b:240.
Aphanothece microscopica Naegeli
1904a:230.
Aphanothece prasina A. Braun
1888a:165.
Apoglossum decipiens J. Agardh
1913:103, 119, 134.
Apoglossum montagneanum J. Agardh
1903a:206, 207.
Arthrocladia villosa (Hudson) Duby
1891:339; 1899b:125; 1900a:45.
Arthrodesmus incrassatus Lagerheim
1888a:161.
var. cycladatus Lagerheim
1888a:161.
Arthrodesmus incus Hass
1888a:161.
Arthrodesmus minutus Ralfs
1888a:161.

Arthrodesmus notochondrus Lagerheim
1888a:161.
Arthrodesmus octocornis Ehrenberg
1888a:161.
Arthrodesmus quadridens Wood
var. aequalis Lagerheim
1888a:161.
Arthrospira gomontiana Setchell
1905b:235.
Ascocyclus balticus Reinke
1891:339.
Ascocylus globosus Reinke
1891:338.
Ascocyclus orbicularis (J. Agardh) Magnus
1891:339; 1894:240; 1900a:45; 1905b:227; 1911:269.
Ascophyllum mackaii (Turner) Holmes et Batters
1900a:45; 1905b:229, 230.
Ascophyllum nodosum (Linneaus) LeJolis
1882:47; 1888:81; 1888a:154; 1888b:312; 1894:235; 1900a:45; 1901a:133; 1903a:212; 1905b:230, 232; 1908d:161; 1911:274; 1914:3, 4; 1917:83.
NOTE: AUTHOR ALSO REPORTED AS LEJOLIS [1882, 1888] AND STACKHOUSE [1888a].
forma scorpioides (Kuetzing) Reinke
1901c:291, 292; 1911:274.
NOTE: AUTHOR ALSO REPORTED AS REINKE [1901c].
Asparagopsis delilei (C. Agardh) Lamouroux
1901b:255, 266.
Asperococcus compressus Griffiths
1880a:163.
Asperococcus echinatus (Mertens) Greville
1880a:163; 1894:239; 1900a:45; 1905b:228; 1906a:108; 1911:270.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [1880a].
var. vermicularis (Griffiths) Harvey
1906b:125; 1911:270.
Asperococcus sinuosus
1913:107.
Asterocytis ramosus (Thwaites) Gobi
1911:275.
Avrainvillea longicaulis (Kuetzing) Murray & Boodle
1901:90; 1901b:245, 246, 263.
Avrainvillea nigricans Decsne.
1901b:245, 246, 263.
Bambusina brebissonii Kuetzing
1888a:159.
Bangia atropurpurea
forma fuscopurpurea
1913:111.
Bangia ciliaris Carmichael
1900a:48; 1905b:230; 1918:144.

Bangia fuscopurpurea (Dillwyn) Lyngbye
1880a:162; 1888b:312; 1894:234; 1900a:48; 1903:18; 1905b:230; 1911: 275; 1913:111, 133.
NOTE: AUTHOR ALSO REPORTED AS LYNGBYE [1880a, 1888b].

Bangia vermicularis
1913:111.

Batrachospermum anatinum Sirodot
1905b:241.

Batrachospermum australe Collins
1900a:110.

Batrachospermum boryanum Sirodot
1905b:241.

Batrachospermum corbula Sirodot
1905b:241.

Batrachospermum ectocarpum Sirodot
1905b:241.

Batrachospermum macrosporum (Wood) Collins
1906a:110.

Batrachospermum moniliforme Roth
1888a:153.
var. chlorosum Sirodot
1905b:241.
var. typicum Sirodot
1905b:241.

Batrachospermum pyramidale Sirodot
1894:234; 1905b:241.

Batrachospermum vagum C. Agardh
1883:55; 1888a:153; 1894:233; 1905b:241.
var. flagelliforme Sirodot
forma tenuissima Collins
1906a:110.

Batrachospermum virgatum Sirodot
1905b:241.

Beggiatoa alba Trevis
var. minima Warming
1888a:164.

Beggiatoa mirabilis Cohn
1888a:164.

Blodgettia confervoides Harvey
1901b:243; 1902b:13.

Bolbocoleon piliferum Pringsheim
1900a:43; 1906b:124; 1911:265.

Bonnemaisonia hamifera Hariot
1913:119.

Boodlea composita (Hooker et Harvey) Brand
1913:104.

Bostrychia mazei Crouan
1901b:257, 267.

Bostrychia moritziana
var. intermedia J. Agardh
1901b:257, 267.

Bostrychia rivularis Harvey
1880a:158; 1888b:310, 311, 314; 1900a:48; 1901a:135; 1905b:232, 233.
Bostrychia tenella (Vahl) J. Agardh
1901b:242, 257, 267.
Botryoglossum platcarpum
1913:118.
Botryophora occidentalis (Harvey) J. Agardh
1901b:247, 264.
Brachytrichia quoyii (C. Agardh) Bornet et Flahault
1890:175; 1899b:126; 1900a:41.
Brachytrichia rivularioides Zanardini
1890:175.
Bryopsis arbuscula
1919:207.
Bryopsis corticulans Setchell
1913:106.
Bryopsis harveyana J. Agardh
1901b:244, 263.
Bryopsis hypnoides Lamouroux
1906b:124; 1913:105.
Bryopsis pennata Lamouroux
1901b:244, 263; 1919:203, 205.
Bryopsis plumosa (Hudson) C. Agardh
1880a:165; 1882:47; 1884:30; 1888:79; 1888a:155; 1888b:311; 1899a:70; 1900a:43; 1905b:226; 1906b:124, 125; 1911:268; 1919:207.
NOTE: AUTHOR ALSO REPORTED AS C. AGARDH [1882, 1888, 1888a], LAMOUROUX [1880a, 1884], AND (KUETZING) AG. [1888b].
Bryothamnion seaforthii (Turner) Kuetzing
1901b:257, 258, 259, 267; 1904:182.
Bryothamnion triangulare (Gmelin) Kuetzing
1901b:231; 257, 267.
Bulbochaete brebissonii Kuetzing
1901d:412; 1918:143.
Bulbochaete elatior Pringsheim
1918:143.
Bulbochaete furberae Collins
1918:142, 143, 145.
Bulbochaete intermedia DeBary
1901d:413; 1905b:240.
var. Supra mediana Hirn
1918:143.
Bulbochaete monile
1901d:413.
Bulbochaete nana Wittrock
1901d:413.
Bulbochaete nordstedtii Wittrock
1901d:413.
Bulbochaete rectangularis Wittrock
1888a:154.
Bulbocoleon piliferum Pringsheim
1894:244.

Calliblepharis ciliata Kuetzing
1880a:159.
Callithamnion americanum Harvey
1880a:162; 1913:124.
Callithamnion baileyi Harvey
1880a:161; 1882:47; 1888:82; 1900a:48; 1901a:135; 1905b:233; 1906a: 112; 1911:279.
var. boreale Harvey
1900a:48; 1901a:135.
var. laxum Farlow
1900a:48.
var. rochei Harvey
1900a:48.
Callithamnion borreri C. Agardh
1882:47; 1888:82; 1888b:313.
Callithamnion byssoideum Arnold
1880a:162; 1882:47; 1888:83; 1888b:313; 1900a:49; 1901b:258; 1905b:233.
var. jamaicensis Collins
1901b:258, 267.
var. unilaterale Harvey
1884:29; 1900a:49.
Callithamnion corymbosum
1880a:162; 1882:47; 1888:83; 1900a:49; 1900b:131; 1901b:258, 267; 1905b:233; 1906a:112.
NOTE: AUTHOR VARIOUSLY REPORTED AS C. AGARDH [1880a], LYNGBYE [1982, 1883], (ENG. BOT.) C. AGARDH [1900a, 1905b, 1906a, AND (ENG. BOT.) LYNGBYE 1901b.
var. secundatum Harvey
1900a:49.
Callithamnion cruciatum C. Agardh
1882:47; 1888:10; 1888b:312.
Callithamnion daviesii Harvey
1906d:194.
var. secundatum Lyngbye
1906d:194.
Callithamnion floccosum Farlow
1880a:162; 1911:279.
NOTE: AUTHOR ALSO REPORTED AS C. AGARDH [1880a].
var. pacificum
1913:124.
Callithamnion halliae Collins
1906a:111.
Callithamnion hypneae Crouan
1901b:258.
Callithamnion lenormandi Suhr ex Kuetzing
1911a:186, 187.
Callithamnion luxurians J. Agardh
1906d:194.
Callithamnion membranaceum Magnus
1883:56; 1888:82.
Callithamnion microptilum Grunow
1901b:259.

Callithamnion pikeanum
1913:124.
Callithamnion polyspermum J. Agardh
1913:124, 135.
Callithamnion pylaisaei Montagne
1880a:162; 1911:280.
Callithamnion roseum (Roth) Harvey
1888b:313; 1900a:49; 1905b:234.
Callithamnion rothii Lyngbye
1880a:162; 1911:280; 1913:127.
NOTE: AUTHOR ALSO REPORTED AS FARLOW [1911].
Callithamnion seirospermum Griffiths
1882:47; 1888:83.
Callithamnion subulatum Harvey
1913:124.
Callithamnion tenue Harvey
1882:47; 1888:83; 1888b:313.
Callithamnion tetragonum C. Agardh
1880a:161; 1882:47; 1888:10; 1900a:49; 1901a:134, 135; 1905b:234.
NOTE: AUTHOR ALSO REPORTED AS (WITH.) C. AGARDH [1900a, 1901a, 1905b].
Callithamnion thuyoideum
1913:124.
Callithamnion variabile C. Agardh
1901c:292.
Callithamnion virgatulum Harvey
1906d:192, 193.
Callophyllis flabellulata Harvey
1913:116, 133.
Callophyllis furcata Farlow
1913:116, 133.
forma dissecta Farlow
1913:116.
Callophyllis lacinata Harvey
1913:116.
Callophyllis obtusifolia
1913:116.
Callophyllis variegata (Bory) Kuetzing
1913:116, 133.
Callymenia californica
1913:116.
Callymenia ornata (Postels et Ruprecht) J. Agardh
1913:116, 133.
Callymenia phyllophora J. Agardh
1913:116, 124, 133.
forma orbicularis Setchell et Gardner
1913:116.
Callymenia reniformis (Turner) J. Agardh
1900a:49; 1913:116, 133; 1916a:171.
Caloglossa lepricurii (Montagne) J. Agardh
1900a:49; 1901b:255, 266; 1905b:232.

Calothrix aeruginea (Kuetzing) Thuret
1891:336; 1900a:41; 1901b:241, 262; 1905b:223; 1908d:160; 1911:262.
NOTE: AUTHOR ALSO REPORTED AS THURET [1911].

Calothrix braunii Bornet et Flahault
1905b:237; 1911a:185.

Calothrix confervicola (Dillwyn) C. Agardh
1880a:167; 1882:46; 1888:77; 1888a:162; 1888b:310; 1900a:41; 1901b:241, 262; 1905b:223; 1908d:160.
NOTE: AUTHOR ALSO REPORTED AS C. AGARDH [1880a, 1882, 1888, 1888a, 1888b] AND (ROTH) C. AGARDH [1901b, 1905b].

forma purpurea Collins
1911:262.

Calothrix contarenii (Zanardini) Bornet et Flahault
1891:336; 1896:6; 1900:13; 1901b:241, 262.

Calothrix crustacea Thuret
1880a:168; 1884a:130; 1888:77; 1888a:162; 1888b:310; 1891:336; 1900a:41; 1905b:223; 1906a:105; 1911:262; 1911a:185.
NOTE: AUTHOR ALSO REPORTED AS BORNET ET THURET [1888] AND (SCHOUSBOE) BORNET ET THURET [1888b].

forma prolifera (Flahault) Collins
1906a:105.

Calothrix fasciculata C. Agardh
1891:336; 1896:6; 1900a:41; 1911:262.

forma incrustans Collins
1900:13; 1900a:41.

Calothrix fusca (Kuetzing) Bornet et Flahault
1901b:241; 1904a:230; 1905b:237, 239.

Calothrix fusco-violacea Crouan
1900a:41.

Calothrix juliana (Meneghini) Bornet et Flahault
1901b:241.

Calothrix kawraiskyi Schmidle
1911a:185.

Calothrix parasitica (Chauvin) Thuret
1883:55; 1900a:41; 1905b:223; 1911:263.
NOTE: AUTHOR ALSO REPORTED AS THURET [1905b, 1911].

Calothrix parietina (Naegeli) Thuret
1905b:237.

Calothrix pilosa Harvey
1901b:242, 262.

Calothrix prolifera Flahault ex Bornet et Flahault
1906a:105.

Calothrix pulvinata (Mertens) C. Agardh
1888b:310;1891:336; 1894:247; 1900:13; 1900a:41; 1902a:178; 1903a:208; 1905b:223; 1911:263.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1888b, 1911].

Calothrix scopulorum (Weber et Mohr) C. Agardh
1880a:168; 1884a:130; 1888b:310; 1891:336; 1894:246; 1900a:41; 1901c:289; 1905b:223; 1908d:160, 162; 1911:262.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a, 1884a, 1888b, 1911].

Calothrix stagnalis Gomont
1906b:123.
Calothrix vivipara Harvey
1900a:41.
Campylaephora hypneoides J. Agardh
1919:203, 206.
Capsosiphon aureolus (C. Agardh) Gobi
1894:245; 1903:30.
NOTE: AUTHOR ALSO REPORTED AS COLLINS [1903].
Carpomitra cabrerae (Clem) Kuetzing
1913:108, 132.
Castagnea virescens (Carmichael) Thuret
1880a:164; 1894:238; 1896:3; 1900a:45; 1905b:228; 1906a:108; 1911:263, 271.
NOTE: AUTHOR ALSO REPORTED AS THURET [1880a].
Castagnea zosterae (Mohr) Thuret
1880a:164; 1884:30; 1900a:45; 1911:271.
NOTE: AUTHOR ALSO REPORTED AS THURET [1880a, 1884].
Catenella opuntia
1891:335.
var. pinnata (Harvey) J. Agardh
1901b:253, 265.
Caulerpa clavifera C. Agardh
1901:91; 1901b:237; 1902b:12.
Caulerpa cupressoides
var. ericifolia (Turner) Weber van Bosse
1901b:244, 263.
var. mamillosa (Montagne) Weber van Bosse
1901b:244, 263.
var. turneri Weber van Bosse
1901b:244, 263.
var. typica Weber van Bosse
1901b:244; 263.
Caulerpa ericifolia C. Agardh
1901:91; 1901b:237; 1902b:12.
Caulerpa falcifolia
1912:59.
Caulerpa pickeringii
1912:59.
Caulerpa pinnata
forma mexicana (Sonder) Weber van Bosse
1901b:244, 263.
Caulerpa plumaris J. Agardh
1901:91; 1901b:237; 1902b:12.
forma brevipes (J. Agardh) Weber van Bosse
1901b:245, 263.
forma longiseta (J. Agardh) Weber van Bosse
1901b:244, 263.
Caulerpa prolifera (Forsskal) Lamouroux
1901b:245, 263; 1904:182.

Caulerpa racemosa
var. clavifera (Turner) Agardh
1901b:245, 263.
var. clavifera
forma macrophysa (Kuetzing) Weber van Bosse
1901b:245, 263.
Caulerpa taxifolia (Vahl) Agardh
1901b:245, 263.
Caulerpa verticillata J. Agardh
1901b:245, 263.
forma charoides (Harvey) Weber van Bosse
1901b:245, 263.
Centroceras clavulatum Montagne
1902b:14.
Ceramium arborescens J. Agardh
1900a:49.
Ceramium botryocarpum Griffiths
1905b:234; 1911:280.
Ceramium boydenii Gepp
1919:203, 206.
Ceramium byssoideum Harvey
1901b:259, 267.
Ceramium californicum J. Agardh
1913:126, 135.
Ceramium cancellatum
1913:126.
Ceramium capri-cornu (Reinsch) Farlow
1899b:126; 1900a:49; 1905b:234.
Ceramium circinatum (Kuetzing) J. Agardh
1900a:49; 1905b:234.
Ceramium clavulatum Agardh
1901b:259, 267; 1915:96.
Ceramium codicola J. Agardh
1913:126, 135.
Ceramium ceslongschampsii Chruvin
1880a:161.
Ceramium diaphanum Roth
1880a:161; 1888b:313; 1906a:112; 1913:126.
var. tenuissimum Lyngbye
1927:148.
Ceramium fastigiatum Harvey
1880a:161; 1882:47; 1888:83; 1888b:313; 1900a:49; 1901b:259, 267; 1905b:234.
Ceramium gracillimum Harvey
1901b:259, 267.
Ceramium hooperi Harvey
1894:230; 1900a:49; 1911:280.
Ceramium japonicum Okamura
1919:203, 206.
Ceramium nitens (C. Agardh) J. Agardh
1901b:259, 267.

Ceramium pedicellatum J. Agardh
1899b:126; 1900a:49.
Ceramium roseolum Crouan
1906d:195.
Ceramium rubrum (Hudson) C. Agardh
1880a:161; 1882:47; 1888:83; 1888a:153; 1888b:313; 1894:230; 1896:5; 1900a:49; 1902a:177; 1905b:234; 1906b:125; 1906d:196; 1911:280; 1913:125, 126, 135; 1914:4; 1915:94, 95; 1927:3B, 14B.
var. corymbosum J. Agardh
1900a:49.
var. decurrens (Kuetzing) Harvey
1900a:49.
var. pacificum Collins
1913:125.
var. proliferum Harvey
1900a:49; 1905b:234; 1911:280.
forma radians
1913:125.
var. secundatum (Lyngbye) Harvey
1900a:49; 1905b:234.
var. squarrosum
1911:280.
Ceramium squarrosum (Harvey) J. Agardh
1900a:49; 1911:280.
NOTE: AUTHOR ALSO REPORTED AS HARVEY [*1911*].
Ceramium strictum (Kuetzing) Harvey
1880a:16;; 1882:47; 1888:83; 1888a:161; 1888b:313; 1899a:70; 1900a:49; 1905b:234; 1911:280; 1913:126, 135.
NOTE: AUTHOR ALSO REPORTED AS HARVEY [*1880a*, *1882*, *1888*, *1888a*, *1911*, *1913*].
forma proliferum
1906a:112.
Ceramium tenuissimum (Lyngbye) J. Agardh
1882:47; 1888:83; 1888b:313; 1900a:49; 1901b:259, 267; 1905b:234; 1913:126, 135; 1927:3B, 14B.
NOTE: AUTHOR ALSO REPORTED AS J. AGARDH [*1882*, *1888*].
var. arachnoideum (J. Agardh) Farlow
1900a:49; 1905b:235.
var. patentissimum Harvey
1888b:313; 1900a:49.
var. pygmaeum (Kuetzing) Hauck
1901b:259, 267.
Ceratocolax hartzii Rosenvinge
1927:12B.
Ceratothamnion arbuscula
var. pacificum
1913:124.
Ceratothamnion pikeanum (Harvey) J. Agardh
1913:135.
forma laxum Setchell et Gardner
1913:124.

Chaetomorpha aerea (Dillwyn) Kuetzing
1880a:167; 1896:4; 1900a:43; 1901b:243; 1905b:225; 1908d:163; 1911:266.
forma linum (Fl. Dan.) Collins
1911:266.
Chaetomorpha brachygona Harvey
1901b:243, 263.
Chaetomorpha californica Collins
1906a:106.
Chaetomorpha cannabina (Areschoug) Kjellman
1901b:243; 1901d:413.
Chaetomorpha chelonum Collins
1907a:198; 1909c:196.
Chaetomorpha clavata (Agardh) Kuetzing
1901b:243, 263.
Chaetomorpha herbipolensis Lagerheim
1907a:199; 1909c:196.
Chaetomorpha linum (Fl. Dan.) Kuetzing
1884a:130; 1838:78; 1888b:311; 1899a:70; 1900a:43; 1901b:243, 263.
1905b:225; 1908d:163; 1911:266; 1915:91.
NOTE: AUTHOR ALSO REPORTED AS KUETZING [1888, 1888b] AND (O.F. MUELLER) KUETZING [1815].
var. brachyarthra Kuetzing
1901b:243; 263.
Chaetomorpha melagonium (Weber et Mohr) Kuetzing
1880a:167; 1891:338; 1894:237, 243; 1896:4; 1899a:70; 1901b:243;
1908d:163; 1909a:25; 1911:272; 1927:B7, 10B.
forma rupincola Areschoug
1900a:43; 1901d:413; 1911:266.
forma typica Kjellman
1900a:43; 1901b:263; 1911:266.
Chaetomorpha piguotiana (Montagne) Kuetzing
1880a:167; 1888b:311; 1894:243; 1901b:243; 1908d:163; 1911:266.
NOTE: AUTHOR ALSO REPORTED AS MONTAGNE [1880a].
Chaetomorpha sutoria Berkeley
1880a:167.
Chaetomorpha tortuosa Dillwyn
1880a:167.
Chaetophora cornu-damae (Roth) C. Agardh
β draparnaldioides Nordstedt et Wittrock
1905b:240.
Chaetophora endivaefolia C. Agardh
1888a:156.
Chaetophora incrassata (Hudson) Hazen
1905b:240.
forma draparnaldioides (Wittrock et Nordstedt) Collins
1905b:240.
Chaetophora maritima (Kjellman) Rosenvinge
1884a:130; 1903a:210; 1908b:126.
NOTE: AUTHOR ALSO REPORTED AS KJELLMAN [1884a, 1908b].
Chaetophora pellicula
1903a:210.

Chaetophora pisiformis (Roth) C. Agardh
1888a:156; 1905b:240.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1888a].
Chaetophora subcutanea Lyngbye
1927:12B.
Chaetophora tuberculosa Agardh
1888a:156.
Chaetopteris plumosa (Lyngbye) Kuetzing
1908a:116; 1927:8B.
Chamaedoris annulata (Lamouroux) Montagne
1901b:247, 264.
Chamaesiphon incrustans Grunow
1916:92.
Champia kotschyana
1919:207.
Champia parvula (C. Agardh) Harvey
1882:47; 1884:29; 1888:84; 1888b:313; 1900a:49; 1901b:255, 266; 1905b:232; 1919:206.
NOTE: AUTHOR ALSO REPORTED AS HARVEY [1882, 1884, 1888].
Chantransia alariae Jonsson
1906d:192; 1911:276.
Chantransia barbadensis Vickers
1906d:195.
Chantransia corymbifera Thuret ex Le Jolis
1896:5; 1906d:195, 196.
NOTE: AUTHOR ALSO REPORTED AS THURET [1896].
Chantransia dasyae (Collins) Collins
1911a:186.
Chantransia daviesii (Dillwyn) Thuret
1880a:162; 1894:233; 1900a:49; 1906d:194; 1911:276.
NOTE: AUTHOR ALSO REPORTED AS THURET [1880a] AND (ENGL. BOT.) THURET [1894].
Chantransia dictyotae (Collins) Collins
1911a:186.
Chantransia dufourii Collins
1911a:187.
Chantransia efflorescens
1906d:195.
var. thuretii Bornet
1906d:196.
Chantransia flexuosa (Vickers) Collins
1911a:186.
Chantransia hallandica Kylin
1913:113, 133.
Chantransia hermanni (Roth) Kuetzing
1894:233.
Chantransia hoytii (Collins) Collins
1911a:186.
Chantransia macounii Collins
1913:113, 114, 133.

Chantransia macrosporum Wood
1906a:110.
Chantransia minima (Collins) Collins
1911a:186.
Chantransia moniliformis Rosenvinge
1913:113, 133.
Chantransia nemalionis (De Notaris) Ardisson et Straforello
1913:114.
Chantransia roseolum (Crouan) Bornet
1906d:195.
Chantransia saviana (Meneghini) Ardissone
1901b:251; 265.
Chantransia secundata (Lyngbye) Thuret
1900a:49; 1906d:192, 194; 1911:276.
NOTE: AUTHOR ALSO REPORTED AS (LYNGBYE) NAEGELI [1906].
Chantransia thuretii Bornet
1900a:49.
Chantransia virgatula (Harvey) Thuret
1880a:162; 1894:233; 1900a:49; 1905a:172; 1905b:231; 1906d:192, 194; 1911:276.
NOTE: AUTHOR ALSO REPORTED AS THURET [1880a].
var. luxurians (J. Agardh) Rosenvinge
1911:276.
forma tenuissima Collins
1906d: 194.
Chara contraria A. Braun
1901d:416.
Chara fragilis Desv.
1901d:416.
Cheilosporum californicum
1913:129.
Cheilosporum frondescens
1913:129.
Cheilosporum macmillani
1913:130.
Cheilosporum planiusculum
1913:130.
Chlorococcum endozoicum Collins
1911:263.
Chlorochytrium dermatocolax Reinke
1905:97.
Chlorochytrium inclusum Kjellman
1905:97; 1913:101; 1927:85.
Chlorochytrium knyanum
1905:99.
Chlorochytrium lemnae Cohn
1905:97, 98.
Chlorochytrium schmitzii Rosenvinge
1900:11; 1900a:43; 1905:97; 1911:263.
Chlorocystis cohnii (Wright) Reinhard
1905:97; 1911:263.

Chlorodesmis comosa
1912:59.
Chondria atropurpurea
1913:120.
Chondria baileyana Harvey
1901b:256, 266; 1905b:232.
Chondria dasyphylla (Woodword) Agardh
1900a:49; 1901b:256, 266.
forma floridana Collins
1906a:111.
Chondria sedifolia Harvey
1900a:49.
Chondria tenuissima (Goodenough et Woodward) C. Agardh
1900a:49; 1901b:256, 266; 1905b:232.
var. baileyana (Harvey) J. Agardh
1900a:49.
forma californica Collins
1906a:111.
Chondriopsis dasyphila Agardh
1882:47; 1888:85.
Chondriopsis tenuissima Agardh
1882:47; 1884:29; 1888:85; 1888b:314.
var. baileyana Farlow
1882:47; 1884:29; 1888b:314.
Chondrus affinis Harvey
1913:114, 133; 1927:3B, 12B.
Chondrus canaliculatus (Agardh) Greville
1915:92.
Chondrus crispus (Linneaus) Stackhouse
1880a:160; 1882:47; 1888:84; 1888a:153; 1888b:313; 1894:232; 1900a: 49; 1901a:133; 1905b:231; 1908d:160; 1911:276; 1913:114, 133.
NOTE: AUTHOR ALSO REPORTED AS (LINNEAUS) LYNGBYE [1913], LYNGBYE [1880a], AND STACKHOUSE [1882, 1888, 1888a].
Chondrus uncialis
1912:59.
Chorda filum (Linneaus) Stackhouse
1880a:164; 1882:47; 1883:55; 1888:81; 1894:237; 1900a:45; 1902a:175; 1905b:229; 1906b:124; 1908a:116; 1911:272; 1913:108, 132; 1927:10B.
NOTE: AUTHOR ALSO REPORTED AS LINNEAUS [1882, 1888], (LINNEAUS) LAMOUROUX [1908a, 1913], AND STACKHOUSE [1880a].
Chorda lomentaria
1913:107.
Chorda tomentosa Lyngbye
1883:55; 1900a:45; 1902a:175; 1905b:242; 1911:272.
NOTE: AUTHOR ALSO REPORTED AS ARESCHOUG [1883].
Chordaria abientina Ruprecht
1913:108, 132.
Chordaria attenuata
1913:107.
Chordaria cladosiphon Kuetzing
1919:203, 205.

Chordaria divaricata Agardh
1880a:164.
Chordaria firma Gepp
1919:205.
Chordaria flagelliformis (Mueller) C. Agardh
1880a:164; 1888b:312; 1894:237; 1900a:45; 1900c:164; 1905b:229, 242, 243; 1908a:116; 1911:272; 1919:203, 205; 1927:108.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1830, 1883b] AND (FL. DAN.) AGARDH [1894, 1900a, 1905b, 1911, 1919].
var. densa Farlow
1900a:45; 1911:272.
Choreocolax polysiphoniae Reinsch
1894:233; 1900a:49; 1904:182; 1911:276.
Chroococcus cohaerens (Brebisson) Naegeli
1905b:235.
Chroococcus limneticus Lemmermann
1918:141.
Chroococcus turgidus Naegeli
1888:76; 1888a:165; 1894:249; 1900a:41; 1901b:239, 262; 1911:259.
NOTE: AUTHOR ALSO REPORTED AS (KUETZING) NAEGELI [1901b].
Chroolepus umbrinum Kuetzing
1888a:156.
Chroothece richteriana Hansgrig
1901b:239, 262.
Chrysymenia halymenoides Harvey
1901b:255, 266.
Chrysymenia orcadensis
1901a:135.
Chrysymenia pseudodichotoma Farlow
1913:118, 134.
Chrysymenia rosea
1901a:135.
var. orcadensis
1901a:135.
Chrysymenia uvaria
1901b:255.
Cladophora aegagropila Kuetzing
1888a:156.
Cladophora albida (Hudson) Kuetzing
1800a:166; 1888b:311; 1900a:43; 1902:114, 119, 120, 121, 125, 127; 1905b:225.
NOTE: AUTHOR ALSO REPORTED AS HUDSON [1880a].
var. refracta Thuret
1900a:43; 1902:119; 1905b:225; 1911:266.
Cladophora (Aegagropila) amphibia Collins
1907a:200.
Cladophora arcta (Dillwyn) Kuetzing
1880a:166; 1894:242; 1900a:43; 1902:114, 115, 116, 117, 118, 127; 1903:18; 1905b:226; 1911:267; 1913:104.
forma b
1913:104.

forma centralis Farlow
1894:242; 1900a:43; 1902:117; 1913:104.
Cladophora arctica (Dillwyn) Kuetzing
1901d:414.
Cladophora baertolonii
var. hamosa Ardissone
1906a:106.
Cladophora callicoma Kuetzing
1905b:240.
Cladophora cartilaginea (Ruprecht) Harvey
1909:19.
Cladophora coalita
1913:104.
Cladophora columbiana
1913:104.
Cladophora composita
1913:104, 105.
Cladophora constricta Collins
1909:19, 20.
Cladophora crispata (Roth) Kuetzing
forma subsimplex Collins
1906a:107.
Cladophora crystallina (Roth) Kuetzing
1901b:243, 263.
Cladophora diffusa Harvey
1902:126; 1913:104.
Cladophora expansa (Mergens) Kuetzing
1880a:167; 1888:78; 1888a:7; 1888b:311; 1894:243; 1896:3; 1900a:43; 1902:114, 122, 123, 124, 127; 1902a:178; 1903:27; 1905b:226; 1907a: 197; 1908d:160, 162; 1910:9; 1911:267.
NOTE: AUTHOR ALSO REPORTED AS KUETZING [1880a, 1888, 1888a, 1888b, 1891, 1907a, 1910].
var. glomerata Thuret
1902:123; 1905b:226.
Cladophora fascicularis (Montagne) Kuetzing
1901b:243; 1915:91.
NOTE: AUTHOR ALSO REPORTED AS KUETZING [1901b].
Cladophora flavescens Harvey
1902:124; 1911:267.
NOTE: AUTHOR ALSO REPORTED AS (ROTH) KUETZING [1911].
Cladophora flexuosa (Griffiths) Harvey
1880a:166; 1888b:311; 1894:243; 1900a:43; 1901d:414; 1902:114, 119, 121, 122, 125, 127; 1911:267: 1913:104.
NOTE: AUTHOR ALSO REPORTED AS GRIFFITHS [1880a] AND HARVEY [1888b].
forma densa Collins
1902:121.
forma floridana Collins
1906a:106.
Cladophora fracta (Fl. Dan.) Kuetzing
1880a:167; 1888:78; 1888a:156; 1900a:43; 1902:114, 124, 127.
NOTE: AUTHOR ALSO REPORTED AS FL. DAN. [1880a] AND KUETZING [1838, 1888a].

forma flavescens (Harvey) Collins
1902:124.
forma marina Hauck
1902:124.
forma reflexa Collins
1906a:107.
Cladophora fuliginosa Kuetzing
1901b:243, 263.
Cladophora glaucescens (Griffiths) Harvey
1880a:166; 1888b:311; 1894:243; 1900a:43; 1902:114, 120, 121, 127; 1903:28; 1911:267; 1913:103.
NOTE: AUTHOR ALSO REPORTED AS GRIFFITHS [1880a] AND HARVEY [1886b].
Cladophora glomerata (Linneaus) Kuetzing
1905b:240.
Cladophora gracilis (Griffiths) Kuetzing
1880a:167; 1882:47; 1888:78; 1888a:156; 1888b:311; 1894:243; 1900a:43; 1902:114, 120, 121, 122, 123, 136, 127; 1905b:226; 1909:20; 1911:267.
NOTE: AUTHOR ALSO REPORTED AS GRIFFITHS [1880a] AND KUETZING [1882, 1888, 1889a].
forma elongata Collins
1902:122; 1911:267.
var. expansa Farlow
1900a:43; 1902:122; 1911:267.
forma subflexuosa Collins
1911:267.
var. tenuis Farlow
1900a:43; 1902:122, 123.
var. vadorum (Areschoug) Collins
1902:122.
Cladophora graminea Collins
1909:19, 20.
Cladophora hamosa
forma refracta Hauck
1888b:311; 1902:125.
Cladophora hariotina Howe
1915:91.
Cladophora herpestica (Montagne) Kuetzing
1901b:244.
Cladophora hirta Kuetzing
1900a:43; 1902:114, 121, 122, 123, 126, 127; 1911:267.
Cladophora howei Collins
1909:18, 20.
Cladophora hutchinsiae (Dillwyn) Kuetzing
1888b:311; 1900a:43; 1901b:243, 263; 1902:114, 126, 127.
NOTE: AUTHOR ALSO REPORTED AS KUETZING [1888b].
var. diffusa (Harvey) Farlow
1900a:43.
var. distans (Agardh) Kuetzing
1902:126; 1913:104.
Cladophora hystrix (Stromfelt) De Toni
1902:114, 116, 117, 127; 1905b:242; 1913:104.

Cladophora intertexta Collins
1901b:243, 244, 263.

Cladophora laetevirens (Dillwyn) Harvey
1880a:167; 1888a:156; 1894:243; 1900a:43; 1902:114, 121, 122, 125; 1911:267; 1913:104.
NOTE: AUTHOR ALSO REPORTED AS DILLWYN [1880a], HARVEY [1888a] AND KUETZING [1900a].

var. glomerata Le Jolis
1902:126.

Cladophora lanosa (Roth) Kuetzing
1880a:166; 1888:78; 1894:242; 1900a:43; 1902:114, 118, 119; 1905b:226; 1911:268.
NOTE: AUTHOR ALSO REPORTED AS ROTH [1880a] AND KUETZING [1888].

var. uncialis (Harvey) Thuret
1900a:43; 1902:118; 1905b:226, 243.
NOTE: AUTHOR ALSO REPORTED AS (FL. DAN.) THURET [1902].

Cladophora microcladioides Collins
1909:17, 20; 1913:104.

Cladophora magdelanae Harvey
1900a:43; 1902:114, 124; 1905b:226.

Cladophora pellucida (Hudson) Kuetzing
1909:19.

Cladophora polyacantha Montagne
1906a:106.

Cladophora refracta (Roth) Areschoug
1880a:166; 1888b:311; 1900a:43; 1901c:290; 1902:114, 119, 120, 124, 125, 127; 1911:267.
NOTE: AUTHOR ALSO REPORTED AS ROTH [1880a] AND ARESCHOUG [1900a, 1901c, 1911].

Cladophora repens (J. Agardh) Harvey
1901b:244.

Cladophora rudolphiana (Agardh) Kuetzing
1882:47; 1888:78; 1900a:44; 1902:114, 120, 127; 1905a:168; 1905b:226.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1888, 1905], (AGARDH) HARVEY [1900a, 1905b], AND KUETZING [1882].

Cladophora rupestris (Linneaus) Kuetzing
1880a:166; 1894:243; 1900a:44; 1902:114, 125, 127; 1909:20, 1911:267.
NOTE: AUTHOR ALSO REPORTED AS LINNEAUS [1880a].

Cladophora sagraeana Montagne
1906d:192.

Cladophora saxatilis
1913:104.

Cladophora scopaeformis (Ruprecht) Harvey
1901d:414; 1913:104.

Cladophora sonderi Kuetzing
1902:116, 117.

Cladophora spinescens Kuetzing
1902:114, 116, 118, 119, 127; 1913:104.

Cladophora stimpsoni Harvey
1913:104.

Cladophora trichocoma (Agardh) Kuetzing
1901b:244, 263; 1913:104.
NOTE: AUTHOR ALSO REPORTED AS KUETZING [1901b].
Cladophora uncialis Harvey
1880a:166; 1902:118.
NOTE: AUTHOR ALSO REPORTED AS "FL. DAN" [1880a].
Cladophora utriculosa
var. laetevirens Hauck
1902:126.
Cladosiphon balticus Gobi
1906c:157.
Cladostephus spongiosus (Lightfoot) Agardh
1880a:164; 1900a:45.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a].
Cladostephus verticillatus (Lightfoot) Agardh
1880a:164; 1888:80; 1900a:45.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a, 1888].
Clathrocystis aeruginosa Henfrey
1888a:165.
Clanthrocystis roseo-ersinca Cohn
1880a:168; 1882:46; 1888:76; 1888a:165; 1888b:310.
Closterium acerosum Ehrenberg
1888a:162.
Closterium angustatum Kuetzing
1888a:162.
Closterium costatum Corda
1888a:162.
Closterium juncidum Ralfs
1888a:162.
Codiolum gregarium A. Braun
1883:55; 1894:242; 1900:12; 1900a:44; 1911:263.
Codiolum longipes Foslie
1883:55; 1894:242; 1900a:44; 1901c:290; 1905b:242, 243.
Codiolum petrocelidis Kuckuck
1900:12; 1900a:44.
Codiolum pusillum (Lyngbye) Foslie
1903c:232.
forma americanum Foslie
1901c:290, 292; 1903:232.
forma longipes (Foslie) Collins
1911:263.
Codiolum refracta Areschoug
1901c:290.
Codium adhaerens (Cabr.) Agardh
1901b:246, 263; 1901d:416; 1913:105.
Codium fragile (Suringar) Hariot
1919:203, 205.
forma californica (J. Agardh) Hariot
1913:105.
forma novae zelandiae (J. Agardh) Collins
1913:105.

Conferva foeniculacea Hudson
1900c:162.
Conferva glaucescens Griffiths
1902:120.
Conferva globulosa Kuetzing
1888a:157.
Conferva gracilis Griffiths
1902:121.
Conferva hutchinsiae Dillwyn
1902:126.
Conferva implexa Dillwyn
1927:8B.
Conferva lanosa Roth
1902:118; 1927:8B.
Conferva laetevirens Dillwyn
1902:126.
Conferva littoralis Linneaus
1927:8B.
Conferva melagonium Weber et Mohr
1927:B7.
Conferva percursa Agardh
1927:B5.
Conferva refracta Wyatt
1902:119, 120, 125.
Conferva rubra Hudson
1927:14B.
Conferva rudolphiana Agardh
1902:120.
Conferva rupestris Linneaus
1902:125.
Conferva sonderi Kuetzing
1902:116.
Conferva torta Mertens
1927:6B.
Conferva uncialis F. Dan.
1902:118.
Conferva vadorum Areschoug
1902:122.
Constantinea sitchenis
1913:129.
Constantinea subulifera Setchell
1913:129, 136.
Corallina aculeata
1913:130.
Corallina capillacea Harvey
1901b:231, 261, 268.
Corallina cubensis Montagne
1901:261, 268.
Corallina gracilis Lamouroux
forma densa Collins
1906a:112.

Cosmarium excavatum Nordstedt
1888a:160.
Cosmarium lagoense Nordstedt
1888a:160.
Cosmarium moniliforme Ralfs
forma elliptica
1888a:160.
Cosmarium octogonum Delphine
var. constrictum Lagerheim
1888a:160.
Cosmarium oculiferum Lagerheim
1888a:160.
Cosmarium ornatum Ralfs
1888a:160.
Cosmarium orthostichum Lund
1888a:160.
var. trigonum Lagerheim
1888a:160.
Cosmarium pardialis Cohn
1888a:160.
Cosmarium polymorphum
1888a:160.
Cosmarium portianum Arch.
var. brasiliense Wille
1888a:160.
Cosmarium pseudogranatum Wolle
1888a:160.
Cosmarium pseudopyramidatum Lund
1888a:160.
Cosmarium pseudotaxichondrum Nordstedt
subspec. trichondrum Lagerheim
1888a:160.
var. quadridentulum Lagerheim
1888a:160.
Cosmarium quadrifarium Lund
1888a:160.
Cosmarium quinarium Lund
1888a:160.
Cosmarium subcruciforme Lagerheim
1888a:160.
Cosmarium taxichondrum Lund
1888a:160.
var. bidentulum Lagerheim
1888a:160.
Cosmarium willei Lagerheim
1888a:160.
Cosmarium wolleanum Lagerheim
subspec. granuliferum Lagerheim
1888a:160.
Costaria turneri Greville
1913:109, 132.

Crouania attenuata (Bonnemaison) J. Agardh
1901b:258, 267.
Cruoria pellita
1900:11.
Cruoriella armorica Crouan
1901b:260, 267.
Cryptoglaena americana Davis
1900a:41.
Cryptonemia crenulata J. Agardh
1901b:260, 267.
Cryptonemia obovata J. Agardh
1913:128, 135.
Cryptosiphonia grayana
1913:128.
Cryptosiphonia woodii J. Agardh
1913:120, 128, 136.
Cylindrospermum catenatum Ralfs
1899:9, 11.
Cylindrospermum limicola Kirchner
1896a:121.
Cylindrospermum majus
1888a:163; 1905b:236.
Cylindrospermum minutissimum Collins
1896a:120; 1901c:289.
Cylindrospermum minutum Wood
1896a:121
Cylindrospermum muscicola Kuetzing
1888a:163; 1896a:121; 1901b:240.
Cylindrospermum stagnale (Kuetzing) Bornet et Flahault
1901c:289, 292.
Cymathere triplicata (Postels et Ruprecht) J. Agardh
1913:109, 132.
Cymopolia barbata (Linneaus) Lamouroux
1901b:231, 242, 247, 264; 1902b:13, 14.
Cymopolia mexicana J. Agardh
1901b:248; 1902b:13, 14.
Cystoclonium armatum Harvey
1919:206.
Cystoclonium gracilarioides
1913:117.
Cystoclonium purpurascens (Hudson) Kuetzing
1880a:160; 1882:47; 1888:84; 1888b;313; 1894:232; 1896:5; 1900a:49; 1906b:125; 1906d:196; 1911:277.
NOTE: AUTHOR ALSO REPORTED AS KUETZING [1880a, 1882, 1888, 1888b].
var. cirrhosum Harvey
1900a:49; 1911:277.
forma stellatum Collins
1906a:111; 1911:277.
Cystophyllum fusiforme Harvey
1919:206.
Cystophyllum geminatum (Agardh) J. Agardh
1913:111, 132.

var. arborescens
1913:119.
Delesseria lepricurii Montagne
1888b:313; 1905b:233.
Delesseria montagneana Agardh
1903a:206, 207.
Delesseria montagnei Kjellman
1903a:204, 206, 207.
var. angustifolia Rosenvinge
1903a:206, 207.
forma rostrata (Rosenvinge) Collins
1908a:116.
var. typica Rosenvinge
1903a:207.
Delesseria quercifolia
1913:119.
var. linearis Collins
1906a:111; 1913:119.
Delesseria revolutae
1903a:206.
Delesseria serrata
1913:119.
Delesseria sinuosa (Goodenough et Woodward) Lamouroux
1880a:159; 1888a:153; 1888b:313; 1894:231; 1900a:50; 1908a:116; 1911:278; 1916a:180; 1927:3B, B13.
var. lingulata Agardh
1911:278; 1927:B13.
forma quercifolia (Turner) Agardh
1911:278.
Delesseria spinulosa (Ruprecht) J. Agardh
1903a:205, 207.
Derbesia marina (Lyngbye) Kjellman
1901d:415.
Derbesia vaucheriaeformis (Harvey) J. Agardh
1899b:126; 1900a:44; 1901d:415.
Dermatophyton radians Peter
1909c:196.
Dermocarpa farlowii Boergesen
1911:260.
Dermocarpa prasina (Reinsch) Bornet et Flahault
1891:335; 1894:249; 1900a:41; 1904:182; 1911:260.
NOTE: AUTHOR ALSO REPORTED AS (REINSCH) BORNET [1891, 1894] AND (REINSCH) BORNET ET THURET [1900a].
Dermocarpa schousboei (Thuret) Bornet
1891:335.
Dermocarpa vickersiae Collins
1911a:184.
Dermocarpa violacea Crouan
1900a:41.
Desmarestia aculeata (Linnaeus) Lamouroux
1880a:165; 1882:47; 1884a:131; 1888:79; 1894:238; 1899b:127; 1900a:45; 1903a:211; 1905b:228; 1908a:116; 1911:270; 1913:107, 132; 1914:3; 1927:B9.
NOTE: AUTHOR ALSO REPORTED AS LAMOUROUX [1880a, 1882, 1884a, 1888].

forma media (Agardh) J. Agardh
1913:107.
Desmarestia ligulata (Turner) J. Agardh
1913:107, 132.
forma herbacea (Turner) J. Agardh
1913:107.
Desmarestia viridis (Mueller) Lamouroux
1880a:165; 1888:79; 1894:238; 1900a:46; 1905b:228; 1908c:133, 134; 1911:270; 1913:107.
NOTE: AUTHOR ALSO REPORTED AS LAMOUROUX [1880a, 1888] AND (FL. DAN.) LAMOUROUX [1894, 1900a, 1905b, 1908c, 1911].
Desmidium aptogonum Brebisson
1888a:159.
var. acutius Nordstedt
1888a:159.
Desmidium graciliceps Lagerheim
forma major Lagerheim
1888a:159.
Desmotrichum balticum Kuetzing
1896:4; 1900a:46; 1905b:227; 1911:270.
Desmotrichum scopulorum
1896:4.
Desmotrichum undulatum (J. Agardh) Reinke
1894:240; 1896:1, 4; 1900a:46; 1905b:227; 1911:270.
Dichothrix compacta (Agardh) Bornet et Flahault
1901c:290.
Dichotrix gypsophila (Kuetzing) Bornet et Flahault
1905b:238.
Dichothrix hosfordii (Wolle) Bornet et Flahault
1897:96; 1905b:238.
NOTE: AUTHOR ALSO REPORTED AS (WOLLE) BORNET [1897].
Dichothrix orsiniana (Kuetzing) Bornet et Flahault
1905b:238.
Dichothrix penicillata Zanardini
1901b:242, 262.
Dichothrix rupicola Collins
1901c:290, 292.
Dictyerpa jamaicensis Collins
1901b:251, 265.
Dictyoneuron californicum Ruprecht
1913:109, 132.
Dictyopteris delicatula Lamouroux
1901b:249, 264; 1911a:184.
Dictyopteris justii Lamouroux
1901b:249, 265.
Dictyopteris plagiogramma Montagne
1901b:249, 265.
Dictyosiphon chordaria Areschoug
1899b:126.
Dictyosiphon corymbosus Kjellman
1900c:165, 166.

Dictyosiphon ekmani Areschoug
1899b:126; 1900a:46; 1900c:162, 165, 166.
Dictyosiphon foeniculaceus (Hudson) Greville
1880a:165; 1894:239; 1896c:461; 1900a:46; 1900c:163, 164, 166; 1905b: 242; 1911:270; 1913:107, 132.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [1880a, 1896c].
var. americanus Collins
1900a:46; 1900c:163, 165; 1905b:228.
subs. flaccidus Kjellman
1884:30; 1888b:311; 1900c:165; 1904:182.
NOTE: AUTHOR ALSO REPORTED AS ARESCHOUG [1884, 1888b].
Dictyosiphon hippuroides (Lyngbye) Areschoug
1894:239; 1900a:46; 1900c:163, 164, 165; 1905b:242, 243; 1911:271.
NOTE: AUTHOR ALSO REPORTED AS (LYNGBYE) KUETZING [1900c].
var. fragilis (Harvey) Kjellman
1900a:46; 1900c:163, 164, 166.
Dictyosiphon hispidus Kjellman
1896c:461; 1900a:46; 1900c:163, 164, 165; 1911:271.
Dictyosiphon macounii Farlow
1900a:46; 1900c:162, 164, 166.
Dictyosphaeria favulosa (Agardh) Descaine
1901b:247, 264; 1902b:13.
Dictyota bartayresiana Lamouroux
1901b:250, 265.
Dictyota bidentata
1912:59.
Dictyota binghamiana J. Agardh
1906a:109; 1906d:193.
Dictyota cervicornis Kuetzing
1901b:250, 265.
Dictyota ciliata Agardh
1901b:250, 265.
Dictyota dentata Lamouroux
1901b:250, 265.
Dictyota dichotoma (Hudson) Lamouroux
1901b:242, 250; 265; 1902b:13; 1908c:134; 1919:206.
Dictyota divaricata Lamouroux
1901b:250, 265.
Dictyota fasciola (Roth) Lamouroux
1901b:250, 265; 1902b:13.
Dictyota indica Sonder
1919:203, 206.
Dictyota kunthii
1906a:109.
Dictyota liturata J. Agardh
1906a:109.
Dictyota pappeana Kuetzing
1906a:109.
Dictyurus occidentalis J. Agardh
1901b:257, 267.

Digenea simplex (Wulfen) C. Agardh
1901b:256, 266; 1902b:14.
Dilophus alternans J. Agardh
1901b:250, 265.
Dilophus flabellatus Collins
1906a:108, 109.
Dilophus guineensis (Kuetzing) J. Agardh
1901b:250, 265.
Dilophus marginatus J. Agardh
1906a:109.
Diplochaete solitaria Collins
1901b:242, 262.
Docidium dilatatum Lund
1888a:161.
Draparnaldia glomerata (Vaucher) Agardh
1838a:156; 1905b:240.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1888a].
Draparnaldia plumosa (Vaucher) Agardh
1905b:240.
Dumontia filiformis
var. tenuis
1919:207.
Ecballocystis willeana
1913:101.
Ectocarpus aecidioides Rosenvinge
1896:4; 1900a:46; 1905b:226; 1911:269.
Ectocarpus amphibius Harvey
1905b:226.
Ectocarpus brachiatus Harvey
1880a:164; 1882a:70.
Ectocarpus confervoides (Roth) Le Jolis
1882:47; 1888:79; 1888a:155; 1888b:311; 1891:338; 1894:240; 1896:2; 1900a:46; 1905b:226, 242; 1911:268; 1913:106, 131; 1914:4.
forma acuminatus Collins et Setchell
1913:106.
var. brumalis Holden
1900:13; 1900a:46; 1905b:227.
forma corticulatus Saunders
1913:106.
forma halliae (J. Agardh) Collins
1906a:107.
var. hiemalis (Crouan) Kuckuck
1900a:46.
forma irregularis Collins
1906a:107.
var. siliculosus Kjellman
1882:47; 1888:79; 1888a:155; 1888b:311; 1891:338; 1894:240.
var. subulatus Hauck
1900a:46.
Ectocarpus dasycarpus Kuckuck
1900a:46.

Ectocarpus duchassaingianus Grunow
1901b:248.
Ectocarpus durkeei Harvey
1880a:165.
Ectocarpus elegans Thuret
1899b:126; 1900a:46.
Ectocarpus farlowii Thuret
1800a:165.
Ectocarpus fasciculatus Harvey
1880a:165; 1888:80; 1891:338; 1894:240; 1900a:46; 1911:269.
var. abbreviatus (Kuetzing) Sauvageau
1901a:133; 1911:269.
var. polyrhizus Collins
1911:269.
var. refractus (Kuetzing) Ardissone
1911:269.
Ectocarpus firmus Agardh
1880a:165.
Ectocarpus granulosus (Eng. Bot.) Agardh
1880a:165; 1888:79; 1888b:311; 1900a:46; 1911:269; 1913:106, 131.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a, 1888, 1888b].
var. tenuis Farlow
1888:79; 1900a:46.
Ectocarpus griffithsianus Le Jolis
1882a:70; 1911:270.
Ectocarpus hamulosus
1912:58, 59.
Ectocarpus littoralis (Linneaus) Harvey
1880a:165; 1888:80; 1888a:155; 1888b:312; 1919:207; 1927:8B.
NOTE: AUTHOR ALSO REPORTED AS HARVEY [1880a] AND LYNGBYE [1888, 1888a, 1888b].
var. brachiatus Agardh
1888b:312.
Ectocarpus longifructus Harvey
1891:338.
Ectocarpus lumbricalis Kuetzing
1891:337.
Ectocarpus lutosus Harvey
1899b:126; 1900a:46.
Ectocarpus mitchellae Harvey
1882:47; 1888:80; 1891:337, 338, 341; 1900a:46; 1901b:248, 264; 1915:91, 92.
Ectocarpus mucronatus Saunders
1913:106, 131.
Ectocarpus ovatus Kjellman
1896c:459; 1899b:126; 1900a:46.
Ectocarpus oviger Harvey
1913:106.
Ectocarpus parasiticus Sauvageau
1906b:125.
Ectocarpus penicillates J. Agardh
1900a:46.

Ectocarpus polycarpus Kjellman
1896c:459.
Ectocarpus ramellosus Kuetzing
1888b:312.
Ectocarpus reptans Crouan
1905b:227.
Ectocarpus sandrianus Zanardini
1891:338.
Ectocarpus siliculosus (Dillwyn) Lyngbye
1880a:165; 1900a:46; 1905b:227; 1911:269; 1913:106, 131; 1919:205.
NOTE: AUTHOR ALSO REPORTED AS LYNGBYE [1880a] AND (DILLWYN) AGARDH [1900a, 1905b].
Ectocarpus sphaerophorus Carmichael
1880a:164.
Ectocarpus subcorymbosus Farlow
1900a:46; 1905b:227.
Ectocarpus terminalis Kuetzing
1888b:311; 1900a:46; 1911:269.
Ectocarpus tomentosoides Farlow
1900a:46; 1911:269.
Ectocarpus tomentosus (Hudson) Lyngbye
1880a:165; 1888b:311; 1900a:46; 1902:118.
NOTE: AUTHOR ALSO REPORTED AS LYNGBYE [1880a].
Ectocarpus virescens Thuret
1891:338; 1915:92.
Ectocarpus viridis Harvey
1880a:165.
Egregia menziesii (Turner) Areschoug
1913:110, 132.
Elachista chondri Areschoug
1901a:133.
Elachista fasciculata
var. major (Reinke) Gran
1900a:46.
Elachistea fucicola (Velley) Fries
1880a:164; 1888:80; 1888b:312; 1891:339; 1894:238; 1900a:46; 1901a: 133; 1905b:228; 1911:271.
NOTE: AUTHOR ALSO REPORTED AS FRIES [1880a, 1888, 1888b].
Elachista lubrica Ruprecht
1891:339; 1894:238; 1900a:46; 1905b:242; 1908a:116; 1911:271.
Elachista stellaris
var. chordae Areschoug
1891:339; 1899b:126; 1900a:46.
Endocladia muricata (Harvey) J. Agardh
1913:114, 133.
forma inermis Setchell et Gardner
1913:144.
Endoderma perforans Huber
1911:265.
Endoderma strangulans Howe
1915:91.

Enteromorpha hopkirkii McCalla
1894:246; 1896:2, 3; 1900a:44; 1903:20, 26, 27, 28, 31; 1905b:224; 1908d:160, 162.
NOTE: AUTHOR ALSO REPORTED AS HARVEY [1896, 1903].

Enteromorpha intesinalis (Linneaus) Link
1880a:166; 1891:336; 1894:245; 1896:2; 1900a:44; 1901b:242, 262; 1901d:411; 1902a:175; 1903:14, 18, 19, 20, 21, 23, 24, 31; 1905b: 224; 1908c:160, 162; 1911:264; 1913:102; 1915:91; 1919:203, 205; 1927:6B.
NOTE: AUTHOR ALSO REPORTED AS (LINNEAUS) GREVILLE [1915, 1919, 1927].

forma bullosa Hauck
1906a:106.

forma clavata J. Agardh
1903:23; 1908a:116; 1911:264; 1913:102.

var. compressa Rosenvinge
1903:25.

forma cylindracea J. Agardh
1900a:44; 1901d:411, 412; 1903:23; 1905b:224; 1908a:116, 1911:264; 1913:102.

forma maxima J. Agardh
1900a:44; 1901d:411; 1903:23; 1911:264; 1913:102.

var. micrococca Rosenvinge
1903:20.

var. minima Rosenvinge
1903:24.

forma tenuis Collins
1903:23.

Enteromorpha lingulata J. Agardh
1903:21, 22.

Enteromorpha linza (Linneaus) J. Agardh
1894:245; 1900a:44; 1901d:410; 1903:3, 10, 18, 19, 23, 24; 1911:264; 1913:102.

forma crispata J. Agardh
1901d:411; 1903:24; 1905b:224.

forma lanceolata J. Agardh
1901d:411; 1903:24.

Enteromorpha marginata J. Agardh
1884a:131; 1896:2; 1900a:44; 1903:19, 25, 31; 1911:264; 1913:102.

Enteromorpha micrococca Kuetzing
1891:336; 1894:245; 1896:2; 1896c:458, 459; 1900a:44; 1901d:411; 1903:19, 20, 25, 31; 1906a:106; 1913:102; 1927:3B, B5, 6B.

forma bullosa Collins
1906a:106.

var. subsalsa Kjellman
1900a:44; 1903:19, 20; 1913:102; 1927:3B, 6B.

Enteromorpha minima Naegeli in Kuetzing
1896c:458, 459; 1900a:44; 1901d:411; 1903:19, 20, 24, 31; 1905b:224, 242; 1911:264; 1913:102.
NOTE: AUTHOR ALSO REPORTED AS NAEGELI [1900a, 1905b, 1911, 1913].

forma glacialis Kjellman
1903:25.

forma rivularis Collins
1903:24.
Enteromorpha percursa (C. Agardh) J. Agardh
1900a:44; 1903:2, 19, 26, 27, 31; 1905b:225; 1911:264; 1927:3B, B5.
var. ramosa J. Agardh
1903:26.
var. simpliciuscula
1903:26.
Enteromorpha plumosa Kuetzing
1903:27; 1911:264; 1919:203, 205.
NOTE: AUTHOR ALSO REPORTED AS DE TONI [*1903*].
Enteromorpha prolifera (Mueller) J. Agardh
1896:2; 1900a:44; 1901b:242, 262; 1901d:411; 1903:19, 21, 22, 26, 31; 1905b:225; 1911:264; 1913:102; 1915:91; 1919:203, 205; 1927:3B, 6B.
NOTE: AUTHOR ALSO REPORTED AS (FL. DAN.) J. AGARDH [*1896, 1903, 1911, 1913, 1919, 1927*] *AND AS J. AGARDH* [*1900a, 1905b*].
var. arctica (J. Agardh) Rosenvinge
1903:22.
var. trabeculata Rosenvinge
1903:22.
var. tubulosa (Kuetzing) Reinbold
1903:19, 22.
Enteromorpha ramulosa (Eng. Bot.) Hooker
1896:2; 1900a:44; 1903:19, 29, 31.
Enteromorpha salina Kuetzing
1903:19, 22.
var. polyclados Kuetzing
1903:19, 22.
Enteromorpha torta (Mertens) Reinbold
1896:3; 1899b:126; 1900a:44; 1903:19, 26, 31; 1927:3B, 6B.
Enteromorpha tubulosa J. Agardh
1903:22.
Entocladia viridis Reinke
1906b:124.
Entocladia wittrockii Wille
1891:340.
Entoderma wittrockii (Wille) Lagerheim
1900a:44.
Entophysalis granulosa Kuetzing
1888b:309; 1896:1; 1900a:41; 1905a:172; 1908d:162; 1911:259.
Entophysalis magnoliae Farlow
1900a:41.
Epicladia flustrae Reinke
1896:2; 1900a:44; 1905b:225; 1911:265.
Erythroglossum woodii J. Agardh
1913:119, 134.
Erythrophyllum delesserioides J. Agardh
1913:116, 133.
Erythrotrichia bertholdii Batters
1918:144.

Erythrotrichia ceramicola (Lyngbye) Areschoug
1880a:162; 1888b:312; 1900a:50; 1905b:231; 1908c:134; 1911:275; 1911a:187; 1913:112, 133.
NOTE: AUTHOR ALSO REPORTED AS ARESCHOUG [1880a].
Erythrotrichia ciliaris Berthold
1918:144.
Erythrotrichia discigera Berthold
1918:144.
Erythrotrichia obscura Berthold
1918:144.
Erythrotrichia rhizoidea Cleland in Collins
1918:144, 145.
Euastrum compactum Wolle
var. major Lagerheim
1888a:160.
Euastrum inerme Lund
1888a:160.
Euastrum pinnatum Ralfs
1888a:160.
Euastrum ventricosum Lund
1888a:160.
Euastrum wollei Lagerheim
var. quadrigibberum Lagerheim
1888a:160.
Eucheuma echinocarpum Areschoug
1901b:253, 265.
Eucheuma isiforme (C. Agardh) J. Agardh
1904:182.
Eucheuma nudum
1913:117.
Euteromorpha linza
1903:14.
NOTE: ALMOST CERTAINLY A MISSPELLING FOR ENTEROMORPHA.
Euthora cristata (Linneaus) J. Agardh
1880a:160; 1894:232; 1899b:125; 1900a:50; 1901a:135; 1908a:115, 116; 1911:278; 1915:94.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a].
Euthora fruticulosa (Ruprecht) J. Agardh
1908a:115; 1913:117, 134.
Farlowia compressa J. Agardh
1913:128.
Farlowia mollis (Harvey et Bailey) Farlow et Setchell in Setchell et Gardner
1913:128, 136.
Fauchea lacinata J. Agardh
1913:117, 134.
Fucus acinarius
1901b:232
Fucus aculeatus Linneaus
1927:B9.
Fucus areschougii Kjellman
1896:5; 1900a:46; 1905b:229; 1911:274.

Fucus bacciferus Turner
1917:78.
Fucus ceranoides Linneaus
1880a:163; 1900a:46; 1905b:230.
Fucus denatus Linneaus
1927:14B.
Fucus distichus Linneaus
1880a:163; 1927:B11.
Fucus edentatus De la Pylaie
1894:235; 1896:5; 1900a:46; 1908a:116; 1913:111.
Fucus evanescens Agardh
1880a:163; 1894:235; 1896:5; 1900a:46; 1905b:229; 1908a:116; 1908d:161; 1911:274; 1913:111, 132; 1927:B11.
forma cornutus Kjellman
1913:111.
forma macrocephalus Kjellman
1913:111.
forma pergrandis Kjellman
1913:111.
forma typica Agardh
1927:B11.
Fucus filiformis Gmelin
1894:235; 1900a:46; 1913:111.
Fucus filum Linneaus
1927:10B.
Fucus flagelliformis
1927:10B.
Fucus furcatus Agardh
1880a:163; 1888b:312; 1911:274; 1913:111.
Fucus inflatus Linneaus
1911:274; 1913:111, 132; 1927:B11.
NOTE: AUTHOR ALSO REPORTED AS VAHL [1927].
forma distichus (Linneaus) Boergesen
1927:B11.
forma edentatus (De la Pylaie) Rosenvinge
1913:111.
forma filiformis (Gmelin) Setchell et Gardner
1913:111.
forma linearis (Oeder) Rosenvinge
1913:111; 1927:B11.
Fucus larix Turner
1927:14B.
Fucus linearis Oeder
1927:B11.
Fucus lycopodioides Linneaus
1927:B13.
Fucus marinus
1901:231.
Fucus miclonensis De la Pylaie
1911:274.

Fucus minimus
1901b:231.
Fucus natans Linneaus
1917:78.
Fucus nodosus Linneaus
1880a:162; 1917:83.
Fucus platycarpus Thuret
1894:235; 1896:5; 1900a:46; 1905b:229; 1911:274.
Fucus plicatus Hudson
1927:12B.
Fucus serratus Linneaus
1880a:163.
Fucus sinuosus Goodenough et Woodward
1927:B13.
Fucus triqueter
1901b:232.
Fucus turbinatus
1901b:232.
Fucus vermicularis Turner
1912:58.
Fucus vesiculosus Linneaus
1880a:163; 1882:47; 1888:81; 1888a:154; 1888b:312; 1894:235; 1896:5; 1900a:46; 1901b:232; 1905b:229, 230; 1908d:161; 1911:257, 274; 1914: 3; 1927:B11.
var. gracillimus Collins
1900:14; 1900a:47.
var. laterifructus Greville
1894:235; 1905b:230; 1911:274.
forma limicola Collins
1906a:109.
var. sphaerocarpus Farlow
1900a:47; 1905b:230; 1911:275.
var. spiralis (Linneaus) Agardh
1900a:47; 1905b:229, 230; 1911:275.
NOTE: AUTHOR ALSO REPORTED AS FARLOW [*1900a*].
Furcellaria fastigiata (Hudson) Lamouroux
1901a:133.
Galaxaura cylindrica (Solier) Decsne.
1901b:252, 265.
Galaxaura lapidescens (Solier) Lamouroux
1901b:252, 265; 1902b:15.
NOTE: AUTHOR ALSO REPORTED AS LAMOUROUX [*1902b*].
Galaxaura marginata (Ell. & Solier) Lamouroux
1901b:252, 265.
Galaxaura obtusa (Ell. & Solier) Lamouroux
1901b:252, 265.
Galaxaura rugosa (Solier) Lamouroux
1901b:252, 265.
Galaxaurata obtusata (Ell. & Solier) Lamouroux
1906a:110.
NOTE: THIS IS PROBABLY GALAXAURA OBTUSA.
Galothrix scopulorum (Weber & Mohr) Agardh
1905b:243.

Gastroclonium uvarium
1919:207.
Gelidium amansii Lamouroux
1913:114, 133.
Gelidium australe J. Agardh
1919:203, 204, 206.
Gelidium cartilagineum
1919:207.
Gelidium coerulescens Crouan
1901b:252, 265.
Gelidium corneum
var. sericeum
1919:207.
Gelidium crinale (Turner) J. Agardh
1888a:152; 1888b:313; 1891:340; 1900a:50; 1901b:253, 265; 1905b:231; 1911:276; 1913:114, 133.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1888a, 1888b].
forma luxurians Collins
1906a:111.
Gelidium latifolium
1913:114.
Gelidium rigidum (Vahl) Agardh
1901b:253, 257, 265.
Gelidium supradecompositum Kuetzing
1901b:253, 265.
Gelidium unilaterale
1912:59.
Gelinaria dentata Crouan
1906a:112.
Gigartina canaliculata Harvey
forma laxa Collins
1906a:111.
Gigartina chamissoi (Agardh) J. Agardh
1915:92.
Gigartina exasperata Harvey & Bailey
1912:58; 1913:115, 133.
forma microphylla (Harvey) Collins
1913:115.
Gigartina lessonii (Bory) J. Agardh
1915:93.
Gigartina mamillosa (Good.& Woodw.) J. Agardh
1880a:160; 1894:232; 1900a:50; 1911:276; 1913:115, 133.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a].
forma dissecta
1913:115.
forma latissima Harvey
1913:115.
forma subsimplex Setchell
1913:115.
forma vulgaris Harvey
1913:115.

Gigartina microphylla
1913:115.
Gigartina mollis
1912:58; 1913:128.
Gigartina papillata
forma cristata
1913:115.
forma dissecta
1913:115.
forma subsimplex
1913:115.
Gigaratina radula
var. exasperata
1913:115.
forma microphylla
1913:115.
Gloeocapsa crepidinum Thuret
1888a:165; 1888b:309; 1894:249; 1900a:41; 1905a:172; 1908d:162; 1911:259.
Gloeocapsa magma (Brebisson) Kuetzing
1904a:229.
Gloeocapsa quaternata (Brebisson) Kuetzing
1901b:239, 240, 241.
Gloeocapsa violacea (Chorda) Rab.
1905b:235.
Gloeocystis paroliniana Naegeli
1888a:158.
Gloeocystis rupestris (Lyngbye) Rab.
1904a:230; 1905b:239.
Gloeocystis scopulorum Hansgrig in Foslie
1903d:155, 163; 1911:266.
NOTE: AUTHOR ALSO REPORTED AS HANSGRIG [1911].
Gloeocystis vesiculosa Naegeli
1904a:230.
Gloeocystis zostericola Farlow
1900a:44.
Gloeothece confluens Naegeli
1888a:165.
Gloeotrichia natans (Hedwig) Rab.
1901b:242.
Gloiopeltis furcata (Post. & Rup.) J. Agardh
1913:127, 135.
Gloiosiphonia californica (Farlow) J. Agardh
1913:127.
Gloiosiphonia capillaris (Hudson) Carmichael
1880a:161; 1894:229; 1899a:70; 1899b:124; 1900a:50; 1900d:210; 1905b: 235; 1906b:125; 1911:280; 1913:127, 135.
NOTE: AUTHOR ALSO REPORTED AS CARMICHAEL [1880a].
Gloiosiphonia verticillaris Farlow
1913:127, 135.

Gloiotrichia pisum (Agardh) Thuret
1888a:162; 1905b:238.
NOTE: AUTHOR ALSO REPORTED AS THURET [1888a].
Gobia baltica (Gobi) Reinke
1904:182; 1906c:157.
Gomontia holdenii Collins
1897:95, 97.
Gomontia polyrhiza (Lagerheim) Bornet & Flahault
1894:242; 1897:95, 96; 1900a:44; 1901b:244, 263; 1901d:415; 1905b:226; 1906c:159; 1911:268; 1913:105.
Gomphosphaeria aponina Kuetzing
1908d:160; 1911:260.
Goniotrichum elegans (Chauvin) Le Jolis
1880a:162; 1888:82; 1891:336; 1900a:50; 1901b:251, 265; 1905b:230; 1911a:187; 1919:203, 204, 206.
NOTE: AUTHOR ALSO REPORTED AS (CHAUVIN) ZAN, [1891] AND ZANARD. [1880a, 1888].
Goniotrichum humphreyi Collins
1901b:251, 265.
Goniotrichum ramosum (Thwaites) Hauck
1891:336; 1900a:50; 1905b:230.
Gracilaria armata Harvey
1901b:253.
Gracilaria blodgettii Harvey
1901b:253, 266.
Gracilaria caudata J. Agardh
1901b:253, 266.
Gracilaria cervicornis (Kuetzing) J. Agardh
1901b:253, 266.
Gracilaria compressa (Agardh) Greville
1901b:253, 266; 1906b:125.
Gracilaria confervoides (Linneaus) Greville
1901b:253, 254, 266; 1903c:231, 232; 1913:105, 117, 134; 1915:93; 1919:203, 204, 206.
Gracilaria cornea J. Agardh
1901b:253, 266.
Gracilaria curtissiae J. Agardh
1901b:253, 266.
Gracilaria damaecornis J. Agardh
1901b:254, 266.
Gracilaria divaricata Harvey
1901b:254; 266.
Gracilaria domingensis Sonder
1901b:254, 266.
Gracilaria ferox J. Agardh
1901b:254, 266.
Gracilaria filiformis
1912:59.
Gracilaria krugiana
1901b:254.

Gracilaria multipartita (Clementi) J. Agardh
1880a:159; 1882a:71; 1884:29; 1888b:313; 1899b:123; 1900a:50; 1901b: 254, 266; 1903c:231, 232; 1905b:231; 1919:203, 206.
NOTE: AUTHOR ALSO RECORDED AS (CLEMENTI) HARVEY [1919], AGARDH [1880a, 1882a, 1884, 1888b].
var. angustissima Harvey
1884:30; 1888:85; 1888a:153; 1888b:313; 1900a:50; 1903c:231, 232; 1905b:231; 1911:278.
Gracilaria wrightii (Turner) J. Agardh
1901b:254, 266.
Grateloupia affinis (Harvey) Okamura
1919:203, 206.
Grateloupia cutleriae (Binder) J. Agardh
1913:127, 135.
Grateloupia dichotoma J. Agardh
1901b:260, 267.
Grateloupia filicina (Wulf.) J. Agardh
1901b:260, 267; 1919:203, 206.
Grateloupia pinnata (Post. & Rupr.) Setchell
1913:127, 135.
Grateloupia prolongata J. Agardh
1901b:260, 267.
Grateloupia ramosissima Okamura
1919:204, 206.
Griffithsia bornetiana Farlow
1882:47; 1884:29; 1888:83; 1900a:50; 1900b:131; 1905b:233.
Griffithsia corallina Agardh
1880a:161; 1919:207.
Griffithsia opuntioides
1913:123.
Griffithsia schousboei Montagne
1913:123, 135.
Griffithsia tenuis Agardh
1899b:126; 1900a:50.
Grinnellia americana (Agardh) Harvey
1882:47; 1884:29; 1888:85; 1888b:313; 1900a:50; 1905b:232.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [1888], HARVEY [1882; 1884].
Gymnogongrus dendroides
1912:59.
Gymnogongrus furcellatus
1901b:234.
Gymnogongrus griffithsiae (Turner) Martius
1891:340; 1899b:126; 1900a:50; 1901a:133, 134; 1903c:232.
Gymnogongrus japonicus Suringar
1919:206.
Gymnogongrus norvegicus (Turner) J. Agardh
1880a:160; 1900a:50; 1903c:232; 1911:277; 1913:114, 133.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a].
Gymnosorus variegatus
1901b:249, 264.
Gymnogongrus vermicularis J. Agardh
1912:58.

Hormactis balani Thuret
1890:175.
Hormactis farlowii Bornet
1890:175.
Hormactis quoyii (Agardh) Bornet & Flahault
1890:175.
Hormidium parietinum (Vaucher) Kuetzing
1901d:412.
Hormiscia penicilliformis (Roth) Fries
1905b:225, 243; 1911:268; 1913:105.
NOTE: AUTHOR ALSO REPORTED AS (ROTH) ARESCHOUG [1911].
Hormiscia wormskjoldii (Mert.) Fries
1913:105.
Hormothamnion enteromorphoides Grunow
1901b:241, 262.
Hormotrichum carmichaelii Harvey
1880a:167.
Hormotrichum collabens Kuetzing
1880a:167.
Hormotrichum speciosum Carmichael
1880a:167; 1913:105.
Hormotrichum wormskjoldii
1913:105.
Hormotrichum younganum Dillwyn
1880a:167.
Hyalotheca dissiliens Breb.
1888a:159; 1905b:240.
Hyalotheca mucosa Ehrenberg
1888a:159.
Hydroclathrus cancellatus Bory
1901b:248, 264.
Hydrocoleum glutinosum (Agardh) Gomont
1900a:42; 1905b:223.
Hydrocoleum holdenii Tilden
1905a:169; 1905b:223.
Hydrocoleum lyngbyaceum Kuetzing
1896:1; 1900a:42.
var. rupestre Kuetzing
1900a:42.
Hydrocoleum majus Holden
1900a:42.
Hyella caespitosa Bornet & Flahault
1894:249; 1900a:42; 1905a:172; 1911:260.
Hyella fontana Huber & Jardin
1897:95, 97.
Hymenena fimbriata
1913:118, 119.
Hymenena latissima
1913:119.
Hypnea divaricata Greville
1901b:254, 266.

Hypnea fruiticulosa Kuetzing
1901b:254.
Hypnea musciformis (Wulf.) Lamouroux
1882:47; 1884:30; 1888:84; 1900a:50; 1901b:254, 266; 1906a:111.
NOTE: AUTHOR ALSO REPORTED AS LAMOUROUX [1882, 1884].
Hypnea nidifica J. Agardh
1901b:254.
Hypnea nigrescens
1919:207.
Hypnea valentiae (Turner) Mont.
1901b:254, 266.
Hypoglossum denticulatum
1903a:205, 206, 207.
Hypriea coulteri
1912:59.
Ilea fulvescens (Agardh) J. Agardh
1900a:44; 1902a:175; 1903:3, 20, 30, 31; 1905b:225; 1908d:160, 162, 1911:264; 1927:3B, 6B.
Iridaea cordata
1913:115.
Iridaea laminarioides Bory
1913:114, 115, 133.
forma cordata (Turner) Setchell & Gardner
1913:115.
forma minor
1913:115.
forma parvula Kjellman
1913:115.
forma punicea (Post. & Rupr.) Setchell & Gardner
1913:115.
Iridaea mertensiana
1913:117.
Iridaea minor
1913:115.
Iridaea punicea
1913:115.
Isactis centrifuga Bornet
1901a:136.
Isactis plana (Harvey) Thuret
1888b:310; 1900a:42; 1901:136; 1905b:224.
NOTE: AUTHOR ALSO REPORTED AS THURET [1888b].
Ismoplea sphaerophora (Harvey) Kjellman
1899b:126; 1900a:47.
Isoptera regularis Okamura
1919:204, 206.
Isymenia angusta J. Agardh
1906a:110.
Janczewskia verrucaeformis Solms.
1913:120, 134.
Jania rubens Lamouroux
1902b:14.

Kallymenia reniformis (Turner) J. Agardh
1884a:132; 1899b:126; 1916a:173, 181.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1884a].
Laminaria agardhii Kjellman
1905a:168; 1905b:226, 229; 1911:272; 1914:3.
forma angustissima Collins
1906a:108; 1911:272.
forma vittata Setchell
1905b:229.
forma zostericola Collins
1906a:108.
Laminaria andersonii Farlow
1913:108, 132.
Laminaria apoda
1913:109.
Laminaria bullata Kjellman
1913:108, 132.
forma amplissima Setchell & Gardner
1913:109.
forma angusta Setchell & Gardner
1913:108.
forma cuneata Setchell & Gardner
1913:109.
forma subsimplex Setchell & Gardner
1913:108.
Laminaria caperata De la Pyl.
1900a:47; 1911:273.
Laminaria dermatodea
1880:118; 1880a:163; 1913:109.
Laminaria digitata (L.) Lamouroux
1891:339; 1894:237; 1900:12; 1900a:47; 1902a:177; 1911:27, 280; 1913:108.
NOTE: AUTHOR ALSO REPORTED AS LAMOUROUX [1894].
var. complanata Foslie
1900a:47; 1911:273.
var. ensifolia (Kuetzing) Foslie
1894:237; 1900a:47; 1911:273.
NOTE: AUTHOR ALSO REPORTED AS LE JOLIS [1894].
Laminaria epherema Setchell
1913:109, 132.
Laminaria fascia
1913:107.
Laminaria flexicaulis Le Jolis
1880a:163.
Laminaria groenlandica Rosenvinge
1927:38, 108.
Laminaria intermedia
var. cucullata Foslie
1900a:47; 1911:273.
var. longipes Foslie
1900a:47.

var. ovata Foslie
1900a:47.
Laminaria longicruris De la Pyl.
1880:118; 1880a:163; 1894:236; 1899b:124; 1900:12; 1900a:47; 1902a:177; 1906c:159; 1911:257, 273, 281; 1914:3, 4.
Laminaria longipes Bory
1880:117; 1906a:108.
Laminaria phyllitis (Stackhouse) Lamouroux
1900a:47.
Laminaria platymeris De la Pyl.
1880a:163; 1894:236; 1900a:47; 1900d:210; 1902a:176; 1911:273.
Laminaria saccharina (Linneaus) Lamouroux
1880:118; 1880a:163; 1888:81; 1888b:312; 1894:236; 1899a:70; 1900a:47; 1905b:229; 1911:273; 1913:109, 132; 1919:207; 1927:B9.
NOTE: AUTHOR ALSO REPORTED AS LAMOUROUX [1880, 1880a, 1888].
var. caperata Farlow
1888:9; 1911:273.
forma complanata Setchell & Gardner
1913:109.
forma membranacea J. Agardh
1913:109.
Laminaria sessilis
1913:109.
Laminaria solidungula J. Agardh
1927:3B; 10B.
Laminaria stenophylla (Harvey) J. Agardh
1900a:47; 1902a:175; 1911:273.
Laurencia botryoides
1919:204.
Laurencia cervicornis Harvey
1901b:255, 266.
Laurencia grevilleana
1913:122.
Laurencia implicata
1901b:255, 266.
Laurencia obtusa (Hudson) Lamouroux
1901b:242, 243, 251, 255, 266; 1919:203, 204, 206.
Laurencia paniculata J. Agardh
1902b:14.
Laurencia papillosa (Forsk) Greville
1901b:255, 266.
Laurencia perforata Montagne
1901b:256, 266.
Laurencia pinnatifida (Gmel.) Lamouroux
1901b:254; 1913:120, 129, 134.
Laurencia thuyoides
1919:204.
Laurencia tuberculosa
var. gemmifera (Harvey) J. Agardh
1901b:256, 266.

Lithothamnion californicum Foslie
1913:129.
Lithothamnion circumscriptum Stromfelt
1896:5; 1900a:50.
Lithothamnion colliculosum Foslie
1900a:50.
forma densum Foslie
1911:281.
forma roseum Foslie
1911:281.
Lithothamnion compactum Kjellman
1900a:50; 1927:B15.
Lithothamnion conchatum
1913:129.
Lithothamnion evanescens Foslie
1900a:50; 1911:281.
Lithothamnion fasciculatum (Lamouroux) Areschoug
1894:228.
Lithothamnion flabellatum Rosenvinge
1900a:50.
Lithothamnion foecundum Foslie
1900a:50.
Lithothamnion glaciale Kjellman
1905b:243; 1927:B15.
Lithothamnion incrustans Phil.
1901b:260, 268.
Lithothamnion laeve (Stromfelt) Foslie
1900a:50; 1911:281; 1927:B15.
Lithothamnion laevigatum Foslie
1900a:50; 1905b:235; 1911:281.
Lithothamnion lenormandi (Areschoug) Foslie
1900a:50; 1901b:260, 268; 1911:281.
Lithothamnion marginatum Setchell & Foslie
1913:129.
Lithothamnion mediocre Foslie & Nichols
1913:129.
Lithothamnion norvegicum (Areschoug) Kjellman
1900a:50.
Lithothamnion polymorphum (Linneaus) Areschoug
1880a:159; 1894:228; 1900a:50.
NOTE: AUTHOR ALSO REPORTED AS ARESCHOUG [1880a].
Lithothamnion reclinatum Foslie
1913:129.
Lithothamnion ungeri Kjellman
1900a:50.
var. fastigiatum Foslie
1900a:50.
Lithophyllum lenormandi Rosanoff
1894:228.
Litosiphon pusillus Harvey
1899b:126.

Lomentaria ovalis
1913:154.
var. coulteri
1913:118.
forma subarticulata (Turner) Harvey
1913:118.
Lomentaria rosea (Harvey) Thuret
1880a:160; 1900a:50; 1901a:135.
NOTE: AUTHOR ALSO REPORTED AS THURET [1880a].
Lomentaria uncinata Meneghini
1884:29; 1888:84; 1888b:313; 1900a:50; 1905b:232.
var. filiformis Harvey
1888:84; 1888b:313; 1900a:50.
var. robusta Harvey
1888b:313.
Lophosiphonia obscura (Agardh) Falkenberg
1901b:257, 267; 1913:122, 134.
Lophosiphonia villum (J. Agardh) Setchell & Gardner
1913:121, 122, 134.
Lophura floccosa
1919:207.
Lyngbya aesturarii (Mert.) Liebmann
1882:46; 1888:76; 1888a:163; 1888b:310; 1894:247; 1896:3; 1900a:42; 1901b:240, 262; 1902:123; 1903:27; 1905a:172; 1905b:222, 235; 1906b:123; 1907a:197; 1908d:160, 162; 1910:9; 1911:261; 1927:3B, 4B.
NOTE: AUTHOR ALSO REPORTED AS (JERG.) LIEBM. [1894], LIEBMANN [1882, 1888, 1888a, 1888b].
Lyngbya aestuarii
forma aeruginosa Gomont
1911:261.
forma limicola Gomont
1911:261.
forma symplocoidea Gomont
1911:261.
Lyngbya confervoides Agardh
1900a:42; 1905a:172; 1908d:160; 1911:261.
forma violacea Collins
1901b:240, 262.
Lyngbya ferruginea Harvey
1880a:167; 1927:4B.
AUTHOR ALSO REPORTED AS AGARDH [1880a].
Lyngbya gracilis (Meneghini) Rabenhorst
1896c:458; 1900a:42.
Lyngbya holdenii De Toni
1911:261.
Lyngbya lagerheimii (Moebius) Gomont
1900a:42; 1911:261.
NOTE: AUTHOR ALSO REPORTED AS GOMONT.
Lyngbya lutea Gomont
1894:248; 1900a:42; 1905b:222; 1911:261.
NOTE: AUTHOR ALSO REPORTED AS (AGARDH) GOMONT [1900a, 1905b].

Lyngbya luteo-fusca Agardh
1888a:163.
Lyngbya majuscula (Dillwyn) Harvey
1888b:310; 1900a:42; 1901b:240, 262.
NOTE: AUTHOR ALSO REPORTED AS HARVEY [1888b; 1901b].
Lyngbya ochracea Thuret
1888a:163; 1905b:236.
NOTE: AUTHOR ALSO REPORTED AS (KUETZING) THURET [1905b].
Lyngbya putalis Montagne
1901b:240.
Lyngbya semiplena (Agardh) J. Agardh
1894:248; 1900a:42; 1906b:123; 1908d:162; 1911:261.
NOTE: AUTHOR ALSO REPORTED AS J. AGARDH [1911].
Lyngbya subtilis Holden
1900a:42; 1905b:222; 1906:113; 1908d:162.
Lyngbya tenerrima Thuret
1888b:310; 1894:248.
Lyngbya versicolor (Wartm.) Gomont
1901b:240.
Lyngbya wollei Farlow
1888a:163.
Macrocystis pyrifera (Turner) Agardh
1913:110, 132.
Mastigocoleus testarum Lagerheim
1894:247; 1900a:42; 1901b:241, 262; 1905b:223; 1906c:159.
1911:263.
Melobesia amplexifrons
1913:129.
Melobesia corallinae Crouan
1888:87; 1900a:50; 1901a:134; 1911:281.
Melobesia farinosa Lamouroux
18880a:159; 1882:47; 1888:87; 1888b:314; 1900a:50; 1901b:260, 268.
Melobesia lejolisii Rosanoff
1880a:159; 1888:86; 1894:229; 1900a:50; 1901b:260, 268; 1905b:235;
1911:281.
Melobesia lenormandi Rosanoff
1894:228.
Melobesia lichenoides Areschoug
1911:281.
Melobesia macrocarpa Rosanoff
1900a:50.
Melobesia marginata
1913:129.
Melobesia membranacea (Esper) Lamouroux
1880a:159; 1888:86; 1900a:51; 1901b:260, 268.
NOTE: AUTHOR ALSO REPORTED AS LAMOUROUX [1880a, 1888, 1901b].
Melobesia pustulata Lamouroux
1880a:159; 1888:87; 1894:229; 1900a:51; 1901b:260, 268; 1911:281.
Melobesia zostericolum
forma mediocris
1913:129.

Mesogloia andersonii Farlow
1913:108, 113, 132.
Mesogloia divaricata (Agardh) Kuetzing
1882:47; 1884:29; 1888:80; 1888b:312; 1899a:70; 1900a:47; 1902a:178; 1904:182; 1905b:229; 1911:272.
NOTE: AUTHOR ALSO REPORTED AS KUETZING [1882, 1884, 1888]; (AGARDH) J. AGARDH [1902].
Mesogloia simplex Saunders
1913:108, 132.
Mesogloia vermicularis Agardh
1880a:168.
Mesotaenium braunii De Bary
1904a:230.
Micrasterias depauperata Nordstedt
1888a:160.
Micrasterias dichotoma Wolle
1888a:160.
Micrasterias muricata Ralfs
1888a:160.
Micrasterias truncata Brebisson
1868a:160.
var. minor Wolle
1888a:160.
Microchaete grisea Thuret
1884a:130; 1900a:42; 1905b:223; 1908b:126.
Microchaete nauschonensis Collins
1918:141.
Microcladia borealis Ruprecht
1909:17; 1913:126, 135.
Microcladia californica Farlow
1913:126, 135.
Microcladia coulteri Harvey
1913:126, 135.
Microcoleus ochthonoplastes Thuret
1888a:14; 1888b:310; 1894:247; 1900a:42; 1901b:240, 262; 1903c:233, 234; 1905b:223; 1911:261.
NOTE: AUTHOR ALSO REPORTED AS (FL. DAN.) THURET [1894, 1900a, 1901b, 1903c, 1905b].
Microcoleus lacustris (Rabenhorst) Farlow
1897:96.
Microcoleus tenerrimus Gomont
1901b:240, 262; 1903c:233, 234; 1911:262.
Microcoleus terrestris Desmaz.
1888a:164.
Microcoleus vaginatus (Vaucher) Gomont
1901b:240.
Microcoleus versicolor Thuret
1888a:164.
Microdictyon agardhianum Decne.
1902b:13.
Microdicyton umbilicatum (Velley) Zan.
1901b:247, 264.

Microspongium gelatinosum Reinke
1900a:47.
Microspora abbreviata (Rab.) Lagerheim
1905b:239.
Microspora amoena (Kuetzing) Rabenhorst
1905b:239.
Microspora crassior (Hansg.) Hazen
1905b:239.
Microspora stagnorum (Kuetzing) Lagerheim
1905b:239.
Mikrosyphar porphyrae Kuckuck
1918:143.
Monostroma angicavum Kjellman
1903:13, 14.
Monostroma articum Wittrock
1903:11, 13, 14, 31; 1909a:24, 25.
NOTE: AUTHOR ALSO REPORTED AS COLLINS [1909a].
var. intestiniforme Rosenvinge
1903:11, 14; 1909a:24.
Monostroma blyttii (Areschoug) Wittrock
1882a:70; 1894:246; 1903:10, 12, 31; 1911:265.
NOTE: AUTHOR ALSO REPORTED AS MARTINDALE [1903], AND WITTROCK [1882a].
Monostroma collinsii
1903:18.
Monostroma crassiusculum Kjellman
1903:12.
Monostroma crepidinum Farlow
1882a:70; 1888:77; 1888b:310; 1900a:44; 1903:11, 16, 31; 1905b:224.
Monostroma cylindraceum Kjellman
1903:13, 14.
Monostroma fuscum (Post. & Rupr.) Wittrock
1900a:44; 1901d:409, 410; 1903:11, 12, 15; 1909a:24, 25; 1911:265; 1914:4
forma blyttii (Wittrock) Collins
1903:12, 31; 1913:102.
forma splendens (Wittrock) Collins
1903:12; 1913:102.
Monostroma grevillei (Thuret) Wittrock
1888a:157; 1900a:44; 1903:11, 12, 13, 14, 15, 31; 1905b:224; 1909a:23.
NOTE: AUTHOR ALSO REPORTED AS LE JOLIS [1888a].
var. arctica
1903:13, 14.
forma lactuca
1903:15.
var. vahlii (J. Agardh) Rosenvinge
1903:13, 14; 1909a:24.
Monostroma groenlandicum J. Agardh
1899b:126; 1900a:44; 1901d:410; 1903:10, 11, 18, 31; 1905b:242;
1911:265.
Monostroma lactuca
1903:15, 1909a:23, 24, 25.

Monostroma latissimum (Kuetzing) Wittrock
1888a:158; 1891:341; 1900a:44; 1901a:134; 1902a:175; 1903:10, 11, 16, 17, 31; 1905b:224, 238; 1909a:26; 1911:265; 1913:102.
NOTE: AUTHOR ALSO REPORTED AS WITTROCK [1888a].

Monostroma leptodermum Kjellman
1900a:44; 1903:11, 15, 31; 1911:265; 1913:103.

Monostroma lubricum Kjellman
1903:12.

Monostroma orbiculatum Thuret
1909a:25, 26.
forma varians Collins
1909a:26.

Monostroma pulchrum Farlow
1880a:168; 1899b:124; 1900a:44; 1903:11, 14, 15, 16, 31; 1905b:224; 1909a:25; 1911:265.

Monostroma quaternarium (Kuetzing) Desmar.
1891:341; 1902a:175; 1903:11, 17, 31.

Monostroma saccodeum Kjellman
1903:13, 14.

Monostroma splendens Kjellman
1901d:410; 1903:12.

Monostroma undulatum Wittrock
1903:11, 14, 15, 31; 1909a:25.
var. farlowii Foslie
1900a:44; 1903:11, 14, 15; 1905b:242; 1911:265.
NOTE: AUTHOR ALSO REPORTED AS ROSENVINGE.

Monostroma vahlii J. Agardh
1888a:157; 1891:341; 1899b:126; 1900a:44; 1901d:410; 1903:13.

Monostroma zostericolum Tilden
1903:16; 1913:103.

Mougeotia genuflexa (Dillwyn) Agardh
1905b:239.

Mougeotia robusta (De Bary) Wittrock
1905b:239.

Murrayella periclados (Agardh) Schmitz
1901b:257, 267.

Mycoidea parasitica Cunningham
1901b:243.

Myriactis pulvinata Kuetzing
var. minor Farlow
1882:47; 1888:80; 1900a:47; 1905b:228.

Myrionema balticum (Reinke) Foslie
1900a:47.

Myrionema corunnae Sauvageau
1906c:158; 1911:271.

Myrionema foecundum (Stromf.) Foslie
1900a:47.

Myrionema globosum (Reinke) Foslie
1900a:47.

Myrionema leclancherrii Harvey
1882a:71.

Myrionema orbiculare J. Agardh
1884a:131; 1911:269.

Myrionema strangulans Greville
1880a:164; 1894:238; 1911:271; 1913:108, 132.
Myrionema vulgare Thuret
1884a:131; 1888b:312; 1900a:47; 1906c:158; 1911:271; 1913:108.
Myriotrichia clavaeformis Harvey
1888:79; 1900a:47.
var. filiformis Farlow
1888b:311.
Myriotrichia filiformis Harvey
1900a:47.
Nemalion multifidum (Web. & Mohr) J. Agardh
1880a:160; 1883:55; 1894:233; 1900a:51; 1905b:231; 1906d:190; 1911:276.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a, 1894].
Nemastoma bairdii Farlow
1900a:51.
Neomeris dumetosa Lamour.
1901b:247, 264.
Nereocystis luetkeana (Mert.) Postels & Ruprecht
1913:110, 132.
Nitella acuminata A. Braun
1901d:416.
Nitella opaca Agardh
1901d:416.
Nitophyllum crytoneuron (Mont.) De Toni
1915:95.
Nitophyllum latissimum (Harvey) J. Agardh
1913:119, 134.
Nitophyllum multilobum
1913:119.
Nitophyllum ruprechtianum J. Agardh
1913:118, 119, 134.
forma flabelligerum (J. Agardh) Nott
1913:118.
Nitophyllum spectabile Eaton
1913:119, 134.
Nitophyllum steonoglossum
1913:119.
Nitophyllum violaceum J. Agardh
1913:119, 134.
Nodularia harveyana (Thwaites) Thuret
1884a:130; 1888a:163; 1900a:42; 1908d:162; 1911:262.
NOTE: AUTHOR ALSO REPORTED AS THURET [1884a, 1888a, 1911].
Nodularia litorea (Kuetzing) Thuret
1884a:130.
Nodularia spumigena Mert.
1908d:162.
var. genuina Born. & Flah.
1911:262.

var. litorea (Kuetzing) Bornet & Thuret
1900a:42; 1911:262.
NOTE: AUTHOR ALSO REPORTED AS BORNET & FLAHAULT [1911].
var. major (Kuetzing) Bornet & Flah.
1900a:42; 1905b:223.
Nostoc collinum Kuetzing
1888a:163.
Nostoc commune Vaucher
1901b:240; 1905b:236.
Nostoc expansum
1912:58, 59.
Nostoc microscopicum Carmichael
1901b:240; 1905b:236.
Nostoc muscorum Agardh
1888a:163; 1904a:230; 1905b:242.
Nostoc parmelioides Kuetzing
1905b:236.
Nostoc punctiforme Hariot in Bornet & Flahault
1918:143.
Nostoc pruniforme Agardh
1905b:237.
Nostoc quoyii
1890:175.
Nostoc rupestre Kuetzing
1904a:230.
Nostoc sphaericum Vaucher
1888a:163; 1908d:160; 1911:262.
Nostoc sphaeroides Kuetzing
1888a:163.
Nostoc verrucosum Vaucher
1901b:240.
Nostochopsis lobatus Wood
1905b:237.
Notheia anomala
1912:59.
Ochlochaete ferox Huber
1908d:157.
Odonthalia aleutica (Agardh) J. Agardh
1913:122, 123, 135.
Odonthalia dentata (L.) Lyngbye
1927:148.
forma angusta Harvey
1908a:116.
Odonthalia floccosa (Esper) Falkenberg
1913:122, 123, 135.
forma comosa Setchell & Gardner
1913:122, 123.
forma macracantha (Kuetzing) Setchell & Gardner
1913:122, 123.
forma typica
1913:123.

Oscillatoria laetevirens Crouan
1900a:42; 1905a:172; 1911:260.
Oscillatoria limosa
1894:248; 1900a:42; 1905b:235; 1911:260.
Oscillatoria margaritifera Kuetzing
1900a:42; 1911:260.
Oscillatoria nigro-viridis Thwaites
1900a:42; 1911:260.
Oscillatoria princeps Vaucher
1900a:42; 1901b:239; 1905b:223, 235, 238.
forma purpurea Collins
1901:239.
Oscillatoria proboscidea Gomont
1901b:239.
Oscillatoria salinarum Collins
1906a:105.
Oscillatoria splendida Greville
1905b:236.
Oscillatoria subuliformis Kuetzing
1894:248.
Oscillatoria tenuis Agardh
1900a:42; 1901b:239; 1905b:236; 1908d:162; 1911:260.
var. natans (Kuetzing) Gomont
1905b:236.
Ostracoblabe implexa
1897:96.
Ostreobium quekettii Born. & Flah.
1900a:42; 1906c:159.
Padina durvillaei Bory
1901b:249, 264.
Padina pavonia Gaillon
1901b:249; 1902b:13; 1919:207.
Palmella rupestris Lyngbye
1882a:70.
Palmellococcus marinus Collins
1908d:160; 1911:263; 1927:3B; B5.
Palmellococcus miniatus
1907a:198.
Pediastrum angulosum
1901d:409.
Pediastrum boryanum
1901d:409.
Pediastrum boryanum
1901d:409.
Pediastrum ehrenbergii A. Br.
1888a:9.
Pelvetia fastigiata
forma limitata
1913:111.
Pelvetiopsis limitata (Setchell) Gardner
1913:111, 132.

Penicillus capitatus Lamour.
1901:91; 1901b:245, 263; 1902b:12.
Penicillus dumetosus (Lamour) Decsne.
1901b:245, 246, 263.
Penium digitus Breb.
1888a:162.
Penium margaritaceum Breb.
var. punctulatum Ralfs
1888a:162.
Penium minutum Cleve
1888a:162.
Percursaria percursa Rosenvinge
1903:26.
Petrocelis cruenta J. Agardh
1880a:160; 1883:56; 1894:229; 1900a:51; 1908d:158, 159; 1911:280.
Petrocelis hennedyi (Harvey) Batters
1908d:159.
Petrocelis middendorffii (Ruprecht) Agardh
1908d:158, 159; 1911:280.
Peyssonnelia dubyi Crouan
1894:229; 1896:5; 1901b:260, 267.
Peyssonnelia rosenvingii Schmitz
1896:5; 1911:280.
Peyssonnelia rubra (Greville) J. Agardh
1901b:260, 267.
Phaeosaccion collinsii Farlow
1888a:155; 1899b:126; 1900a:47; 1911:268.
Phloeospora biachiata
1882a:70.
Phloeospora pumila Kjellman
1927:B9.
Phormidium ambiguum Gomont
1900a:42.
Phormidium autumnale (Agardh) Gomont
1900a:42.
Phormidium corium (Agardh) Gomont
1900a:42; 1905b:236; 1911:261.
NOTE: AUTHOR ALSO REPORTED AS GOMONT [1911].
Phormidium favosum (Bory) Gomont
1900a:42; 1905:236.
Phormidium fragile (Meneghini) Gomont
1894:248; 1900a:42; 1911:261.
NOTE: AUTHOR ALSO REPORTED AS GOMONT [1894, 1911].
Phormidium papyraceum Gomont
1927:3B, 4B, B7.
Phormidium persicinum (Reinke) Gomont
1900a:42; 1900:11; 1911:261.
NOTE: AUTHOR ALSO REPORTED AS GOMONT [1911].
Phormidium retzii (Agardh) Gomont
1901b:239; 1904a:230; 1905b:236, 243.
forma fasciculatum (Breb.) Gomont
1906b:122.

Phormidium uncinatum (Agardh) Gomont
1905b:236.
Phormidium valderianum (Delponte) Gomont
1900a:42.
Phuyllophora traillii Holmes
1891:339.
Phycocelis faecunda
1913:108.
Phycocelis maculans Collins
1896c:459, 462; 1911:271.
Phyllitis fascia (Mueller) Kuetzing
1880a:165; 1882:47; 1888:79; 1888a:154; 1888b:311; 1894:239; 1896c:460; 1900a:47; 1900c:163; 1905b:228, 243; 1911:270; 1913:107, 131.
NOTE: AUTHOR ALSO REPORTED AS KUETZING [1880a, 1882, 1888, 1888a, 1888b, 1896c] AND (FL. DAN.) KUETZING [1894, 1900a, 1900c, 1905b, 1911].

var. caespitosa (Agardh) Farlow
1894:239; 1905b:228.
Phyllitis zosterifolia Reinke
1896c:460; 1899b:127; 1900a:47; 1905b:242.
Phyllobium dimorphum Klebs
1905:99.
Phyllophora brodiaei (Turner) J. Agardh
1880a:160; 1883:56; 1888:84; 1888b:313; 1900a:51; 1901a:134; 1901b: 234; 1903c:232; 1905b:231; 1911:276, 277.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a, 1888, 1888a, 1888b].
var. interrupta (Greville) Rosenvinge
1908a:116; 1927:128.
forma pygmaea Darb.
1908a:116.
Phyllophora membranifolia (Good. & Woodw.) J. Agardh
1880a:160; 1888:84; 1888b:313; 1900a:51; 1905b:231; 1911:277.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a, 1888, 1888b].
Phyllophora rubens (Good. & Woodw.) Grey
1899b:127.
Phyllophora traillii Holmes
1900a:51; 1905b:231; 1911:277.
See also: 1891:339.
Phyllospora menziesii
1913:110.
Pikea californica Harvey
1913:128, 136.
Pilinia diluta Wood
1905a:210.
Pilinia endophytica Collins
1908d:156; 1911:266.
Pilinia lunatiae Collins
1908b:122, 123, 125, 127.
Pilinia maritima (Kjellman) Rosenvinge
1900a:44; 1903a:210; 1908b:122, 126.
Pilinia minor Hansgrig in Foslie
1908b:122, 124; 1908d:156.
Pilinia morsei Collins
1908b:122, 126, 127.

Plocamium coccineum (Hudson) Lyngbye
1901b:234; 1913:118, 134; 1915:93, 94, 95.
forma compactum Collins
1915:93, 94.
var. flexuosum Harvey
1915:95.
Plocamium leptophyllum Kuetzing
1915:95.
var. flexuosum J. Agardh
1915:95.
Plocamium violaceum Farlow
1913:118, 134.
Plumaria elegans (Bonnem.) Schmitz
1894:230; 1900a:51; 1902a:176; 1906a:112; 1911:279.
NOTE: AUTHOR ALSO REPORTED AS BONNEM. [*1894*].
Pogotrichum filiforme Reinke
1911:270.
Polycystis elabens Kuetzing
1894:249; 1900a:42; 1905a:172; 1908d:162; 1911:259.
NOTE: AUTHOR ALSO REPORTED AS KUETZING [*1908d, 1911*].
Polycystis pallida (Kuetzing) Farlow
1888b:310; 1894:249; 1900a:43.
Polyides rotundus (Gmel.) Greville
1880a:160; 1888:85; 1894:229; 1900a:51; 1911:280; 1911a:187.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [*1880a*], *GREVILLE* [*1888*].
Polysiphonia americana
1905b:232.
Polysiphonia arctica J. Agardh
1927:B13.
Polysiphonia atrorubescens (Dillwyn) Greville
1880a:158; 1884:29; 1888:86; 1888b:314; 1900a:51; 1913:120.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [*1880a, 1884, 1888, 1888b*].
Polysiphonia bipinnata Post. & Rupr.
1913:121; 1927:B13.
Polysiphonia californica
1913:120.
var. plumigera
1913:121.
Polysiphonia cuspidata J. Agardh
1901b:256, 266.
Polysiphonia dendroidea
1915:121.
Polysiphonia dictyurus
1913:120.
Polysiphonia elongata (Hudson) Harvey
1880a:158; 1888:86; 1900a:51; 1905b:232.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [*1880a, 1888a*].
Polysiphonia fastigiata (Roth) Greville
1880a:159; 1891:335, 339; 1894:231; 1900a:51; 1903c:212; 1905b:232; 1911:260, 276, 279.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [*1880a*].

Polysiphonia ferulacea Suhr
1901b:256, 266; 1919:204, 206.
Polysiphonia fibrillosa (Dillwyn) Greville
1880a:158; 1900a:51; 1911:279.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [1880a].
Polysiphonia flexicaulis (Harvey) Collins
1911:279.
Polysiphonia harveyi Bailey
1880a:158; 1882:47; 1888:85; 1888b:314; 1900a:51; 1905b:232; 1911:278.
var. arietina Harvey
1880a:158; 1888:86; 1905b:232.
Polysiphonia havanensis Mont.
1901:256, 266; 1902b:14.
var. binneyi (Harvey) J. Agardh
1901b:256, 266.
Polysiphonia japonica Harvey
1919:206.
Polysiphonia nigrescens (Dillwyn) Greville
1880a:159; 1882:47; 1888:86; 1888a:152; 1888b:313; 1894:231; 1900a:51; 1905b:232; 1908a:116; 1911:279; 1913:134.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [1880a, 1882, 1888, 1888a].
var. affinis (Moore) Harvey
1888:86; 1888b:314; 1900a:51; 1905b:232; 1913:120.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1888, 1888b].
var. durkeei Harvey
1900a:51; 1905b:232.
var. fucoides Harvey
1888b:314; 1900a:51; 1905b:232.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1888b].
Polysiphonia olneyi Harvey
1880a:158; 1882:47; 1888:85; 1894:231; 1899a:70; 1900a:51; 1901c:292; 1902a:178; 1905b:232; 1911:278.
Polysiphonia pecten-veneris Harvey
1901b:256, 266, 1902b:14.
Polysiphonia plumula
1913:121.
Polysiphonia schuebelerii Foslie
1901c:291, 292; 1911:279.
Polysiphonia secunda (Agardh) Zanardini
1901b:256, 267.
Polysiphonia senticulosa
1913:119, 120.
Polysiphonia spinescens
var. sinensis
1919:207.
Polysiphonia subtilissima Montagne
1880a:158; 1896:2; 1900a:51.
Polysiphonia subulata (Ducl.) J. Ag.
1901b:256, 267; 1913:113, 120, 134.
Polysiphonia tenuistriata Hooker & Harvey
1913:120, 134.

Polysiphonia urceolata (Lightfoot) Greville
1880a:158; 1882:47; 1888b:313; 1894:231; 1900a:51; 1900d:210; 1905b: 233, 242; 1911:278; 1913:119, 134; 1919:206.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [1880a, 1882], (DILLWYN) GREVILLE [1888b], AND (LYNGBYE) GREVILLE [1919].
var. formosa (Suhr) Agardh
1880a:158; 1882:47; 1888:85; 1900a:51; 1905b:233; 1911:278.
NOTE: AUTHOR ALSO REPORTED AS HARVEY [1882], AGARDH [1888].
var. patens (Dillwyn) Greville
1880a:158; 1900a:51; 1911:278.
var. senticulosa (Harvey) Collins
1913:119.

Polysiphonia variegata (Agardh) Zanardini
1880a:158; 1882:47; 1884:29, 30; 1888:86; 1888b:314; 1900a:51; 1905b:233.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a, 1882, 1884, 1888, 1888b].

Polysiphonia vestita J. Agardh
1896c:462; 1899b:127; 1900a:51.

Polysiphonia villum
1913:121.

Polysiphonia violacea (Roth) Greville
1880a:158; 1888:86; 1894:231; 1900a:51; 1901c:291, 292; 1902a:177; 1905b:233; 1911:279.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [1880a, 1888].
var. flexicaulis Harvey
1900a:51; 1911:279.

Polysiphonia woodii
1913:121.

Porphyra abyssicola Kjellman
1903a:212; 1913:112, 133.

Porphyra amplissima (Kjellman) Setchell & Hus
1902a:177; 1903a:211, 212; 1911:275; 1913:112, 133; 1916a:171.
NOTE: AUTHOR ALSO REPORTED AS (KUETZING) SETCHELL & HUS [1911].

Porphyra coccinea J. Agardh
1884a:131; 1899b:127; 1900a:51; 1903a:211.

Porphyra laciniata (Lightfoot) Agardh
1882:47; 1882a:70; 1888:82; 1888a:153; 1888b:312; 1894:234; 1900a:51; 1903a:210, 211, 212; 1905b:231, 243; 1911:275.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1882, 1882a, 1888, 1888a, 1888b].
forma epiphytica Collins
1903a:212.
forma umbilicalis Agardh
1903a:211, 212.

Porphyra leucosticta Thuret
1882a:70; 1884a:131; 1888b:312; 1900a:51; 1903a:210, 211, 212; 1905b:231; 1911:275.

Porphyra linearis Greville
1903a:212; 1905b:243.

Porphyra miniata (Lyngbye) Agardh
1884a:131; 1894:234; 1900a:51; 1902a:177; 1903a:211, 212; 1905b:242; 243; 1911:275; 1913:133.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1884a, 1894, 1900a, 1902a, 1905b]. AND (AGARDH) FL. DAN. 1911.

forma cuneiformis Setchell & Hus
1913:112.
Porphyra naiadum
1913:133.
forma major Hus
1913:112.
forma minor Hus
1913:112.
Porphyra nereocystis Anderson
1913:112, 133.
Porphyra perforata J. Agardh
1913:112, 133.
forma segregata Setchell & Hus
1913:112.
Porphyra tenuissima (Stromf) Setchell & Hus
1903a:211, 212; 1911:275.
Porphyra umbilicalis (L.) J. Agardh
1911:269, 275, 276; 1913:112, 133; 1918:143, 144.
NOTE: AUTHOR ALSO REPORTED AS SETCHELL & GARDNER [1913].
forma epiphytica Collins
1911:275.
Porphyra variegata Kjellman
1913:112, 133.
Porphyra vulgaris Agardh
1880a:162; 1913:112.
Porphyridium cruentum Naegeli
1888a:158.
Postelsia palmaeformis Ruprecht
1913:110, 132.
Prasinocladus subsalsus Davis
1900a:45; 1911:263.
Prasiola crispa
1901d:412.
forma submarina Wille
1927:B7.
Prasiola furfuracea (F. Dan.) Meneghini
1927:B7.
Prasiola gardneri Collins
1906a:106.
Prasiola johanseni Collins
1927:3B, 4B, B7.
Prasiola stipitata Suhr
1916:90, 91; 1927:B7.
Pringsheimia scutata Reinke
1891:340; 1900a:45; 1901b:243, 262; 1908d:157.
Prionitis lanceolata Harvey
1913:127, 135.
Prionitis lyallii Harvey
1913:127, 135.
forma densissima Harvey
1913:128.

var. concinna
1913:124.
Ptilota elegans Bonnem.
1880a:161; 1888b:313; 1911:279.
Ptilota filicina J. Agardh
1913:124, 135.
Ptilota hypnoides Harvey
1913:124, 135.
Ptilota pectinata (Gunner) Kjellman
1894:230; 1896c:461; 1900a:51; 1905b:243; 1906a:112; 1908a:116; 1911:279.
NOTE: AUTHOR ALSO REPORTED AS KJELLMAN [1896a].
forma tenuis Collins
1906a:112.
Ptilota plumosa Agardh
1880a:161.
var. serrata
1880a:161.
Ptilota serrata Kuetzing
1884:30; 1911:279; 1913:124.
Ptilothamnion butleriae
1901b:259.
Ptilothamnion micropterum (Mont.) Bornet
1901b:259.
Punctaria glacialis Rosenvinge
1927:89.
Punctaria latifolia Greville
1880a:165; 1888a:154; 1888b:311; 1894:239; 1900a:47; 1905b:227; 1911:270.
forma crispata (Kuetzing) Collins
1911:270.
var. zosterae Le Jolis
1880a:165; 1888:79; 1888a:154; 1888b:311; 1896:4.
Punctaria plantaginea (Roth) Greville
1880a:165; 1888b:311; 1896:4; 1900a:47; 1905b:228; 1911:270.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [1880a].
Punctaria stipitata Collins
1927:88, 89, 168.
Pylaiella littoralis (L.) Kjellman
1894:241; 1900a:47; 1905b:226, 242; 1908a:116; 1911:268; 1913:106, 131; 1914:4; 1927:88.
var. firma (Agardh) Kjellman
1911:268.
var. firma
forma macrocarpa (Foslie) Kjellman
1913:106.
var. fluviatilis Hauck
1891:338; 1900a:47.
var. robustus Farlow
1894:241; 1900a:47.

var. typica Kjellman
1911:268.
var. varia (Kjellman) Kuckuck
1900a:47; 1911:268; 1913:106.
NOTE: AUTHOR ALSO REPORTED AS KJELLMAN [1900a, 1911].

Ralfsia borneti Kuckuck
1900:12; 1900a:47; 1901a:134; 1905b:229; 1908d:156; 1911:272.

Ralfsia clavata (Carmichael) Farlow
1880a:164; 1888:80; 1888a:155; 1888b:312; 1894:237; 1900a:47; 1905b:229; 1911:272; 1913:108.
NOTE: AUTHOR ALSO REPORTED AS CROUAN [1880a, 1888, 1888a]; (CARMICHAEL) CROUAN [1882b, 1894].
forma laminariae Collins
1911:272.

Ralfsia deusta (Agardh) J. Agardh
1883:56; 1894:237; 1900a:47; 1900d:209; 1905b:243; 1913:108.
NOTE: AUTHOR ALSO REPORTED AS ARESCHOUG [1905b], J. AGARDH [1894, 1900a, 1900d], AGARDH [1883].

Ralfsia pusilla (Stromf.) Holmes & Batters
1894:237; 1896:1; 1900a:48; 1911:272; 1927:10B.
NOTE: AUTHOR ALSO REPORTED AS (STROMF.) BATTERS [1927].

Ralfsia verrucosa Areschoug
1880a:164; 1883:56; 1888a:155; 1888b:312; 1894:237; 1900:12; 1900a:48; 1905b:229; 1906c:158; 1908d:161; 1911:272; 1913:108.
NOTE: AUTHOR ALSO REPORTED AS (ARESCHOUG) J. AGARDH [1894, 1905b, 1913].

Renfrewia parvula Griggs
1913:109.

Rhabdonia coulteri
1913:117.

Rhabdonia tenera Agardh
1880a:160; 1882:47; 1884:29; 1888:85; 1888b:313.

Rhipocephalus phoenix (Ell. & Sol.) Kuetzing
1901b:245, 263; 1902b:12.

Rhizoclonium erectum Collins
1901c:291, 292.

Rhizoclonium hieroglyphicum
var. macromeres Nordstedt
1905b:240.

Rhizoclonium implexum (Dillwyn) Kuetzing
1927:3B, 8B.

Rhizoclonium kerneri Stockmayer
1900a:45; 1913:103.

Rhizoclonium kochianum Kuetzing
1880a:168; 1888:78; 1888a:156.

Rhizoclonium lacustre Kuetzing
1888a:156.
forma americanum Wille
1905b:240.

Rhizoclonium linum Thuret
1884a:130.

Rhizoclonium pachydermum Kjellman
1901c:291.
Rhizoclonium riparium (Roth) Harvey
1880a:168; 1888:78; 1888a:156; 1888b:311; 1891:335; 1894:243; 1905b: 225; 1908d:160; 1913:103.
NOTE: AUTHOR ALSO REPORTED AS HARVEY [1880a, 1888, 1888a]; ROTH [1888b].
var. implexum Rosenvinge
1900a:45; 1901d:414; 1904a:230; 1911:266; 1913:103; 1927:8B.
NOTE: AUTHOR ALSO REPORTED AS (DILLWYN) ROSENVINGE [1911, 1913].
var. polyrhizum Rosenvinge
1900a:45; 1904a:230; 1911:266; 1913:103.
NOTE: AUTHOR ALSO REPORTED AS (LYNGBYE) ROSENVINGE [1911, 1913].
Rhizoclonium tortuosum Kuetzing
1888a:156; 1894:243; 1900a:45; 1901c:290; 1904a:230; 1905b:225; 1911:266.
var. polyrhizum Holden
1900a:45; 1905b:225.
Rhodochorton membranaceum Magnus
1894:230; 1900a:51; 1906c:160; 1911:280.
Rhodochorton parasiticum Holmes
1900:12; 1900a:51; 1911:280.
Rhodochorton penicilliforme (Kjellman) Rosenvinge
1906c:160.
Rhodochorton rothii (Turton) Naegeli
1891:335; 1894:230; 1900:12; 1900a:51; 1900b:131; 1905a:172; 1905b: 234; 1911:280; 1913:127, 135; 1914:4.
NOTE: AUTHOR ALSO REPORTED AS NAEGELI [1900]; (ENG-BOT.) NAEGELI [1894, 1900a, 1905b, 1911, 1914].
Rhododermis elegans Crouan
1906c:160; 1911:281.
Rhododermis georgii (Batters) Collins
1906c:160, 161; 1911:281.
Rhododermis parasitica Batters
1906c:160; 1911:281.
Rhododermis vanheurckii Heydrich
1906c:161.
Rhodomela floccosa
1908a:115; 1913:122.
Rhodomela larix (Turner) Agardh
1913:122, 123, 135; 1927:14B.
Rhodomela lyallii
1913:122.
Rhodomela lycopodioides (L.) Agardh
1906c:159, 160; 1911:279; 1913:122, 123, 134; 1927:B13.
forma flagellaris Kjellman
1908a:116; 1927:B13.
forma setacea Kjellman
1927:B13.
forma tenuissima (Rupr.) Kjellman
1908a:116; 1913:122; 1927:14B.
NOTE: AUTHOR ALSO REPORTED AS KJELLMAN [1927].

forma typica
subforma tenera Kjellman
1911:279.
Rhodomela rochei Harvey
1900a:51; 1905a:169.
Rhodomela subfusca (Woodw.) Agardh
1880a:159; 1894:231; 1896c:461, 462; 1900a:51; 1906c:159, 160; 1911:276, 279; 1919:206.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a, 1896c].
var. gracilis (Harvey) J. Agardh
1880a:159; 1900a:51.
forma gracilior (Harvey) J. Agardh
1905b:233.
var. rochei
1880a:159.
Rhodomela virgata Kjellman
1896c:461; 1900a:51.
Rhodophyllis dichotoma (Lepechin) Gobi
1900a:52; 1902a:176.
Rhodymenia corallina (Bory) Greville
1913:117, 118, 134; 1915:93.
Rhodymenia flabellifolia Bory
1913:118, 134; 1915:93.
Rhodymenia palmata (L.) Greville
1880a:160; 1882:47; 1884a:132; 1888:84; 1888a:153; 1888b:313; 1894:232; 1896c:460; 1900:11; 1900a:52; 1900d:210; 1905b:231, 243; 1906a:108; 1906d:194; 1908a:116; 1913:117, 134; 1914:3; 1915:94; 1916a:170.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [1880a, 1882, 1888, 1888a, 1896c].
forma angustifolia Kjellman
1911:278.
var. latifolia Rosenvinge
1900a:52.
forma mollis Setchell & Gardner
1913:117.
var. sarniensis (Mert.) Greville
1900a:52.
var. sinensis
1919:207.
Rhodymenia palmetta (Esp.) Greville
1913:117, 134.
Rhodymenia pertusa (Post. & Rupr.) J. Agardh
1912:59; 1913:118, 134.
Rhodymenia wilkesii Bailey & Harvey
1912:58, 59.
Rivularia atra Roth
1880a:168; 1888:5; 1894:247; 1900a:43; 1905b:224; 1911:263; 1919:205.
Rivularia beccariana (De Not.) Born. & Flah.
1899:11.
Rivularia biasolettiana Meneghini
1900a:43.

Rivularia bornetiana Setchell
1900a:43.
Rivularia compacta Collins
1899:10, 11.
Rivularia hospita Thuret
1888b:310.
Rivularia minutula (Kuetzing) Born. & Flah.
1899:10, 11.
Rivularia nitida Agardh
1890:175; 1894:247; 1900a:43; 1905b:224; 1911:263.
Rivularia plicata Carmichael
1882a:70; 1911:263.
Rivularia polyotis (J. Agardh) Born. & Flah.
1901a:136.
Rivularia warreniae Thuret
1882a:69.
Rytiphloea capensis
1919:207.
Rytiphloea sinensis Debaux
1919:206.
Saccorhiza dermatodea (De la Pyl.) J. Agardh
1882a:71; 1894:236; 1900a:48; 1911:274.
NOTE: AUTHOR ALSO REPORTED AS DE LA PYL [1882a, 1894].
Sacheria rigida Sirodot
1888a:153.
Sarcophyllis arctica Kjellman
1927:B5, B15.
Sarcophyllis california J. Agardh
1913:128, 136.
Sarcophyllis pygamaea Setchell
1913:129, 136.
Sargassum bacciferum (Turner) J. Agardh
1900a:48; 1901b:232, 248, 264; 1917:78, 81, 83.
forma angustum Collins
1906a:110; 1917:81.
Sargassum filipendula Agardh
1900a;48; 1902b:13; 1905b:230; 1917:78.
forma subedentatum J. Agardh
1900a:48; 1905b:230.
Sargassum fluitans Boergesen
1917:78, 79, 81.
Sargassum hystrix J. Agardh
1917:78, 81.
var. fluitans Boergesen
1917:78.
Sargassum lendigerum (L.) Agardh
1901b:248, 264; 1917:80, 81, 82.
NOTE: AUTHOR ALSO REPORTED AS (L.) KUETZING [1901b].
Sargassum lingifolium (Turner) J. Agardh
1917:81, 82.

Scytonema ambiguum Kuetzing
1888a:162.
Scytonema arcangelii Born. & Flah.
1901b:241.
Scytonema conchophilum Humphrey in Collins
1901b:241, 262.
Scytonema crispum (Agardh) Bornet
1901b:241; 1905b:237.
Scytonema densum (A. Br.) Bornet
1901b:241.
Scytonema figuratum Agardh
1905b:237.
Scytonema guyanense Montagne
1888a:162.
Scytonema hoffmanni Agardh
1888a:162; 1901b:241; 1905b:237.
Scytonema javanicum (Kuetzing) Bornet
1901b:241.
Scytonema myochrous (Dillwyn) Agardh
1897:96; 1905b:237.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1897].
Scytonema ocellatum (Dillwyn) Thuret
1901b:24; 1904a:230; 1905b:237.
Scytosiphon lomentarius (Lyngbye) J. Agardh
1880a:165; 1882:47; 1888:79; 1888a:155; 1888b:311; 1894:239; 1896:4; 1900a:48; 1900c:163, 165; 1905b:228; 1911:270; 1913:107, 131.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a, 1882, 1888, 1888a, 1888b].
var. complanatus Rosenvinge
1896:4; 1900a:48; 1905b:228.
Seirospora griffithsiana Harvey
1900a:52; 1905b:234; 1906b:123.
Sebdenia heteronema Howe
1916a:171, 172, 173.
Siphonocladus membranaceus (Ag.) Bornet
1901b:247, 264.
Siphonocladus tropicus (Crouan) J. Agardh
1901b:247, 264.
Solieria chordalis (Agardh) J. Agardh
1901b:253, 265.
Soranthera ulvoidea Postels & Ruprecht
1913:107, 152.
Sorocarpus uvaeformis Pringsheim
1896c:459; 1899b:127; 1900a:48.
Spatoglossum schroederi (Mert.) J. Agardh
1901b:249, 264.
Spermatochnus australis
1919:207.
Spermothamnion gorgoneum (Montagne) Bornet
1901b:258, 266.
Spermothamnion turneri (Mert.) Areschoug
1882:47; 1888:82; 1900a:52; 1901c:292.
NOTE: AUTHOR ALSO REPORTED AS ARESCHOUG [1882, 1888].

var. variabile Harvey
1901b:258, 267; 1901c:292.
NOTE: AUTHOR ALSO REPORTED AS J. AGARDH [1901b].
Sphacelaria britannica Sauvageau
1911:270.
Sphacelaria cirrhosa (Roth) Agardh
1880a:164; 1882:47; 1888:80; 1900a:48; 1904:182; 1905b:227, 230; 1908d:157, 158; 1911:269.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a, 1882, 1888].
Sphacelaria fusca C. Agardh
1908d:157, 158; 1913:106, 131.
Sphacelaria racemosa Greville
var. arctica (Harvey) Reinke
1900a:48.
Sphacelaria radicans (Dillwyn) Agardh
1880a:164; 1894:240; 1900a:48; 1905a:172; 1905b:225, 227, 230; 1911:269.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1880a].
Sphaerella lacustris
1901d:409.
Sphaerococcus interruptus Greville
1927:128.
Sphaerozosma excavatum Ralfs
1888a:159.
Sphaerozyga carmichaelii Harvey
1888:76; 1888a:163; 1888b:310.

Spirogyra bellis (Hass.) Cleve
1905b:238.
Spirogyra crassa Kuetzing
1888a:159.
Spirogyra decimina (Mueller) Kuetzing
1901b:242; 1903c:233.
var. triplicata Collins
1903c:233.
Spirogyra insignis Kuetzing
1888a:159.
var. hantzschii Petit
1888a:159.
Spirogryra majuscula Kuetzing
1894:241.
Spirogyra nitida (Dillwyn) Link
1905b:238.
Spirogyra porticalis (Mueller) Cleve
forma minor Collins
1906a:105.
Spirogyra varians (Hass.) Kuetzing
1905b:238.
Spirogyra weberi Kuetzing
1888a:159.

Spirulina meneghiniana Zanardini
1896:1; 1900a:43; 1901c:289, 292; 1908d:162; 1911:260.
Spirulina nordstedtii Gomont
1900a:43.
Spirulina subsalsa Oersted
1894:248; 1896:1; 1896c:458; 1900a:43; 1905a:172; 1908d:162; 1911:260.
Spirulina tennuissima Kuetzing
1888:76; 1888a:164; 1888b:310; 1894:248; 1896:1; 1911:260.
Spirulina versicolor Cohn
1896c:458; 1900a:43.
Spondylosium nitens Lund
1888a:159.
Spongomorpha arcta (Dillwyn) Kuetzing
1911:267; 1913:104.
forma congulutinara Collins
1913:104.
Spongomorpha coalita (Ruprecht) Collins
1913:104.
Spongomorpha hystrix Stromfelt
1902:116, 117; 1911:267; 1913:104.
Spongomorpha lanosa (Roth) Kuetzing
1911:268; 1927:8B.
var. uncialis (F. Dan.) Kjellman
1911:268.
Spongomorpha saxatilis (Ruprecht) Collins
1913:104.
Spongomorpha sonderi Kuetzing
1902:116, 117.
Spongomorpha spinescens Kuetzing
1902:117; 1911:268; 1913:104.
Spyridia aculeata Kuetzing
1901b:259, 267.
Spyridia filamentosa (Wulf.) Harvey
1880a:161; 1882:47; 1884:30; 1888:83; 1888b:313; 1900a:52; 1901b:259, 267; 1905b:235.
NOTE: AUTHOR ALSO REPORTED AS HARVEY [1880a, 1882, 1884, 1888, 1888b].
Staurastrum aristiferum Ralfs
forma trigona
1888a:161.
Staurastrum brasilense Nordstedt
1888a:161.
Staurastrum cerastes Lund
forma tetragona
1888a:161.
Staurastrum clepsydra Nordstedt
1888a:161.

Staurastrum echinatum Brebisson
1888a:161.
Staurastrum grallatorium Nordstedt
var. forcipigerum Lagerheim
1888a:161.
Staurastrum inconspicum Nordstedt
1888a:161.
Staurastrum leptacanthum Nordstedt
forma 6 + 4 radiata
1888a:161.
Staurastrum leptocladum Nordstedt
var. cornutum Wille
1888a:161.
Staurastrum luteolum Lagerheim
1888a:161.
Staurastrum macrocerum Wolle
1888a:161.
Staurastrum striolatum Arch.
forma trigona
1888a:161.
Staurastrum tricorne Meneghini
1888a:161.
Staurastrum trifidum Nordstedt
1888a:161.
var. glabrum Lagerheim
1888a:161.
Steonogramme interrupta
1913:118.
Sterrocolax crassior Schmitz
1913:116, 133.
Sterrocolax decipiens Schmitz
1900a:52; 1901a:134; 1905b:231; 1911:277; 1927:12B.
Stichococcus flaccidus (Kuetzing) Gay
1905b:239.
Stichococcus marinus (Wille) Hazen
1905b:225; 1927:3B, B5.
Stictyosiphon griffthsianus (Le Jolis) Holmes & Batters
1900a:48; 1911:270.
NOTE: AUTHOR ALSO REPORTED AS (LE JOLIS) HOLMES [1911].
Stictyosiphon subsimplex Holden
1900a:48; 1905a:169; 1905b:228.
Stictyosiphon tortilis (Rupr.) Reinke
1927:B9.
Stigeoclonium fasciculare Kuetzing
1905b:239.
Stigeoclonium flagelliferum Kuetzing
1905b:239.
Stigeoclonium lubricum (Dillwyn) Kuetzing
1905b:239.
Stigeoclonium tenue (Agardh) Rabenhorst
1888a:156; 1901b:242; 1905b:239.
NOTE: AUTHOR ALSO REPORTED AS KUETZING [1888a].
Stigonema hormoides (Kuetzing) Bornet & Flahault
1904a:230.

Stigonema mamillosum Agardh
1894:247; 1904a:230; 1905b:237, 243.
Stigonema minutum (Agardh) Hass.
1904a:230; 1905b:237.
Stigonema ocellatum (Dillwyn) Thuret
1904a:230.
Stigonema panniforme (Agardh) Born. & Flah.
1905b:237.
Stilophora rhizoides (Ehr.) J. Agardh
1884:30; 1888:81; 1891:339; 1900a:48; 1905b:229.
NOTE: AUTHOR ALSO REPORTED AS LYNGBYE [1884], AGARDH [1888].
forma contorta Holden
1905b:229.
Stragularia pusilla Stromfelt
1896:4; 1927:10B.
Streblocladia camptoclada (Mont.) Falkenberg
1915:95.
Streblocladia spicata Howe
1915:95.
Streblonema chordariae (Farlow) De Toni
1900a:48.
Streblonema fasciculatum Thuret
1896:5; 1900a:48.
Streblonema oligosporum Stromfelt
1906b:125; 1908c:134; 1911:269.
Streblonema parasiticum (Sauvageau) De Toni
1906b:125; 1911:269.
Streblonema reptans (Crouan) Farlow
1900a:48.
Streblonema volubilis Pringsheim
1896:3.
Strepsithalia curvata Sauvageau
1906a:107.
Strepsithalia investiens Collins
1906a:107.
Striaria attenuata (Agardh) Greville
1900a:48; 1900c:163; 1901b:248, 264; 1913:107.
NOTE: AUTHOR ALSO REPORTED AS GREVILLE [1900a, 1900c].
var. ramosissima (Kuetzing) Hauck
1901b:248, 264.
Stypopodium lobatum (Agardh) Kuetzing
1901b:249, 264.
Symphyocladia gracilis (Martens) Falkenberg
1919:203, 204, 206.
Symploca hydnoides Kuetzing
1900a:43; 1901b:262; 1905b:222.
var. fasiculata (Kuetzing) Gomont
1901b:240, 262.
var. genuina Gomont
1901b:240.
Synechococcus aeruginosus Naegeli
1904a:230.

Tellamia contorta Batters
1911:266.
Tetmemorus brebissonii Ralfs
1888a:161.
Tetmemorus granulatus Ralfs
1888a:161.
Tetranema percursum (Agardh) Areschoug
1894:244; 1896:3; 1903:26.
Tetraspora bullosa (Roth) Agardh
1888a:158; 1905b:239.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1888a].
forma cylindrica (Hilse) Rabenhorst
1905b:239.
Tetraspora gelatinosa Kuetzing
forma uniformis Collins
1906a:105.
Tetraspora lubrica Agardh
1888a:158.
var. lacunosa (Duby) Chauv.
1905b:239.
Tolypothrix aegagropila Kuetzing
1888a:162.
Tolypothrix lanata (Desv.) Wartmann
1905b:237.
Tolypothrix setchellii Collins
1897:96, 97.
Tolypothrix truncicola Thuret
1888a:162.
Trentepohlia aurea (L.) Mart.
1904a:230; 1905b:240.
Trentepohlia daviesii Farlow
1906d:194.
Trentepohlia iolithus (L.) Wittrock
1901d:413, 1905b:240.
Trentepohlia virgatula Harvey
1882:47; 1888:82; 1888b:312; 1906d:193; 1911:276.
NOTE: AUTHOR ALSO REPORTED AS FARLOW [1888, 1906d, 1911]; (HARVEY) FARLOW [1888b].
var. secundata Farlow
1906d:194.
Tuomeya fluviatilis Harvey
1894:234; 1905b:241.
Turbinaria trialata Kuetzing
1901b:231, 232, 248, 264.
Turbinaria vulgare Sloane
1901b:248; 1902b:13.
Turnerella mertensiana (Post. & Rupr.) Schmitz
1913:117, 133.
Udotea conglutinata (Sol.) Lamouroux
1901b:246, 263.

Udotea flabellata Lamouroux
1901b:246, 263; 1902b:12.
Ulothrix collabens (Agardh) Thuret
1899b:127; 1900a:45.
Ulothrix flacca (Dillwyn) Thuret
1888a:157; 1888b:310; 1894:244; 1900a:45; 1901d:412; 1905b:225; 1911:264; 1927:3B, B5.
NOTE: AUTHOR ALSO REPORTED AS THURET [1888a].
Ulothrix implexa Kuetzing
1891:336; 1900a:45; 1905b:225; 1911:264.
Ulothrix isogona (Sm.) Thuret
1883:55; 1888b:310; 1894:244; 1911:268; 1913:105.
NOTE: AUTHOR ALSO REPORTED AS THURET [1888b].
Ulothrix parietina
1901d:412.
Ulothrix subtilis Kuetzing
1888a:157.
Ulothrix variabilis Kuetzing
var. marina Wille
1900:12; 1900a:45; 1905b:225; 1927:B5.
Ulothrix zonata (Web. & Mohr.) Kuetzing
1894:244; 1905b:239.
NOTE: AUTHOR ALSO REPORTED AS KUETZING [1894].
Ulva aureola Agardh
1884:131; 1888:78; 1888b:310; 1903:30.
Ulva californica Wille
1903:8, 9.
Ulva clathrata Agardh
1888:78; 1888a:157; 1888b:310; 1903:29, 30.
NOTE: AUTHOR ALSO REPORTED AS PIKE [1903].
var. erecta Le Jolis
1888b:310; 1903:28.
NOTE: AUTHOR ALSO REPORTED AS COLLINS [1888b].
var. prostrata Martindale
1903:29.
var. ramulosa Farlow
1888b:310; 1903:29.
var. rothiana
forma prostrata Farlow
1903:29.
var. ucinata Martindale
1903:29.
Ulva compressa Anderson
1903:30.
var. racemosa Kjellman
1903:25.
Ulva enteromorpha Le Jolis
1882:46; 1888:77; 1888b:310.
var. compressa Le Jolis
1888:77; 1888a:157; 1888b:310; 1903:25, 30; 1911:264.

var. intestinalis Le Jolis
1888:77; 1888a:157; 1888b:310; 1903:23, 30; 1911:264.
var. lanceolata
1888a:157; 1888b:310; 1903:34; 1911:264.
Ulva fasciata Delile
1901b:238, 242, 262; 1903:8, 10; 1904:182; 1909a:24; 1913:103.
forma caespitosa Setchell
1903:10.
forma lobata Setchell
1903:10.
forma taeniata Setchell
1903:10.
Ulva fulvescens Agardh
1927:6B.
Ulva grevillei (Thuret) Wittrock
1909a:12, 13.
Ulva hopkirkii (Mc Calla) Harvey
1888:78; 1888a:157; 1888b:310; 1903:28, 31; 1911:264.
NOTE: AUTHOR ALSO REPORTED AS HARVEY [1888, 1888a].
Ulva intestinalis Linneaus
1903:31; 1927:6B.
NOTE: AUTHOR ALSO REPORTED AS ANDERSON [1903].
Ulva lactuca Linneaus
1882:46; 1888:77; 1888a:157; 1888b:310; 1894:246; 1900a:45; 1901b: 232; 1903:3, 8, 10, 13, 15, 31; 1908a:116; 1909a:23; 1919:205.
NOTE: AUTHOR ALSO REPORTED AS LE JOLIS [1888], (LINNEAUS) LE JOLIS [1888a, 1888b, 1894, 1900a].
var. lactuca Le Jolis
1894:246; 1903:8, 31.
var. latissima Le Jolis
1888:77; 1888b:310; 1903:9, 31; 1913:103.
NOTE: AUTHOR ALSO REPORTED AS (L.) DC. [1913].
var. mesenteriformis (Roth) Collins
1900a:45; 1903:9; 1905b:224.
var. myriotrema
1901d:410.
var. rigida (Agardh) Le Jolis
1888b:310; 1894:246; 1900a:45; 1901b:242, 262; 1901d:410; 1903:8, 9, 31; 1905b:224; 1911:265; 1913:103.
Ulva latissima Linneaus
1880a:166; 1903:8, 9, 31.
var. linza Hervey
1903:24.
Ulva linza Post. & Rupr.
1903:24.
Ulva marginata Le Jolis
1884a:130, 131; 1888b:310; 1896:2; 1903:25.
Ulva merismopedioides
1903:17.
Ulva mesenteriformis J. Agardh
1903:9.

Ulva pavonia
1901b:252.
Ulva percursa Agardh
1884a:131; 1888b:310; 1903:26.
Ulva prolifera
1927:6B.
Ulva rigida
1903:9.
Urococcus foslieanus Hansgrig
1908d:162; 1911:266.
Urospora penicilliformis (Roth) Areschoug
1900a:45; 1901d:413; 1903:18; 1905b:225.
Urospora wormskjoldii
1913:105.
var. vancouverensis
1913:105.
Valonia aegagropila Agardh
1901b:246, 264; 1902b:12.
Valonia ovalis
1913:105.
Valonia ventricosa J. Agardh
1901b:246; 264.
Valonia verticillata Kuetzing
1901b:247, 264.
Vaucheria aversa Hass.
1905b:240.
Vaucheria dillwynii Greville
1888a:154.
Vaucheria gardneri Collins
1907a:201; 202.
forma tenuis Collins
1907a:201.
Vaucheria geminata (Vaucher) DC.
1905b:240; 1907a:201, 202.
var. racemosa (Vaucher) Walz.
1888a:154; 1905b:240.
NOTE: AUTHOR ALSO REPORTED AS WALZ [1888a].
Vaucheria litorea Nordstedt
1888a:154; 1888b:312; 1894:241; 1900a:45; 1905b:226.
NOTE: AUTHOR ALSO REPORTED AS AGARDH [1905b].
Vaucheria longipes Collins
1907:201, 202.
Vaucheria piloboloides Thuret
1880a:166; 1900:13; 1900a:45; 1905b:226.
var. compacta Collins
1900:13; 1900a:45.
Vaucheria pusilla
1901c:290.
Vaucheria sessilis (Vaucher) DC.
1901d:415; 1905b:241.

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ON PROCESSING FIELD AND CULTURE SAMPLES OF DESMIDS (DESMIDIALES, CHLOROPHYTA) FOR SCANNING ELECTRON MICROSCOPY

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A procedure is outlined for preparing both field collected and laboratory grown desmid populations for scanning electron microscopy which avoids the use of the potentially hazardous chemicals glutaraldehyde and osmium tetroxide and reduces preparation time substantially. FAA is utilized both in fixation and mucilage removal, and living material can be prepared for critical point drying in as little as 90 min. Limitations of this procedure are outlined briefly and the use of SEM material in systematic studies is commented upon.

Recognition of the potential of scanning electron microscopy (SEM) as a tool in studies of morphogenesis, cell wall ornamentation, and systematics of desmids (Desmidiales, Chlorophyta) has led to the development of several techniques (Lyon, 1969; Pickett–Heaps, 1973, 1974) for the preparation of desmids for SEM examination. These procedures utilize specimens grown in culture and involve apparent air drying from water or alcohol (Lyon, 1969, see Pickett–Heaps, 1973, p. 114) or critical point drying (Pickett–Heaps, 1973, 1974) after pretreatment in "Glusulase" (a polysaccharidase) for mucilage removal, fixation in glutaraldehyde, post-fixation in osmium tetroxide, and dehydration via an acetone series.

Although these techniques have yielded some excellent scanning electron micrographs (see Pickett–Heaps, 1975), certain limitations apparently exist. Thus, for example, the procedure seems applicable only to specimens growing in unialgal culture. In addition, handling prior to critical point drying involves the use of the potentially hazardous chemicals glutaraldehyde and osmium tetroxide and requires up to 6·5 h. Finally, removal of the copious quantities of mucilage from desmid cell walls commonly appears difficult (Pickett–Heaps, 1973, p. 116; 1975, p. 408–409, 414) and leads to inconsistent results and many unusable preparations.

In conjunction with studies of polymorphic behaviour in field and experimental populations of various desmids, we have developed an SEM preparation procedure which can be utilized directly on field populations as well as on experimental cultures, which avoids the use of glutaraldehyde and osmium tetroxide and which reduces preparation time substantially. In addition, the problem of mucilage removal appears to be minimal, but it has not been solved entirely. This paper outlines the procedure and evaluates its potential in quantitative and qualitative morphological and systematic investigations of desmids.

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MATERIALS AND METHODS

COLLECTION AND MAINTENANCE

Field populations of desmid plankton were gathered by passing 10–20 l of surface water through a No. 25 silk mesh plankton net and transferring the concentrate to a 50 ml storage vial prior to fixation (see below). Desmids in the epiphyton were obtained by hand squeezing quantities of the macrophyte host and collecting the run off in a jar or by retaining the macrophyte sample and subsequently removing the desmids by agitation (Gough & Woelkerling, 1976). Clonal cultures of taxa isolated from acid waters were grown in liquid Waris medium (Waris, 1953) at a pH of 6·0 while taxa isolated from alkaline waters were grown in liquid Bristol's medium (Starr, 1964) at a pH of 8·0; 1 $\mu g\,l^{-1}$ of vitamin B_{12} was added to all containers. Material was maintained at 20°C on a 16/8 h light/dark cycle. References used for desmid identification include Iréneé-Marie (1939), Krieger (1935, 1937, 1939), and Smith (1924).

FIXATION AND MUCILAGE REMOVAL

All fixation was effected with the addition of sufficient FAA (7 : 2 : 1 : 1 :: water : formalin : glacial acetic acid : 95% ethanol) to double the volume of liquid in which the desmids were suspended. Field material was fixed at the time of collection and stored in FAA until studied. Material preserved in FAA for over 15 months yielded good results, and it appears that samples destined for SEM work can be kept in FAA indefinitely. Cells grown in culture were fixed in FAA for a minimum of 30 min but in most cases for 2–48 h.

While FAA itself apparently facilitates the removal of most excess mucilage from the cell walls by acid hydrolysis (see Gough & Woelkerling, 1976), cleaner cells sometimes could be obtained by sonication for 5–45 s in 1·0 N HCl. Caution must be exercised, however, since the use of formaldehyde and HCl may lead to formation of vapours of Bis-chloromethylether, a potentially powerful carcinogen.

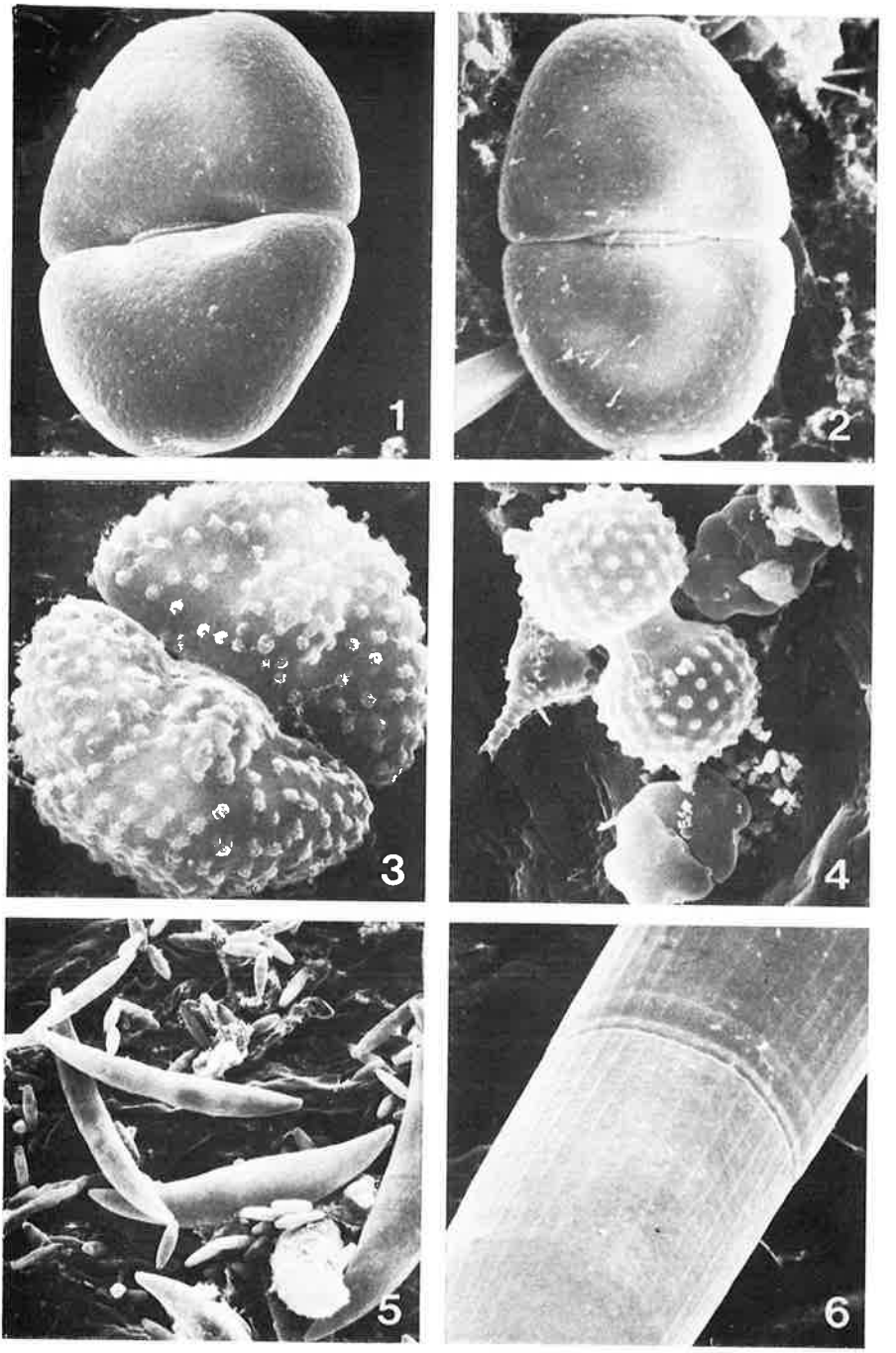
FURTHER HANDLING

After fixation, the cells were collected by suction-filtration from FAA onto a membrane filter fitted to a membrane filter flask assembly. Filter selection was based on criteria outlined by Pickett-Heaps (1973). Pore sizes of 10 μm and 0·45 μm both worked satisfactorily, and the use of gridded filters facilitated recognition of top and bottom sides during later handling. Once on the filters, specimens were partially dehydrated with three successive aliquots of 95% ethanol. Then filters were transferred quickly to petri dishes of 100% ethanol, cut into 6 mm squares with a scalpel, and transferred to vials of 100% ethanol for temporary storage. It is vitally important that filters are not allowed to dry out during the above sequence of steps, or severe collapse and distortion of cells will result.

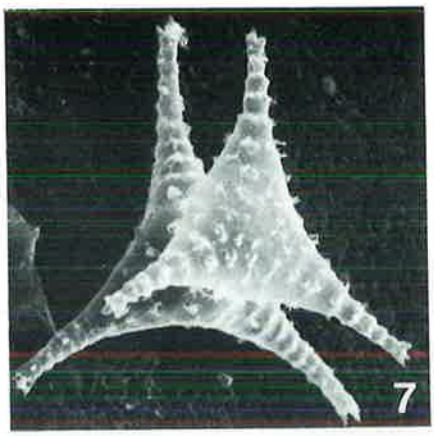
Final processing involved placing the 6 mm squares in plastic baskets, critical point drying (see Pickett-Heaps, 1973 for details) from 100% ethanol in a Denton CPD apparatus, affixing the dried squares to aluminium specimen stubs with double-stick tape, grounding the squares with an edging of silver paint, and coating the specimens with gold-palladium in a Denton Vacuum Evaporator. Specimens were examined at 20 μV using a JOEL JSM-U3 scanning electron microscope, and Polaroid no. 55 P/N film was used for photography.

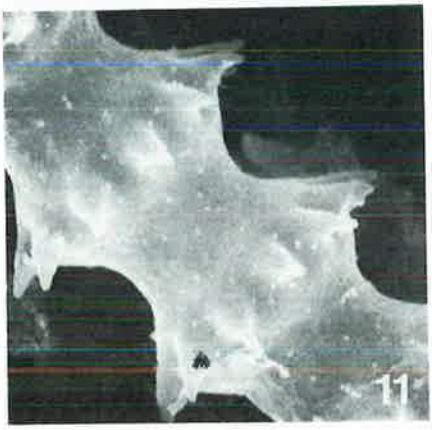
RESULTS AND DISCUSSION

The above procedure has been applied successfully to a variety of desmid genera obtained directly from field samples as well as from clonal cultures, and morphological features of systematic importance are readily visible. In *Cosmarium* (Figs 1–4), for example, punctate and verrucate wall ornamentation patterns are both readily discernable, and comparable results can be obtained for the same species whether cells come from experimental (Fig. 1) or field (Fig. 2) populations. Similarly, cells from cultures of *Closterium* (Figs 5, 6) can be collected on filters in sufficient numbers to enable measurement of cell size and curvature, and data on bands, ribs and other morphological characters of systematic significance can be gathered as well. Cells of radiate taxa (Figs 7–9),



FIGS 1–6. Fig. 1. *Cosmarium granatum* Brebisson in Ralfs 1848: 96. ×1600. Fig. 2. *Cosmarium granatum* Brebisson in Ralfs 1848: 96. ×1600. Fig. 3. *Cosmarium punctulatum* Brebisson 1856: 129. ×2200. Fig. 4. *Cosmarium portianum* Archer 1860: 235. ×925. Fig. 5. *Closterium* sp. A mixed population of several species. ×145. Fig. 6. *Closterium regulare* Brebisson 1856: 148. ×1600.





FIGS 7–12. Fig. 7. *Staurastrum manfeldtii* Delponte 1877: 160. ×660. Fig. 8. *Staurastrum leptocladum* Nordstedt 1869 : 228. ×780. Fig. 9. *Micrasterias radiata* Hassall in West and West 1905: 113. ×475. Fig. 10. *Arthrodesmus bulnheimii* Raciborski 1889: 95. ×200. Fig. 11. *Triploceras gracile* Bailey 1851: 38. Portion of a semicell showing whorls of spines. ×1750. Fig. 12. *Spondylosium planum* (Wolle) W. and G. S. West 1913: 430. ×1400.

spined taxa (Figs 10, 11), and filamentous taxa (Fig. 12) commonly emerge from the processing without collapse, distortion, or excessive mucilage.

In addition to its applicability to both laboratory grown and field populations, this procedure eliminates (assuming HCl is not used) the need for potentially hazardous chemicals such as glutaraldehyde and osmium tetroxide. Living material can be prepared for critical point drying in as little as 90 min, or it can be preserved and stored indefinitely for later use.

The problem of mucilage removal has not been solved entirely. The need for a 3 h polysaccharidase treatment and washing prior to fixation (Pickett–Heaps, 1973) has been eliminated because of the apparent mucilage removal capabilities of FAA (see Gough & Woelkerling, 1976). Total mucilage removal, however, has not been possible with consistency, and in some preparations, no more than approximately 25% of the cells emerged in an acceptably clean condition (i.e., with all features of wall ornamentation clearly evident). A number of other methods of mucilage removal have been attempted (e.g. use of ammonium oxalate, EDTA, dichromate cleaners, sodium hydroxide, detergent) in hopes of obtaining more consistent results, but in all cases the cells were either completely destroyed or the outcome was very erratic as compared with the FAA treatment.

A second difficulty was sometimes encountered in the preparation of large-celled species of *Closterium* where many of the cells would collapse during preparation. Such collapse was minimized, however, if sonication times of only 5 s were used and critical point drying was very carefully regulated.

Excessive detritis or plant fragments (e.g., *Sphagnum* leaves) in field samples occasionally caused membrane filter pores to clog quickly, thereby reducing the ability of desmid cells to adhere to the filter during dehydration and critical point drying. Such debris also commonly obscured cell wall ornamentation (e.g. note debris on cells of *Euastrum* in background of Fig. 4). These problems, however, were usually overcome by filtering potentially troublesome field samples through cheesecloth prior to membrane filtration.

The use of SEM preparations for studies of cell wall morphogenesis and for desmid identification are readily apparent, especially in attempting species determinations in genera such as *Cosmarium* and *Staurastrum* where large numbers of taxa have been separated on differences in wall ornamentation. Their application in gathering quantitative data on intraspecific polymorphism in cell wall morphology requires further study. Present attempts of the authors (unpublished data) to gather quantitative data have been hampered by the expense involved in SEM photography and the time required to obtain the series of photos on populations needed for proper statistical assessment. Especially troublesome is the absolute necessity (for mathematical analyses) of obtaining both end views and face views of the same cell of species of *Cosmarium* and *Staurastrum*, and this difficulty has not been resolved as yet. Similarly we do not know whether cells adhere to membrane filters in random fashion or whether slight differences in morphology result in sufficiently great selectivity to cause subsequent bias in cells used for data collection.

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WISCONSIN DESMIDS. II. AUFWUCHS AND PLANKTON COMMUNITIES OF SELECTED SOFT WATER LAKES, HARD WATER LAKES AND CALCAREOUS SPRING PONDS

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Abstract

This report summarizes the results of summer studies of five soft water lakes, five hard water lakes and six calcareous spring ponds in Wisconsin with respect to the composition of the plankton and aufwuchs communities and the relative role of desmids in those communities. The results are compared with similar data obtained from selected acid bog lakes, alkaline bog lakes and closed bogs. Soft water lakes harbored a greater aufwuchs and plankton desmid diversity than hard water lakes or spring ponds; however, diversity in acid bog lakes was substantially greater than in any other lake type. *Utricularia* contained the greatest desmid diversity and population density in every lake where it occurred. *Staurastrum* was the most prevalent genus in the plankton and it was the only one recorded from hard water lakes and calcareous spring ponds. Desmid aufwuchs population densities were roughly comparable in hard water lakes, soft water lakes and acid bogs and the contribution of desmids to the total aufwuchs population was similar for the latter two lake types. However, the plankton of acid bog lakes generally harbored substantially greater desmid populations and these populations contributed much more to the total population than in any other lake type. Aufwuchs data are presented for several hosts and comparisons of population densities are given among hosts within a given lake and between the same host in different lakes of a given type. Data for other algal groups are also included.

Introduction

Our knowledge of desmids (Desmidiales, Chlorophyta) in hard water lakes, soft water lakes and calcareous spring ponds appears to be limited and almost entirely qualitative in nature. Floristic accounts (e.g., Irénée-Marie 1939, Krieger 1933-1939, Smith 1924) indicate that desmid diversity is lower in hard waters than in soft waters. Smith (1920, p. 8), for example, reports that with one or two exceptions, desmids are not found in the hard waters of southeastern Wisconsin, and Sloey & Blum (1972) found only three desmid species in Lake Winnebago, a hard water lake in east central Wisconsin.

Hard waters are often eutrophic and soft waters are generally oligotrophic (Moss 1972), and differences in desmid diversity have been used in phytoplankton quotients (e.g., Brook 1965, Nygaard 1949, Thunmark 1945) designed to assess the degree of eutrophy. The use of such quotients, however, is fraught with difficulties because soft water environments are not always oligotrophic (nor are hard waters always eutrophic) and because euplanktonic desmids are often difficult to distinguish from tychoplanktonic forms (Brook 1965, Rawson 1956).

West and West (1909) also concluded that desmids are poorly represented qualitatively in hard waters and speculated that the amount of calcium carbonate present in the water may exert a controlling influence on desmid development. Pearsall (1932) regarded waters with low Ca^{++} levels (and therefore with low hardness values) and with a low NO_3^- to PO_4 ratio as more conducive to desmid development, and Wade (1957) classified most desmid species as calciphobic. Pringsheim (1926), however, reported that a few *Micrasterias* spp. seemed to require moderately high calcium concentrations for growth, and West and Fritsch (1927) recorded a few calciphilic *Cosmarium* spp. In addition, several taxa have been reported to be eurytopic (i.e., tolerant of a wide range of chemical conditions; see Fjerdingstad 1965, Hutchinson 1967, Palmer 1969).

Few published accounts exist on the vegetation of calcareous springs, and our knowledge appears to be largely confined to travertine-depositing forms of the out-

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flow streams (e.g., Fritsch 1949, Hynes 1972). Studies of the plankton and aufwuchs communities (e.g., Davis & Gworek 1972, Schmitz 1961, Teal 1957, Whitford 1956) are mostly qualitative in nature and restricted to determinations of dominant species. These investigations invariably emphasize the relative abundance of diatoms, and Whitford (1960) has speculated that several diatom species inhabiting colder springs are incapable of occurring at temperatures above 15°C.

The ponds produced by calcareous springs are characterized by an abundance of dissolved calcium bicarbonate and by high levels of free carbon dioxide (Hynes 1972, p. 51; Ruttner 1963, p. 244). These authors state, furthermore, that the major portion of the gaseous CO_2 is held

Table 1. Study Lakes: Geographic and Biological Host Data.

A. Soft Water Lakes

Lake	County	T	R	S	Reference	Hectares	Aufwuchs Hosts
Ike	Sawyer	42N	5W	14	Sather and Threinin 1969	7.90	Utricularia, Potamogeton
Pine	Chippewa-Rusk	32-33N	9W	23 34-35	Sather and Threinin 1963	106.11	Utricularia, Hygroamblystegium, Potamogeton, Sphagnum
Zielke	Ashland	43N	2W	28	Sather and Threinin 1966	8.59	Utricularia, Nitella
Lake 15-12	Burnett	40N	14W	15	Blackman, Sather, and Threinin 1966	2.75	Utricularia, Equisetum
Lake 20-12A	Barron	36N	10W	20	Sather and Threinin 1964	3.81	Utricularia, Riccia

B. Hard Water Lakes

Lake	County	T	R	S	Reference	Hectares	Aufwuchs hosts
Ripley	Jefferson	6N	13E	7	Poff, Piening and Threinin (1968)	175.37	Nuphar Potamogeton crispus Utricularia Myriophyllum
Fish	Dane	9N	7E	3	Poff and Threinin (1962)	102.06	Myriophyllum Ceratophyllum Utricularia Nuphar
Beulah	Walworth	4N	18E		Poff and Threinin (1961)	338.99	Anacharis Utricularia Myriophyllum Potamogeton pectinatus

Table 1. (continued).

Lake	County	T R S	Reference	Hectares	Aufwuchs hosts
Fowler	Waukesha	8N 17E 33	Poff and Threinin (1963)	31.59	Chara Myriophyllum Potamogeton pectinatus Anacharis
Bruner's Pond	Dane	6N 7E 11	---	<1	Ceratophyllum Myriophyllum Potamogeton pectinatus

C. Calcareous Spring Ponds

Spring	County	T R S	Area (Hectares)	Aufwuchs hosts
A	Waukesha	5N 17E 3	0.01	Anacharis sp. Hippuris vulgaris L.
B	Waukesha	6N 18E 21	0.01	Anacharis sp. Chara sp.
C	Waukesha	6N 18E 21	0.01	Chara sp. Ranunculus longirostris Godron
D	Waukesha	6N 18E 21	0.005	Chara sp. Ranunculus longirostris Godron
E	Waukesha	6N 18E 22	0.002	Chara sp.
F	Waukesha	6N 18E 22	0.002	Chara sp.

by supersaturation and is lost readily to the atmosphere in the outflow stream with the resultant precipitation of calcium carbonate. Although calcareous spring ponds resemble hard water lakes chemically in having alkaline pH readings and high levels of alkalinity and total hardness, they differ significantly from hard water lakes in having an abundance of free CO_2 at all times rather than a paucity or absence of it over extended parts of the day.

Because of the combination of high calcium concentrations and high free CO_2 levels, spring pond environments present a potential opportunity to determine to what extent, if any, calcium levels (e.g., Hutchinson & Pickford 1932, Strøm 1921, Wade 1957) or CO_2 levels (Moss 1972, 1973a-c) exert a controlling influence over the diversity of the desmid flora in natural situations.

This report summarizes the results of summer studies of five soft water lakes, five hard water lakes and six calcareous spring ponds with respect to the composition of the plankton and aufwuchs communities and the relative role of desmids in those communities. The results are compared with similar data obtained from acid bog lakes, alkaline bog lakes and closed bogs (Woelkerling 1975).

Materials and methods

The sites selected for each lake type (Table 1) were chosen on the basis of similar water chemistry (particularly pH, calcium concentration, and total alkalinity – see Table 2). In addition, all soft water lakes contained plants of *Utricularia,* all hard water lakes contained plants of *Myriophyllum,* and the calcareous springs all had at least one macrophyte in abundance within a relatively static pool. In many instances, more than one type of macrophyte was collected at each site for analysis of the aufwuchs. Procedures used in sample collection and preservation and in analysis of the chemical and biological data have been outlined previously (Woelkerling 1975). Samples

Table 2. Summary of water chemistry conditions in the various lake types. All values expressed as mg./l. except for conductivity (μmhos/cm.) and pH (units).

	Spring Ponds		Hard Water Lakes		Soft Water Lakes	
Parameter	Range	Mean	Range	Mean	Range	Mean
Conductivity	520-619	583.8	228-490	375	16-56	31.8
pH	7.3-7.5	7.37	8.30-8.80	8.58	6.5-7.0	6.78
CO_2	24-32	29.3			3-6	4.4
O_2	4.0-9.0	7.7			7-13	10.8
PO_4-P	.014-.030	.0197	.014-.051	.0236	<.005-.072	.0404
Total P	.03-.06	.0417	.01-.08	.042	.02-.22	.092
NO_2-N	.002-.021	.0095	.000-.032	.007	.004-.013	.0094
NO_3-N	2.35-2.94	2.615	<.04-.39	.124	.07-.28	1.36
NH_3-N	.05-.23	.147	<.03-.12		<.03-.15	.072
Org. N	.34-.66	.567	.64-1.48	.962	.44-1.31	.97
Total N	3.07-3.63	3.34	.76-1.53	1.124	.54-1.58	1.186
Total Alkalinity	247-290	271.3	110-324	196.6	0(?)1-19	8.5
Ca^{++}	50-74	66.2	35-63	47.8	2.7-9.1	5.0
Mg^{++}	25-43	36.2				
K^{+}						
Na^{+}						
Cl^{-}	21-32	26.5	13-27	17.8	2-18	6.6
$SO_4^{=}$	27-32	29.5	3-30	18.0	6-14	7.8

from the spring ponds were collected in areas distant from the artesian inlets and in water at least 0.5 m. deep.

Results and discussion

Generic Diversity

Fourteen genera of desmids occurred in the aufwuchs of the soft water lakes whereas only three were found in the aufwuchs of the hard water lakes and none occurred in the spring pond aufwuchs (Table 3). These results support the hypotheses of Pearsall (1932), West and West (1909) and others regarding the presence of a greater desmid diversity in soft waters than in hard waters. *Utricularia* occurred in three of the five hard water lakes and contained the maximum relative desmid diversity in each case (Table 3). It also was present in all five soft water lakes and harbored at least five desmid genera in four of those lakes.

Table 3. The presence (+) or absence (–) of desmid genera in the aufwuchs associated with different hosts at the study sites.

A. Soft Water Lakes

Taxon	Ike Lake		Pine Lake				Zielke Lake		Lake 15-12		Lake 20-12A	
	Potamogeton	Utricularia	Hygroamblystegium	Potamogeton	Sphagnum	Utricularia	Nitella	Utricularia	Equisetum	Utricularia	Riccia	Utricularia
Closterium	–	+	+	–	–	+	+	+	–	+	–	+
Cosmarium	+	+	+	+	+	+	+	–	+	+	+	+
Desmidium	–	–	–	–	+	+	–	–	–	+	–	–
Euastrum	–	+	+	+	+	+	+	–	+	+	–	+
Hyalotheca	–	–	+	+	–	+	–	–	+	+	–	–
Micrasterias	–	–	+	–	–	–	–	–	–	–	–	+
Netrium	–	–	–	+	–	–	–	–	+	–	–	–
Pleurotaenium	+	+	+	–	–	+	–	–	–	+	–	–
Roya	–	+	–	–	–	–	–	–	+	+	–	–
Sphaerozosma	–	–	+	+	–	+	–	–	–	+	+	–
Spondylosium	–	–	–	–	–	–	–	–	–	+	–	–
Staurastrum	–	–	+	+	+	+	–	–	+	+	+	+
Triploceras	–	–	+	–	–	–	–	–	–	+	–	–
Xanthidium	–	–	–	–	–	+	–	–	+	–	–	–

B. Hard Water Lakes

Taxon	L. Ripley				Fish L.				L. Beulah				Fowler L.				Bruner's Pond		
	Nuphar	Potamogeton crispus	Utricularia	Myriophyllum	Ceratophyllum	Myriophyllum	Nuphar	Utricularia	Anacharis	Myriophyllum	Potamogeton pectinatus	Utricularia	Anacharis	Chara	Myriophyllum	Potamogeton pectinatus	Ceratophyllum	Myriophyllum	Potamogeton pectinatus
Cosmarium	–	+	+	+	–	+	+	+	+	+	+	+	–	+	+	+	–	+	+
Closterium	–	–	+	–	–	–	–	–	–	–	–	–	–	+	+	–	–	+	–
Staurastrum	–	–	+	+	–	+	–	+	–	–	–	–	–	+	–	–	–	–	–

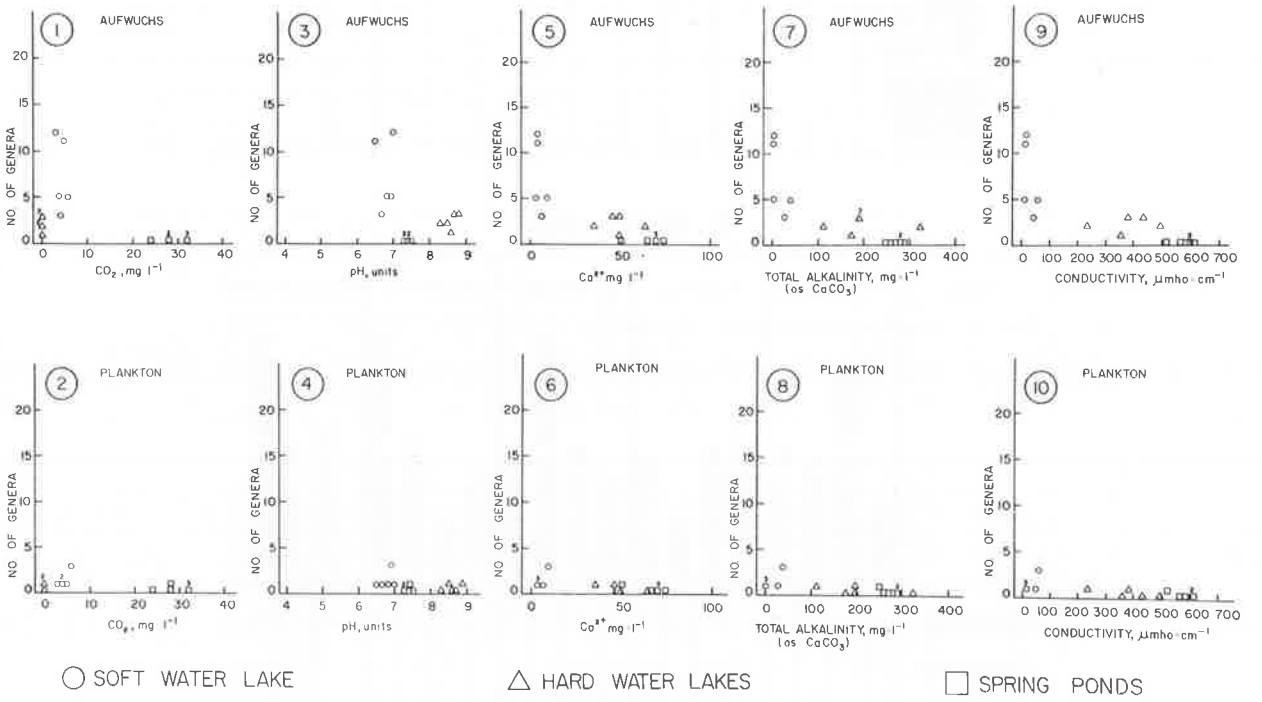
Cosmarium, the most prevalent genus in the aufwuchs, occurred in 15 out of 19 hard water lake macrophyte samples and 11 out of 12 soft water lake macrophyte samples. The other two genera present in the hard water lake aufwuchs, *Closterium* and *Staurastrum,* were detected in four and five of the 19 samples, respectively, and they appeared in seven and eight of the 10 soft water lake samples, respectively (Table 3). The number of genera present in the aufwuchs of a given lake varied from one to 10 in the soft water lakes and from one to three in the hard water lakes. No correlations, however, between water chemistry and generic diversity within a given lake type were evident (see Figs. 1-18, odd numbers).

The plankton samples of the lakes contained only four desmid genera. Pine Lake, which harbored 12 desmid genera in the aufwuchs, contained only plants of *Staurastrum* in the plankton. *Staurastrum* likewise was the only plankton desmid found in Lake 15-12 (11 genera of aufwuchs desmids) and in Zielke Lake (three genera of aufwuchs desmids), while *Desmidium* was the sole planktonic desmid in Lake 20-12a (five genera of aufwuchs desmids). Ike Lake plankton contained *Closterium, Cosmarium,* and *Staurastrum* along with five genera in the aufwuchs. The greater number of taxa in the aufwuchs appears to support the contentions of Griffiths (1928), Hutchinson (1967), Krieger (1933), and others, that the benthic environment contains a more diverse desmid flora.

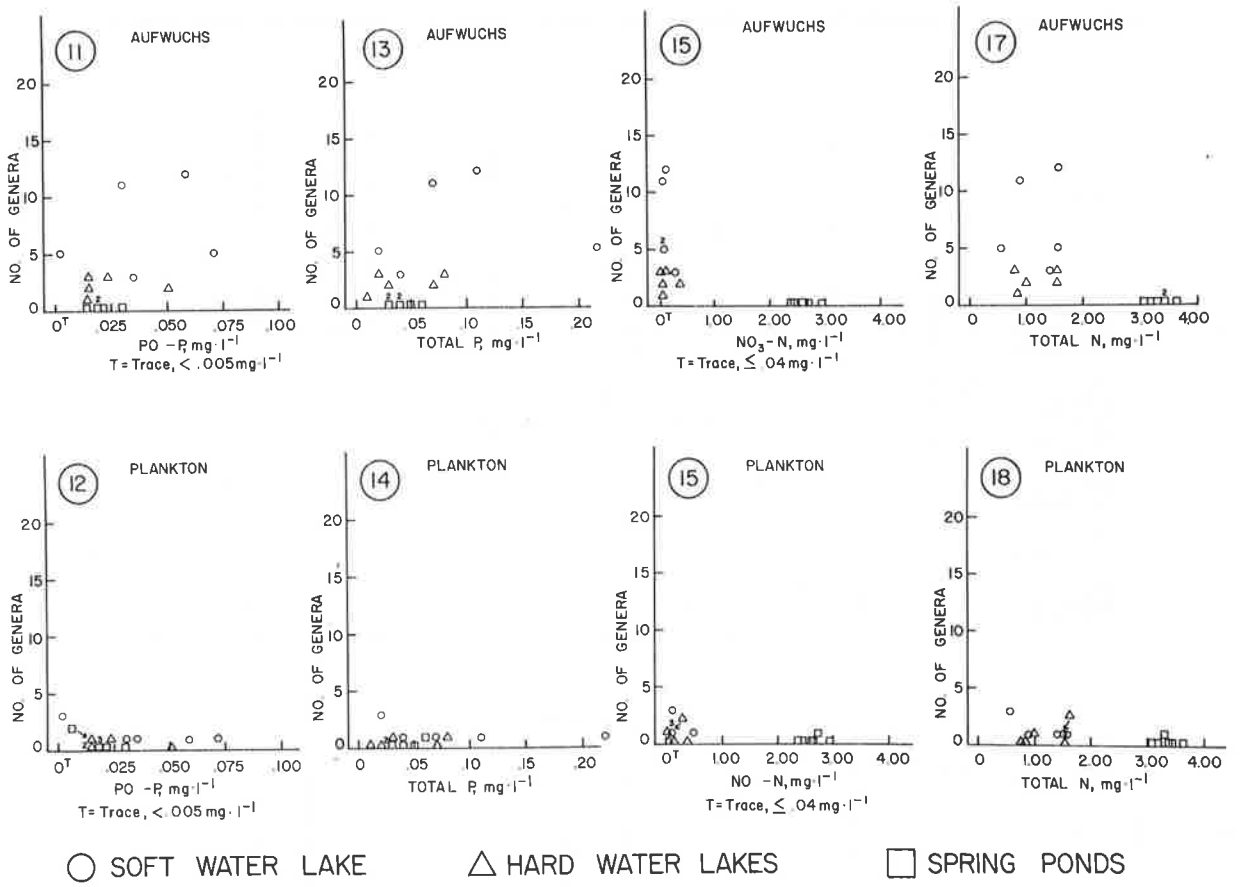
Staurastrum was the only desmid genus found in the plankton of the hard water lakes and the calcareous spring ponds. It occurred in only two of the five hard water lakes and in only one of the six spring ponds. As with the aufwuchs, desmid plankton generic diversity was found to be greater in the soft water lakes than in the hard water environments. However, the presence or absence of *Staurastrum* in the plankton of the hard water lakes or spring ponds does not appear to be correlated obviously with parameters of the chemical environment (Figs. 1-18, even numbers).

Desmid Population Densities

Population densities of desmids in the aufwuchs of soft water lakes ranged from 1.92 x 10^2 organisms/mg. host dry weight on *Potamogeton* in Ike Lake to 1.04 x 10^4 organisms/mg. host dry weight on *Utricularia* in Pine Lake (Table 4). In seven of the 12 samples, these densities



Figs. 1-10. Relationships between the number of desmid genera present in the aufwuchs and the plankton and various chemical parameters at the study sites.



Figs. 11-18. Relationships between the number of desmid genera present in the aufwuchs and the plankton and various chemical parameters at the study sites.

accounted for less than 10% of the total aufwuchs population, and in no case did the desmids account for more than 30.9% of the total population (Fig. 19).

Population densities of desmids in the aufwuchs of hard water lakes ranged from 0 organisms/mg. host dry weight on three different macrophytes in four different lakes to 1.10 x 10^4 organisms/mg. host dry weight on *Utricularia* in Lake Ripley (Table 4). Desmids comprised less than 1% of the total aufwuchs in the majority of instances (Figs. 20-21), and the maximum of 11.3% found on *Utricularia* in Lake Ripley appeared to be exceptionally high.

The range in population densities per mg. host dry weight of desmids in the aufwuchs appeared to be somewhat greater (0 to 1.10 x 10^4) in the hard water lakes than in the soft water lakes (1.92 x 10^2 to 1.04 x 10^4), but a majority of the hosts in hard water lakes harbored densities under 10^2 desmids/mg host dry weight while none of the hosts in the soft water lakes had such low densities.

The maximum population densities of desmids in the aufwuchs were nearly the same in both the hard water and soft water lakes (1.10 x 10^4 vs. 1.04 x 10^4 organisms/mg. host dry weight) and in both instances these maxima occurred on *Utricularia*. While 67% of the aufwuchs samples from the soft water lakes contained desmid populations which contributed over 5% of the total population, only 11% of the aufwuchs samples from the hard water lakes did so. Moreover, the maximum percentage composition of desmids in the aufwuchs of the soft water lakes (30.9% on *Utricularia*) was nearly three times the maximum in hard water lakes (11.3%, also on *Utricularia*). Finally, desmids occurred in all aufwuchs samples from the soft water lakes but were absent from 22% of the aufwuchs samples from hard water lakes. Desmids were not found in the spring pond aufwuchs samples analyzed.

Table 4. Summary of Aufwuchs Population Density Data. Figures expressed as no. organisms per mg dry weight of host tissue.

A. Soft Water Lakes

Lake	Macrophyte Host	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Euglenophyceae	Dinophyceae	Total Population
Ike	Potamogeton	1.92×10^2	-	3.57×10^3	1.64×10^4	1.17×10^3	5.90×10^1	-	2.14×10^4
	Utricularia	3.76×10^3	6.46×10^3	1.01×10^4	1.99×10^4	8.34×10^3	-	-	4.86×10^4
Pine	Hygroamblystegium	2.56×10^3	2.48×10^3	1.75×10^3	6.22×10^3	5.72×10^3	-	-	1.87×10^4
	Potamogeton	5.45×10^3	3.26×10^3	2.60×10^3	3.75×10^3	2.77×10^3	-	3.32×10^2	1.82×10^4
	Sphagnum	1.47×10^3	4.38×10^3	1.01×10^3	7.20×10^3	3.19×10^3	-	-	1.73×10^4
	Utricularia	1.04×10^4	1.10×10^4	2.64×10^3	1.05×10^4	4.34×10^3	-	6.87×10^2	3.96×10^4
Zielke	Nitella	3.99×10^2	1.17×10^3	2.07×10^3	1.76×10^4	2.54×10^3	-	9.40×10^1	2.39×10^4
	Utricularia	7.47×10^2	1.94×10^3	3.74×10^3	3.56×10^4	5.24×10^3	1.49×10^2	-	4.74×10^4
Lake 15-12	Equisetum	2.09×10^3	1.26×10^3	2.53×10^3	2.47×10^3	2.09×10^3	-	-	1.04×10^4
	Utricularia	7.11×10^3	7.87×10^3	6.77×10^3	1.45×10^4	1.15×10^4	-	-	4.78×10^4
Lake 20-12A	Riccia	6.14×10^2	3.00×10^3	4.37×10^3	1.23×10^4	7.08×10^3	-	-	2.74×10^4
	Utricularia	4.13×10^3	7.86×10^3	4.85×10^3	2.10×10^4	1.09×10^4	1.80×10^2	3.59×10^2	4.93×10^4

B. Hard Water Lakes

Lake	Macrophyte host	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Euglenophyceae	Other groups	Total population
Ripley	Myriophyllum	$2.73X10^2$	$5.15X10^3$	$1.40X10^3$	$2.13X10^4$	$5.75X10^3$	---	$5.00X10^1$	$3.39X10^4$
	Nuphar	---	$3.75X10^2$	$5.47X10^2$	$1.66X10^3$	$7.91X10^2$	---	---	$3.37X10^3$
	Potamogeton crispus	$7.1X10^1$	$3.75X10^2$	$3.75X10^2$	$6.54X10^3$	$3.75X10^2$	---	---	$7.74X10^3$
	Utricularia	$1.10X10^4$	$1.38X10^4$	$8.29X10^3$	$5.73X10^4$	$6.59X10^3$	---	$1.15X10^2$	$9.71X10^4$
Fish	Ceratophyllum	---	---	$7.36X10^2$	$1.86X10^3$	$2.05X10^3$	---	---	$4.65X10^3$
	Myriophyllum	$1.96X10^3$	$1.32X10^3$	$2.8X10^1$	$1.19X10^2$	$1.85X10^4$	---	$1.47X10^2$	$2.21X10^4$
	Nuphar	$3.2X10^1$	---	$1.6X10^1$	$7.58X10^2$	$4.19X10^2$	---	---	$1.23X10^3$
	Utricularia	$5.94X10^3$	$7.39X10^2$	$1.88X10^4$	$1.30X10^5$	$5.94X10^3$	---	$4.33X10^2$	$1.62X10^5$

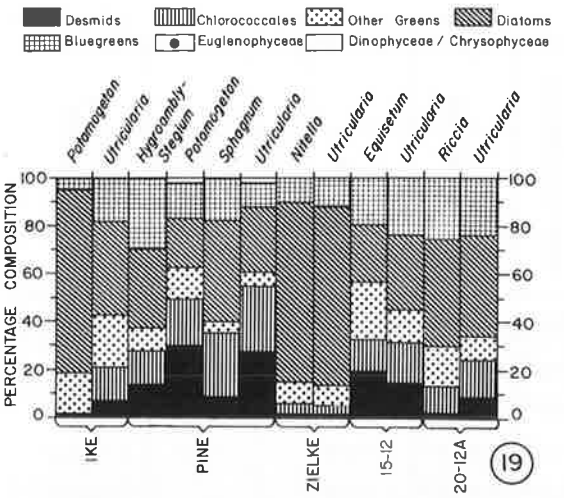
Population densities of desmids in the plankton of soft water lakes ranged from 2.04×10^{-1} to 1.48×10^0 organisms/ml. (Table 5), and in no case did these densities account for more than 6.4% of the total population (Fig. 23). At all localities, the percentage of desmids in the total plankton population was lower than the percentage of

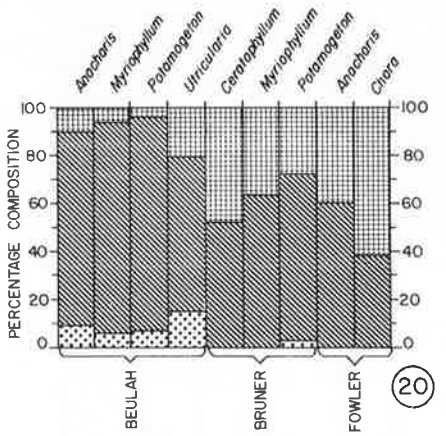
Table 4. (continued).

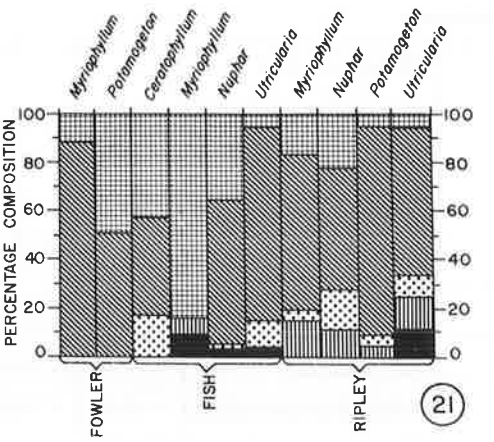
Lake	Macrophyte host	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Euglenophyceae	Other groups	Total population
Beulah	Anacharis	$2.2X10^1$	$7.1X10^1$	$8.88X10^2$	$8.70X10^3$	$1.23X10^3$	---	$4.4X10^1$	$1.10X10^4$
	Myriophyllum	$3.7X10^1$	$1.07X10^2$	$1.30X10^3$	$2.18X10^4$	$1.76X10^3$	---	$1.1X10^1$	$2.50X10^4$
	Potamogeton pectinatus	$1.6X10^1$	$5.2X10^1$	$9.33X10^2$	$1.25X10^4$	$6.84X10^2$	---	$3.2X10^1$	$1.42X10^4$
	Utricularia	$7.7X10^1$	$1.01X10^2$	$2.00X10^3$	$8.47X10^3$	$2.77X10^3$	---	$7.7X10^1$	$1.35X10^4$
Fowler	Anacharis	---	$3.75X10^2$	$7.96X10^2$	$1.47X10^5$	$9.51X10^4$	---	---	$2.43X10^5$
	Chara	$3.69X10^2$	$1.18X10^2$	$1.92X10^2$	$7.38X10^4$	$1.16X10^5$	---	$5.9X10^1$	$1.91X10^5$
	Myriophyllum	$4.61X10^2$	$1.27X10^2$	$2.79X10^2$	$6.88X10^4$	$8.95X10^3$	---	---	$7.86X10^4$
	Potamogeton pectinatus	$5.61X10^2$	$5.61X10^2$	$8.12X10^2$	$1.46X10^5$	$1.40X10^5$	---	---	$2.88X10^5$
Bruner's Pond	Ceratophyllum	---	$3.93X10^2$	$2.06X10^3$	$3.65X10^5$	$3.44X10^5$	---	---	$7.11X10^5$
	Myriophyllum	$3.02X10^3$	$2.66X10^3$	$6.14X10^3$	$5.17X10^5$	$2.95X10^5$	---	---	$8.24X10^5$
	Potamogeton pectinatus	$1.39X10^3$	$1.53X10^3$	$9.60X10^3$	$2.94X10^5$	$1.19X10^5$	---	---	$4.26X10^5$

C. Calcareous Spring Ponds

Spring	Macrophyte Host	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Other groups	Total Population
A	Anacharis sp.	---	---	8.22×10^3	1.72×10^4	---	---	2.54×10^4
	Hippuris vulgaris L.	---	1.36×10^2	7.79×10^3	2.12×10^5	---	---	2.20×10^5
B	Anacharis sp.	---	---	2.11×10^2	3.42×10^4	---	---	3.44×10^4
	Chara sp.	---	1.06×10^2	6.89×10^1	5.23×10^5	2.06×10^1	---	5.23×10^5
C	Chara sp.	---	1.11×10^2	---	8.54×10^5	3.08×10^1	---	8.54×10^5
	Ranunculus longirostris Godron	---	---	9.37 x 10	5.04×10^4	---	---	5.13×10^4
D	Chara sp.	---	9.78×10^2	---	8.09×10^4	7.36×10^2	---	8.26×10^4
	Ranunculus longirostris Godron	---	---	4.19×10^2	2.43×10^4	1.04×10^1	---	2.47×10^4
E	Chara sp.	---	---	7.18×10^1	5.02×10^4	1.16×10^2	---	5.04×10^4
F	Chara sp.	---	4.06×10^2	---	1.94×10^5	2.76×10^2	---	1.95×10^5







Figs. 19-21. Percentage composition of aufwuchs communities associated with various macrophyte hosts. Fig. 19. Soft water lakes. Figs. 20-21. Hard water lakes. (Percentages < 1.0 not indicated).

desmids in the total aufwuchs population associated with *Utricularia,* and with two exceptions (*Potamogeton* in Ike Lake and *Riccia* in Lake 20-12a), the same held true for other hosts.

Desmid plankton population densities in hard water lakes ranged from 0 organisms/ml in three of the lakes to 3×10^0 organisms/ml. and comprised from 0% to 0.5% of the total population (Fig. 23). In most instances, desmids comprised a greater percentage of the total population in the aufwuchs than in the plankton.

Table 5. Summary of Plankton Population Density Data in organisms/ml.

A. Soft Water Lakes

Lake	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Euglenophyceae	Other Groups	Total Population
Ike	1.48×10^0	-	4.90×10^0	8.92×10^0	1.48×10^0	-	6.17×10^0*	2.30×10^1
Pine	4.08×10^{-1}	-	6.63×10^{-1}	4.08×10^{-1}	1.28×10^0	-	1.34×10^1**	1.62×10^1
Zielke	2.04×10^{-1}	-	1.68×10^0	1.40×10^1	8.67×10^{-1}	-	6.63×10^{-1}**	1.74×10^1
Lake 15-12	4.08×10^{-1}	-	3.83×10^0	2.75×10^0	2.14×10^0	-	3.42×10^0**	1.25×10^1
Lake 20-12a	4.10×10^{-1}	4.10×10^{-1}	2.96×10^0	8.20×10^{-1}	6.43×10^0	-	4.29×10^0*	1.53×10^1

*Dinobryon (Chrysophyceae)
**Peridinium (Dinophyceae)

Table 5. (continued).

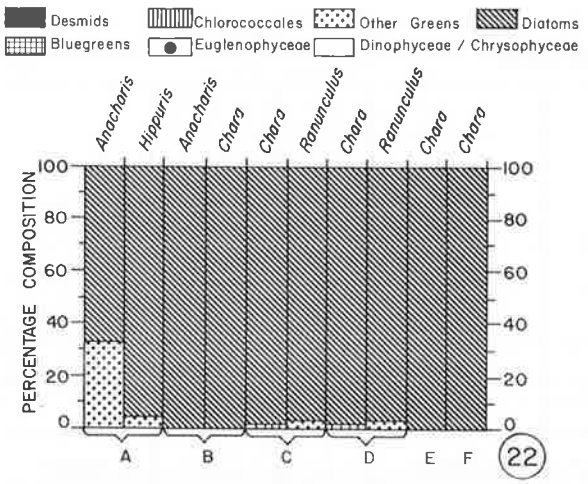
B. Hard Water Lakes

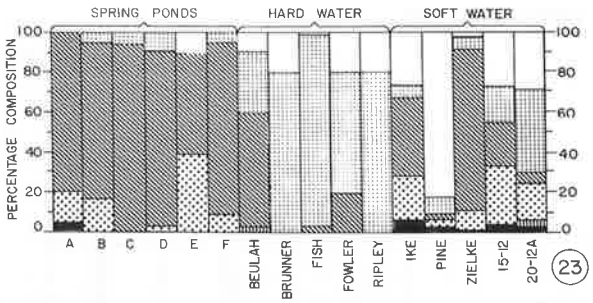
Lake	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Euglenophyceae	Other groups	Total population
Ripley	$3X10^0$	---	---	$1.17X10^3$	$5.29X10^2$	---	---	$1.70X10^3$
Fish	$2X10^0$	$1X10^0$	$1X10^0$	$9X10^0$	$3.51X10^2$	---	$4X10^0$	$3.68X10^2$
Beulah	---	$1X10^0$	---	$3.4X10^1$	$1.8X10^1$	---	$5X10^0$	$5.5X10^1$
Fowler	---	<1	<1	$1X10^0$	$3X10^0$	---	$1X10^0$	$5X10^0$
Bruner's Pond	---	<1	---	$1X10^0$	$1.21X1^2$	---	$3X10^1$	$1.52X10^2$

C. Calcareous Spring Ponds

Spring	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Other groups	Total population
A	5.30×10^{-1}	---	2.25×10^0	1.16×10^1	---	---	1.44×10^1
B	---	---	4.92×10^0	2.46×10^1	1.91×10^0	---	3.14×10^1
C	---	---	---	3.58×10^1	2.76×10^0	---	3.86×10^1
D	---	---	8.43×10^{-1}	4.36×10^1	4.84×10^0	---	4.93×10^1
E	---	---	3.17×10^0	4.04×10^0	---	8.74×10^{-1}*	8.08×10^0
F	---	---	5.27×10^0	6.09×10^1	3.97×10^0	---	7.01×10^1

* Ceratium sp. (Dinophyceae)





Figs. 22-23. Percentage composition of aufwuchs and plankton communities at the study sites. Fig. 22. Percentage composition of aufwuchs communities at the spring pond study sites. Fig. 23. Percentage composition of plankton communities at the study sites. (Percentages < 1.0 not indicated).

In the plankton of Spring A, *Staurastrum* occurred at a density of 5.30×10^{-1} organisms/ml. (Table 5) and comprised 4% of the total population. No desmids occurred in the plankton at the other five locations. The greatest density of planktonic desmids occurred in the hard water lakes (twice the maximum in soft water lakes and six times the greatest value in spring ponds). However, desmids only comprised over 1% of the total population in the five soft water lakes and in one of the spring ponds. In most instances, the percentage contribution of desmids to the total aufwuchs population was greater than to the total plankton population in both the soft water and hard water lakes.

It would appear that desmids form a more conspicuous qualitative component in soft water plankton and aufwuchs communities than in the hard water communities studied, although actual standing crop values for the group often did not differ substantially.

Table 6. Presence (+) or absence (−) of significant differences (95% level) in the population densities of the various groups of algae associated with different hosts at a given soft water lake.

Lake	Hosts Compared	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Total Population
Ike	Potamogeton vs. Utricularia	+	+	+	-	+	+
Pine	Utricularia vs. Hygroamblystegium	+	+	-	-	-	+
	Utricularia vs. Potamogeton	-	+	-	-	-	+
	Utricularia vs. Sphagnum	+	+	-	+	-	+
	Sphagnum vs. Hygroamblystegium	-	-	-	-	-	-
	Sphagnum vs. Potamogeton	+	-	+	+	-	-
	Potamogeton vs. Hygroamblystegium	-	-	-	-	+	-
Zielke	Utricularia vs. Nitella	-	-	-	+	-	+
Lake 15-12	Utricularia vs. Equisetum	+	+	+	+	+	+
Lake 20-12A	Utricularia vs. Riccia	+	+	-	+	-	+

Table 7. Presence (+) or absence (–) of significant differences (95% level) in the population densities of the various groups of algae associated with different hosts at a given hard water lake.

Lake	Hosts compared	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Other groups	Total population
Ripley	Myriophyllum vs. Nuphar	+	+	+	+	+	-	+
	Myriophyllum vs. P. pectinatus	+	+	+	+	+	-	+
	Myriophyllum vs. Utricularia	+	+	+	+	+	-	+
	Nuphar vs. P. crispus	-	-	-	+	-	-	+
	Nuphar vs. Utricularia	+	+	+	+	+	-	+
	P. crispus vs. Utricularia	+	+	+	-	+	-	+

Table 7. (continued).

Lake	Hosts compared	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Other groups	Total population
Fowler	Chara vs. Myriophyllum	+	-	-	-	+	-	+
	Chara vs. P. pectinatus	+	+	+	+	+	-	+
	Chara vs. Anacharis	+	-	-	+	+	-	+
	Myriophyllum vs. P. pectinatus	+	+	+	+	+	-	+
	Myriophyllum vs. Anacharis	+	-	-	+	-	-	+
	P. pectinatus vs. Anacharis	+	-	-	-	+	-	+
Bruner's Pond	Ceratophyllum vs. Myriophyllym	+	+	+	+	+	-	+
	Ceratophyllum vs. P. pectinatus	+	+	-	+	+	-	+
	Myriophyllum vs. P. Pectinatus	+	+	-	+	+	-	+

Table 7. (continued).

Lake	Hosts compared	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Other groups	Total population
Fish	Myriophyllum vs. Ceratophyllum	+	+	+	+	+	+	+
	Myriophyllum vs. Utricularia	+	-	+	+	+	+	+
	Myriophyllum vs. Nuphar	+	+	-	+	+	+	+
	Ceratophyllum vs. Utricularia	+	+	+	+	+	+	+
	Ceratophyllum vs. Nuphar	-	-	+	-	+	+	+
	Nuphar vs. Utricularia	+	+	+	+	+	+	+
Beulah	Anacharis vs. Utricularia	-	-	+	-	+	-	+
	Anacharis vs. Myriophyllum	-	-	+	+	+	-	+
	Anacharis vs. P. pectinatus	-	-	-	+	+	-	+
	Utricularia vs. Myriophyllum	-	-	-	+	+	-	+
	Utricularia vs. P. pectinatus	-	+	+	+	+	-	-
	P. pectinatus vs. Myriophyllum	-	-	-	+	+	-	+

Host to Host Variation Within Lakes

For the soft water lakes, a comparison of all possible pairs of hosts from the same locality revealed statistically significant differences (95% level) in desmid population densities in 60% of the cases (Table 6). In Pine Lake, for example, the population density of desmids associated with *Utricularia* was seven times greater than the population density of desmids associated with *Sphagnum*. Such differences suggest that the most meaningful comparisons between the aufwuchs communities of two or more lakes are those involving the aufwuchs associated with a common host.

In hard water lakes, statistically significant differences occurred 70% of the time in population densitiees of desmids associated with different macrophytes (Table 7). Lake Beulah was a notable exception, however, since desmid populations did not vary significantly in any of the macrophyte comparisons. The greatest magnitude of difference occurred between *Nuphar* and *Utricularia* in Lake Ripley where the desmid population of *Utricularia* exceeded that of *Nuphar* by 10^4 organisms/mg. dry weight of host tissue. Differences of 10^2 were common.

Lake to Lake Variation for Given Hosts

In the soft water lakes studied, *Utricularia* was the only host common to all the localities, and an analysis of the desmid aufwuchs associated with this macrophyte revealed significantly different population densities in 40% of the comparisons (Table 9). Unfortunately, these differences did not appear to be correlated with any general trends in the water chemistry parameters measured. Thus, for example, significant differences in desmid densities also occurred between Pine Lake and Lake 20-12a ciated with differences in calcium levels, alkalinity, and

Table 8. Presence (+) or absence (−) of significant differences (95% level) in the population densities of the various groups of algae associated with different hosts at a given calcareous spring pond.

Spring	Hosts Compared	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Other groups	Total population
A	Anacharis sp. vs. Hippuris vulgaris L.	-	+	-	+	-	-	+
B	Anacharis sp. vs. Chara sp.	-	+	+	+	-	-	+
C	Chara sp. vs. Ranunculus longirostris Godron	-	+	+	+	-	-	+
D	Chara sp. vs. Ranunculus longirostris Godron	-	+	+	+	+	-	+

conductivity, but significant differences in desmid densities also occurred between Pine Lake and Lake 20-12A where calcium levels, alkalinity, and conductivity were virtually identical.

A comparison of the desmid aufwuchs populations on *Myriophyllum spicatum* L. in the five hard water lakes revealed significant differences (95% level) in all but one instance (Table 10). The population density of desmids on *Myriophyllum* in Fish Lake, for example, was 53.0 times more than in Lake Beulah. No correlation between these differences and differences in water chemistry could be detected either.

Data on Other Algal Groups

In addition to the Desmidiales, the aufwuchs communities of the soft water lakes contained members of the Chlorococcales, other Chlorophyceae, Bacillariophyceae, Cyanophyceae, Euglenophyceae, and/or Dinophyceae.

Table 9. Presence (+) or absence (−) of significant differences in the population densities of the various groups of algae associated with Utricularia at different localities of soft water lakes.

Lakes Compared	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Total Population
Ike vs. Pine	+	-	+	+	+	-
Ike vs. Zielke	-	-	+	+	-	-
Ike vs. 15-12	-	-	-	-	-	-
Ike vs. 20-12A	-	-	+	-	-	-
Pine vs. Zielke	+	+	-	+	-	-
Pine vs. 15-12	-	-	+	-	+	+
Pine vs. 20-12A	+	-	-	+	-	+
Zielke vs. 15-12	+	+	-	+	-	+
Zielke vs. 20-12A	-	+	-	+	-	+
15-12 vs. 20-12A	-	-	-	-	-	-

Table 10. Presence (+) or absence (–) of significant differences (95% level) in the population of the various groups of algae associated with Myriophyllum at different localities of hard water lakes.

Lakes compared	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Other groups	Total population
Ripley vs. Fish	+	+	+	+	+	+	+
Ripley vs. Beulah	-	+	-	+	+	-	+
Ripley vs. Fowler	+	+	+	+	-	-	+
Ripley vs. Bruner's Pond	+	+	+	+	+	+	+
Fish vs. Beulah	+	+	+	+	+	+	-
Fish vs. Fowler	+	+	-	+	+	+	+
Fish vs. Bruner's Pond	+	+	+	+	+	+	+
Beulah vs. Fowler	+	+	+	+	+	-	+
Beulah vs. Bruner's Pond	+	+	+	+	+	-	+
Fowler vs. Bruner's Pond	+	+	+	+	+	-	+

Total population densities of aufwuchs ranged from 1.04×10^4 to 4.93×10^4 organisms/mg. dry weight of host tissue (Table 4). At all five localities, the total population density of aufwuchs associated with *Utricularia* was significantly greater (based on statistical comparisons) than that associated with other macrophyte hosts. In most cases total population densities on *Utricularia* were approximately double those on other hosts, but at Lake 15-12, *Utricularia* harbored 4.6 times as many algae per mg. dry weight of host tissue as did *Equisetum*. This greater difference may be due, in part, to the greater surface area per unit weight of *Utricularia* and in part to the greater specific gravity of the silicon impregnated tissues of *Equisetum*.

Of the seven groups of organisms comprising the aufwuchs, the Euglenophyceae and Dinophyceae occurred only sporadically and in such small numbers (Table 4) that they appear to be of little consequence. In no case did either of the groups account for more than 1.8% of the total population (Figs. 19-22). Since taxa belonging to these groups are normally flagellated and actively motile, their occurrence in the aufwuchs probably is fortuitous.

The Bacillariophyceae, in contrast, occurred in substantial numbers in all samples and always accounted for at least 20% of the total number of organisms present (Fig. 19-22). In nine of the 12 samples, diatoms constituted the largest single element in the total population, and in three cases, they accounted for approximately 75% of the organisms present.

Few other general trends emerged regarding aufwuchs community composition. With one exception, the Cyanophyceae comprised between 10 and 30% of the total population and with two exceptions, the same held true for the Chlorococcales. Except for one instance, the miscellaneous Chlorophyceae accounted for 20.7% or less of the total population.

At all five localities, considerable variation occurred in aufwuchs population densities and community composi-

tion from one macrophyte host to another. In Ike Lake, for example, the population densities of Desmidiales, Chlorococcales, other Chlorophyceae, and Cyanophyceae as well as the total population associated with *Potamogeton* were significantly different from those associated with *Utricularia* (Table 6). Although the population densities of Bacillariophyceae did not differ significantly on the two hosts in Ike Lake, the diatoms accounted for less than 50% of the total population on *Utricularia* but over 75% of the total population associated with *Potamogeton.*

Moreover, in cases where significant differences did not occur in total population (e.g., *Potamogeton* vs. *Sphagnum* and *Potamogeton* vs. *Hygroamblystegium* in Pine Lake; see Table 6), significant differences did occur among one or more groups comprising the total population. Indeed, a complete absence of statistically significant differences appeared in only one of the 10 paris of hosts examined (*Sphagnum* vs. *Hygroamblystegium* in Pine Lake).

A comparative analysis of the aufwuchs associated with *Utricularia* at the five localities revealed similar variation (Table 9). Although significant differences in the total population densities did not appear to be present in six of the 10 paris of lakes, significant differences in the population densities of one or more of the components of the total population occurred in four of those six cases. In only two cases (Ike vs. 15-12 and 15-12 vs. 20-12a) was there a total absence of significant differences. Similarly, in the four instances where significant differences occurred in the total population densities, significant differences were present in only some but not all of the components of the total population.

In addition to the Desmidiales, the aufwuchs communities of the hard water lakes included Chlorococcales, other Chlorophyceae, Bacillariophyceae, Cyanophyceae and Dinophyceae. Total population values ranged from 1.23×10^3 organisms/mg. host dry weight on *Nuphar* in Fish Lake to 8.24×10^5 organisms/mg. host dry weight on *Myriophyllum* in Bruner's Pond (Table 4). As with the Desmidiales, total population densities did not seem to be correlated with the water chemistry parameters measured.

In 16 out of the 19 macrophyte samples, the Bacillariophyceae constituted the most important element in the aufwuchs (Figs. 20-21) and accounted for up to 87.9% of the total population. The pennate diatoms greatly outnumbered the centric diatoms; *Fragillaria* and *Cocconeis* were the most common genera. The Cyanophyceae were the second most prevalent group (constituting up to 83.5% of the total population). The 'other Chlorophyceae' comprised 16.3% or less of the total population and the Chlorococcales comprised up to 15.2% of the total but were less than 1% in the majority of instances. Members of the Dinophyceae never accounted for more than 0.7% of the total.

As with the Desmidiales, the populations of other algal groups comprising the aufwuchs were often significantly different from one macrophyte to the next in the same lake. On *Myriophyllum* and *Ceratophyllum* in Fish Lake, for example, significant differences occurred in all categories (Table 7). Likewise, the algal groups associated with *Myriophyllum* differed significantly between lakes in nearly every instance; all Bacillariophyceae population densities were significantly different and only one of the total population comparisons was not (Table 10).

The aufwuchs community of the spring ponds included members of the Chlorococcales, 'other Chlorophyceae,' Bacillariophyceae and Cyanophyceae. Total population densities ranged from 2.47×10^4 organisms/mg. host dry weight on *Ranunculus longirostris* Godron in Spring D to 8.54×10^5 organisms/mg. host dry weight on *Chara* sp. in Spring C (Table 4). In all cases, the Bacillariophyceae was the dominant group, constituting 96% or more of the standing crop (Fig. 22). Pennate forms greatly outnumbered centric ones in each instance, and no one or two genera were conspicuously dominant. The 'other Chlorophyceae' ranked second in abundance but comprised only up to 2% of the total population and was composed exclusively of Zygnemataceae (*Mougeotia* sp., *Spirogyra* sp. and *Zygnema* sp.). These genera formed extensive felt-like mats in all but one spring and were probably adventitious on the macrophytes. Cyanophyceae and the Chlorococcales were of little importance, comprising only 0 to 1% of the total population.

Within a given spring, population densities of the various algal groups differed significantly (at the 95% level) in the majority of instances (Table 8). The Chlorococcales, the Bacillariophyceae and the total populations were significantly different consistently. Comparisons of the standing crops associated with *Chara* sp. at different localities (Table 11) revealed similar trends–the diatom densities and the total population densities were significantly different in nine out of 10 comparisons.

In the soft water lakes, the plankton community contained, in addition to the Desmidiales, members of the Chlorococcales, other Chlorophyceae, Bacillariophyceae, Cyanophyceae, Chrysophyceae, and Dinophyceae.

Table 11. Presence (+) or absence (–) of significant differences (95% level) in the population densities of the various groups of algae associated with Chara sp. at different localities of calcareous spring ponds.

Springs Compared	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Other groups	Total population
B vs. C	–	–	+	+	–	–	+
B vs. D	–	+	+	+	+	–	+
B vs. E	–	+	–	+	+	–	+
B vs. F	–	+	+	+	+	–	+
C vs. D	–	+	–	+	+	–	+
C vs. E	–	+	–	+	–	–	+
C vs. F	–	+	–	+	+	–	+
D vs. E	–	+	–	+	+	–	+
D vs. F	–	+	–	+	+	–	+
E vs. F	–	+	–	+	+	–	+

Euglenophyceae were not detected. Total population densities of plankton ranged from 1.25×10^1 to 2.30×10^1 organisms/ml. (Table 5).

At four of the five localities, one of two flagellates *Dinobryon* (Chrysophyceae) or *Peridinium* (Dinophyceae) accounted for at least 25% of the total population, and in Pine Lake, *Peridinium* was the dominant phytoplanter with 83% of the total population (Fig. 23). This contrasts markedly with the aufwuchs community where members of the Chrysophyceae were not detected and members of the Dinophyceae never accounted for more than 1.8% of the total population (Fig. 19).

Considerable variation occurred in the population densities of the other groups. The Bacillariophyceae were the most abundant element in the plankton of Ike Lake and Zielke Lake whereas the Cyanophyceae were most numerous in Lake 20-12a and the other Chlorophyceae most common in Lake 15-12. Members of the Chlorococcales occurred only in the plankton of Lake 20-12a and there accounted for only 2.7% of the total population.

The plankton samples of the hard water lakes contained the same groups of organisms as the aufwuchs did with one exception: *Dinobryon* (Chrysophyceae) occurred in four of the lakes, usually in association with *Ceratium* (Dinophyceae). These two genera accounted for 20% of the total population in one instance (Fig. 23). Total population densities varied considerably (Table 5) and, as in the aufwuchs, the Bacillariophyceae and the Cyanophyceae comprised the bulk of the total population. In two of the lakes the diatoms were most frequent (up to

68.7%) whereas in the other three the blue-greens were most common (up to 79.0%). The Chlorococcales were present in four of the five lakes in quantities ranging from 0.3% to 20.0% of the total population.

Other components of the plankton of the spring ponds included the 'other Chlorophyceae' (the same genera as in the aufwuchs; probably dislodged from the benthic mat), the Bacillariophyceae, the Cyanophyceae and the Dinophyceae. Diatoms were also dominant in these communities, comprising 50-93% of the total population (Fig. 23). The 'other Chlorophyceae' and the Cyanophyceae were more conspicuous in the plankton than the aufwuchs, however, and constituted 0-39% and 0-10% of the total population, respectively. The Dinophyceae (*Ceratium* sp.) accounted for 11% of the total in Spring E but were not represented at the other localities. The Chlorococcales were not represented. Total population densities of the plankton ranged from 8.08×10^{0} to 7.01×10^{1} organisms/ml. (Table 5).

Comparisons with bog lakes

A comparison of the results emerging from this study with those emerging from work on bog lakes in northern Wisconsin (Woelkerling 1975) has revealed both similarities and differences regarding desmid diversity, population densities, community composition and host-aufwuchs interaction.

Generic Diversity

Acid bog lakes harbored the greatest diversity of desmids in both the aufwuchs and the plankton (Table 12); soft water lakes contained the next highest diversity followed by closed bogs, alkaline bogs, hard water lakes and calcareous spring ponds. The soft water environments (acid bog lakes, alkaline bog lakes, closed bogs and soft water lakes) supported several times the number of desmid genera that the hard water environments did. As in the soft water and hard water lake samples, *Utricularia* in the acid bog and alkaline bog lakes harbored the greatest aufwuchs generic diversity in almost every instance (*Utricularia* was not found in the closed bogs visited).

Staurastrum was the most prevalent desmid genus in the plankton and it was the only one recorded from the hard water lakes and calcareous spring ponds.

Desmid Population Densities

Similar maximum population densities and mean population densities for desmids in the aufwuchs occurred in soft water lakes, hard water lakes and acid bogs (Table 12). Values for alkaline bog lakes and closed bogs were some-

Table 12. A comparison of the number of desmid genera present and desmid population densities for all six lake types.

	Total no. of desmid genera present		Desmid Population Densities in the Aufwuchs (no. of organisms per mg host dry weight)		Desmid Population Densities in the Plankton (no. of organisms per ml)	
Lake Type	Aufwuchs	Plankton	Range	Mean	Range	Mean
Acid bog	22	18	1.69×10^{2} - 1.63×10^{4}	3.66×10^{3}	8.2×10^{-2} - 2.7×10^{2}	2.2×10^{1}
Alkaline bog	10	4	0 - 1.97×10^{3}	5.13×10^{2}	5.1×10^{-1} - 4.8×10^{0}	1.9×10^{0}
Closed bog	12	--	0 - 1.12×10^{3}	3.87×10^{2}	---	---
Soft Water	14	4	1.92×10^{2} - 1.04×10^{4}	3.24×10^{3}	2.0×10^{-1} - 1.5×10^{0}	5.8×10^{-1}
Hard Water	3	1	0 - 1.10×10^{4}	1.33×10^{3}	0 - 3×10^{0}	1×10^{0}
Spring Pond	0	1	---	---	0 - 5.3×10^{-1}	8.8×10^{-2}

what less. Although desmid aufwuchs diversity was much lower in the hard water lakes than in any of the soft water environments, standing crops in the hard water lakes were similar to or exceeded those in the soft water habitats. Maximum population densities were obtained on *Utricularia* in every lake type where this macrophyte occurred. Desmid plankton population densities (Table 12) were substantially higher in the acid bog lakes than in the hard water lakes or the spring ponds although the mean density for the hard water lakes was comparable to the value for the alkaline bog lakes.

The greatest ranges and means in percent contribution of desmids to the total aufwuchs population (Table 13) were associated with acid bog lakes and soft water lakes. Intermediate values were associated with alkaline bog lakes and closed bogs and the lowest values were in association with the hard water environments. Similar trends were evident with the plankton data (Table 13); mean percent contribution of desmids to the plankton population of acid bog lakes was 22 and 155 times greater than the value for spring ponds and hard water lakes, respectively but only eight and five times greater than the values for alkaline bog lakes and soft water lakes, respectively. The maximum value for the acid bog lakes (70.4%) was considerably higher than the values for the other lake types.

Host to Host Variation Within Lakes

Acid bog lakes, soft water lakes and hard water lakes had a greater percentage of statistically significant differences in the desmid populations from one host to another (67%, 60% and 70%, respectively) than did the alkaline bog lakes or closed bogs (3% and 33%, respectively). The reasons for these differences and the apparent uniformity of the aufwuchs communities of the alkaline bog lakes are not clear.

Significant differences nearly always occurred between *Utricularia* and another host; in the hard water lake L. Ripley, desmid populations on *Utricularia* were greater than those on *Nuphar* petioles by 10^4 organisms/mg. host dry weight and in the acid bogs and soft water lakes, desmid densities on *Utricularia* exceeded those on *Sphagnum* by ca. 7-52 times. A notable exception to the above occurred in alkaline bog lakes where significant differences in the desmid densities between *Utricularia* and another host only occurred 36% of the time.

The presence of numerous significant differences in population densities of the aufwuchs add support to the

Table 13. A comparison of the contribution of desmids to the total aufwuchs and plankton populations for all six lake types.

	Contribution of Desmids to the total aufwuchs population (%)		Contribution of Desmids to the total plankton population (%)	
Lake Type	Range	Mean	Range	Mean
Acid bog	2.5 - 27.5	10.7	0.2 - 70.4	15.5
Alkaline bog	0 - 10.1	3.4	1.5 - 2.3	2.0
Closed bog	0 - 17.8	4.2	---	---
Soft Water	0.9 - 30.0	11.3	1.2 - 6.4	3.2
Hard Water	0 - 11.3	1.6	0 - 0.5	0.1
Spring Pond	---	---	0 - 4.0	0.7

hypothesis (see Woelkerling 1975) that the composition of benthic communities may be influenced markedly by the nature of the substratum – in this case the type of host. This hypothesis is further strengthened by population density data for aufwuchs groups other than the Desmidiales (see Tables 6-8).

Lake to Lake Variation for Given Hosts

Utricularia occurred in all acid bog lakes and soft water lakes, and significant differences in the desmid populations occurred 24% of the time from lake to lake in the acid bogs and 40% of the time in the soft water lakes. Lake to lake variations in desmid densities associated with *Utricularia* were generally much less than variations between *Utricularia* and other hosts at a given site. Likewise, significant differences in desmid populations associated with *Sphagnum* in the closed bogs occurred only 18% of the time. In contrast to this apparent uniformity between lakes of a given type, desmid populations on *Myriophyllum* in the hard water lakes varied significantly 80% of the time.

Additional comments

Several results emerging from this investigation require further comment. One concerns the greater diversity of desmid taxa in the aufwuchs as compared to the plankton. *Sphagnum* long has been recognized (e.g., Brook 1959, Griffiths 1928, Krieger 1933) as harboring a qualitatively rich desmid flora; this richness may be due in part to the ability of *Sphagnum* to reduce the pH of surrounding waters (Skene 1915, Rose 1953), thereby increasing the availability of free CO_2 which Moss (1973a, 1973c) feels would favor desmid development. In view of the results of the current investigation which indicate that *Utricularia* has a qualitatively more diverse and a quantitatively greater desmid flora than other macrophyte hosts examined (including *Sphagnum*), studies appear warranted to determine whether *Utricularia* also possesses some physiological mechanism which would favor desmid development. Sculthorpe (1967) provides no information on this topic.

Recent culture work has attempted to shed some light on desmid growth in relation to water chemistry. Tassigny (1971) reported somewhat decreased growth rates of four species at higher calcium concentrations, but Moss (1972) observed that calcium levels as high as 100 ppm did not cause decreased growth rates for four typically oligotrophic desmids. Moss (1973a) also suggested that many desmids are selected against in hard water habitats because of typically higher pH's which limit the availability of free carbon dioxide.

The paucity of desmids in hard water environments, particularly spring ponds, may lend support to the hypotheses of Strøm (1921), Wade (1957), Tassigny (1971) and others that the growth of most desmids is restricted to waters with low Ca^{++} concentrations. However, the presence of abundant free CO_2 in the spring ponds suggests that the desmid flora should be much more diverse if Moss's (1973a) conclusions regarding desmid distribution are correct (see Woelkerling & Gough 1975 for further discussion). The lack of development of a significant desmid flora in spring ponds may not be due to a direct chemical effect, however. Thus, for example, the extent to which diatoms may be able to outcompete other forms at these temperatures and chemical conditions in unknown, and further studies in this area are required.

Further study likewise is needed to determine the potential environmental indicator value of quantitative data on the aufwuchs communities associated with macrophyte hosts. The heterogeneity of the aufwuchs in all of the lake types examined resulted in no clear cut trends. The most obvious trends – those showing a greater generic diversity in the aufwuchs than in the plankton and those showing a greater diversity in soft water habitats than in hard water environments – are more qualitative than quantitative in nature. Unfortunately current studies on the value of qualitative data are hampered by the rather chaotic state of desmid systematics.

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ON THE REMOVAL AND QUANTIFICATION OF ALGAL AUFWUCHS FROM MACROPHYTE HOSTS

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Abstract

Accurate population density measurements of algal aufwuchs associated with macrophyte hosts appears to be fraught with uncertainties. This account details a procedure involving aufwuchs removal by agitation and acid hydrolysis with subsequent quantification by a special Sedgwick-Rafter cell counting technique. The aufwuchs removal efficiency from five hosts of widely differing morphology was calculated to be 98.0% (95% confidence limits: 96.3%, 99.7%) after five 45 second agitation cycles.

Introduction

The removal and quantification (by counting) of algal aufwuchs from macrophyte hosts has received the attention of a number of investigators, and various techniques have been developed. Methods of removal include agitation (Foerster & Schlichting 1965, Knudson 1957), grinding (Douglas 1958), using jets of water and brushing (Hickman 1971), and scraping (Sladeckova 1962, Young 1945). Subsequent quantification by counting has involved the use of inverted microscope techniques (Knudson 1957), the use of membrane filters (Foerster & Schlichting 1965), the use of transects on glass slides (Hickman 1971, Sladeckova 1962), or the use of Sedgwick-Rafter or similar counting cells (Douglas 1958, Slack *et al.* 1973, Sladeckova 1962, Young 1945), and in all of the above investigations results have been expressed in terms of number of organisms per unit of host surface area.

Little objective information, however, appears to be available on the precision and reliability of the various removal techniques, and in cases where such data are presented (e.g., Foerster & Schlichting 1965), a potentially high degree of variability is indicated, thus necessitating the use of 'correction factors'. Moreover, quantification procedures, especially those involving the use of Sedgwick-Rafter cells, apparently assume that similar results (in terms of accuracy) emerge, regardless of the counting regime employed. Woelkerling *et al.* (1975), however, have shown that such assumptions cannot be made. Finally, some authors (e.g. Hickman 1971) note that difficulties may occur in attempting to determine host surface area (see Sladeckova 1962, p. 298 for methods), and this may, in turn, affect results that are expressed in terms of numbers of organisms per unit of host surface area.

These limitations have contributed to the widespread adoption of indirect measurements with the use of artificial substrates (see APHA 1971, Sladeckova 1962 for methods). Artificial substrates, however, not only suffer from the drawback of permitting only indirect measurement, but they also may permit a particular type of selective colonization (Herbst & McNelly 1973, Hickman 1971, Tippet 1970). This, of course, could produce misleading results. Moreover, any natural selectivity resulting from differences in macrophyte host biology (e.g., surface texture, chemical secretion) cannot be detected satisfactorily with the use of artificial surfaces. Thus accurate quantitative (i.e., population density) measurements of algal aufwuchs associated with macrophyte hosts still appears to be fraught with uncertainties.

Preliminary observations on the role of desmids (Desmidiales, Chlorophyta) in Wisconsin lake communities supports the contentions of Griffiths (1928), Hutchinson (1967), Krieger (1933), and others that desmids can occur in substantial numbers in aufwuchs associated

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with macrophyte hosts and that the desmid aufwuchs may be of greater ecological importance than the desmid plankton in a given lake. Consequently, quantitative measurement of aufwuchs appears essential to an understanding of desmid ecology in lakes, and the present investigation has been undertaken in hopes of developing a procedure which would 1) permit direct measurement of aufwuchs on natural substrates, 2) allow consistently for virtually complete removal of aufwuchs from a wide variety of macrophyte host types, and 3) result in a quantification procedure which involves a reliable counting regime, yields population density data, and avoids expressing results in terms of numbers per unit of host surface area.

The procedure

Since aufwuchs attachment to the host surface commonly appears to be effected by mucilage-like polysaccharides (O'Colla 1962), it was hypothesized that aufwuchs removal could be accomplished by a combination of agitation and acid hydrolysis of the polysaccharides with FAA (10:7:2:1::95% ethanol: water: formalin: glacial acetic acid). Initial experiments were conducted on the aufwuchs associated with *Myriophyllum spicatum* L., but the work was eventually extended to include five macrophytes of widely varing morphology (Table 1).

The procedure for the removal and the subsequent quantification which resulted from these experiments may be summarized as follows:

1. Place macrophyte material in a wide mouth jar, add enough FAA to just cover plants, cap jar, and agitate by shaking vigorously (ca. 2 shakes per second) for 45 seconds.
2. Decant through cheesecloth into another container; return macrophyte fragments retained by cheesecloth to original sample. (Removal of material from cheesecloth can be facilitated, where necessary, by rinsing with jets of distilled water from a squirt bottle.)
3. Repeat steps 1-2 until five agitation cycles have been completed.
4. Dry macrophyte material at 70° C for 24 hrs; weigh on an analytical balance.
5. Compute the *total* population of aufwuchs organisms in the accumulated decantation using Sedgwick-Rafter cell counts (Woelkerling *et al.*, 1975; express results in terms of number of organisms per unit dry wt. of macrophyte host.

To insure more accurate results, several factors should be taken into account in applying the above procedure. Care must be exercised in collecting to avoid dislodging very loosely attached forms. The authors generally collected enough 5-15 cm portions of host material to fill a 250 ml jar; subsequent agitation was carried out in a 1000 ml container.

TABLE I

Salient morphological features of the macrophytes studied

Macrophyte	Salient morphological features
Myriophyllum spicatum L.	Numerous finely divided leaves.
Utricularia sp.	Finely divided leaves; carnivorous bladders.
Potamogeton pectinatus L.	Coarse, thread-like leaves from multiple stems.
Sphagnum sp.	Numerous, small, closely appressed leaves.
Nuphar sp. (petioles)	Cylindrical, relatively smooth petioles.

Another aspect concerns the Sedgwick-Rafter cell counting (see Woelkerling *et al.* (1975) for details of the procedure). In the present study the authors employed a regime of 2 counts on each of 12 S-R cells. The volume of the decanted material was adjusted, where necessary, to insure individual Whipple grid tallies of 5-25 at a total magnification of 200x (20x obj.; 10x ocular). This density range appeared to avoid overcrowding and excessive clumping of organisms on the one hand and yet permitted tallies of taxa present in relatively low numbers on the other hand. Dilution was effected with the addition of FAA. Concentration was accomplished with a plankton centrifuge (Kahl Scientific Instrument Corporation, El Cajon, California, Model 020WA106) set at 14,000 rpm and a flow rate of 100 ml/min. The efficiency of the instrument was previously determined (unpublished data) to be 96-99% from comparisons of the residue and effluent counts with the membrane filter technique of McNabb (1960).

The total population (T) of organisms was computed from the equation

$$T = dv \quad (1)$$

where d is the density of organisms per ml of the sample and v is the total volume of the sample's liquid in ml. The procedure for determining d for Sedgwick-Rafter cell counts is outlined in APHA (1971).

Calculation of aufwuchs removal efficiencies

To determine the efficiency of aufwuchs removal, the washing liquid from each 45 second agitation-washing cycle was collected and analyzed separately for each macrophyte. Curves resulting from plots of total counts of aufwuchs present in each fraction vs. washing number for the five macrophytes, displayed an orderly pattern which suggested an exponential decrease (Fig. 1a). Exponential regressions performed with a Hewlett-Packard 1900 B programmable calculator determined approximate functional relationships between total count and washing number for each macrophyte. The equations obtained were of the form:

$$Y_x = ae^{bx} \quad (2)$$

where Y_x is proportional to the number of organisms removed in the X-th washing, e = 2.718, the base of

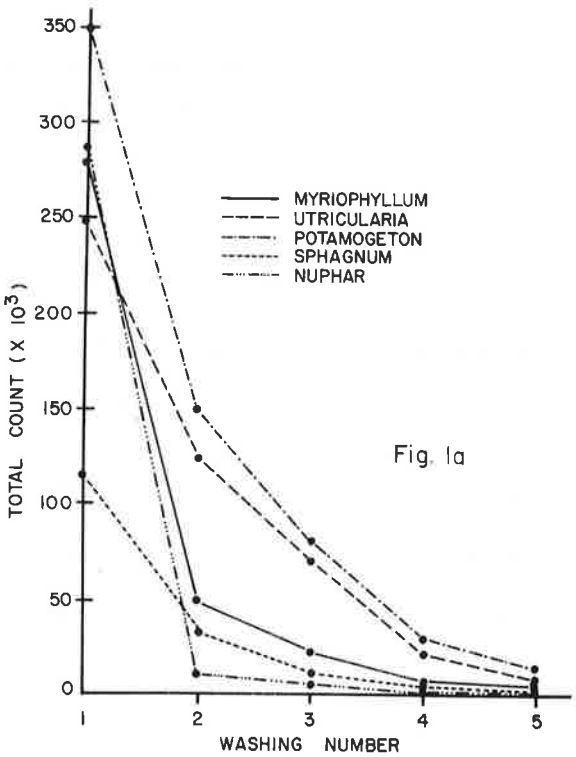

Fig. 1a. Total count vs. washing number for the five macrophytes.

natural logarithms, and a an b are constants determined by regression. The correlation coefficient between Y_x (estimated) and Y_x (observed) ranged from .93 to .98, indicating good curve fits in all cases. Before performing the regressions, the observed Y_x values were transformed to a common scale by assigning a value of 1.000 to the highest count (washing 1) of each macrophyte and computing all other values as fractions of this maximum value.

For a given macrophyte, the total number of organisms removed after n washings is proportional to

$$T_n = \sum_{x=1}^{n} Y_x = ar(1-r^n)/(1-r) \quad (3)$$

and the total number of organisms present is proportional to

$$T = \sum_{x=1}^{\infty} Y_x = ar/(1-r) \quad (4)$$

where Y_x is estimated using equation (2) and $r = e^b$. Efficiencies, E_n, expressed as percent removal of aufwuchs can be calculated by

TABLE II

Exponential equations (regressed) for each macrophyte, efficiencies predicted by each equation and mean efficiencies and confidence intervals.

Macrophyte	Equation	Washing number 1	2	3	4	5	6	7	8	9
		Efficiency (%)								
Myriophyllum spicatum L.	$Y = 1.363\ e^{-.846X}$	57.1	81.6	92.1	96.6	98.6	99.4	99.7	99.9	(100)*
Utricularia sp.	$Y = 2.256\ e^{-.738X}$	52.2	77.2	89.1	94.8	97.5	98.8	99.4	99.7	99.9
Potamogeton pectinatus L.	$Y = 1.877\ e^{-.688X}$	49.7	74.7	87.3	93.6	96.8	98.4	99.2	99.6	99.9
Sphagnum sp.	$Y = 1.319\ e^{-.694X}$	50.0	75.0	87.5	93.7	96.9	98.4	99.2	99.6	99.8
Nuphar sp.	$Y = 3.383\ e^{-1.920X}$	85.3	97.9	99.7	100.0	100.0	100.0	100.0	100.0	100.0
95% confidence interval	lower limit	40.3	69.3	85.7	92.4	96.3	98.1	99.1	99.5	99.7
	upper limit	77.5	93.3	97.5	99.0	99.7	99.9	99.9	100.0	100.0

(5) $$E_n = 100\ T_n / T_x$$

For each macrophyte, efficiencies were calculated for several washing numbers and, as a measure of the variability between macrophytes, 95% confidence intervals were established for each washing number (see Table II). In Fig. 1b, the confidence intervals are plotted against washing numbers. Variability is seen to be the greatest after the first washing (95% confidence limits: 40.3%, 77.5%) and to decline steadily with successive washings until after the ninth washing, the removal efficiency is over 99% (95% confidence limits: 99.7%, 100.0%). If one assumes that the macrophytes studied here represent a range in host morphology likely to be encountered in the field, then the removal efficiency can be expected to fall between 96.3% and 99.7% after five washings.

Discussion

Expressing total population densities in terms of dry weights of macrophyte hosts appears to offer some advantages over results expressed in terms of unit surface area of hosts. Dry weights can be easily and accurately determined whereas estimating surface areas can be laborious and prone to errors. The morphology of many macrophyte species is known to vary from site to site (e.g., *Potamogeton pectinatus* L.). Moreover some species, and even single plants, can vary substantially in morphology at different water depths (Fassett 1957). In addition, most surface area values are based on an average size and shape, a procedure which can introduce errors in the final results. Finally, the morphology of many macrophytes is of such a complex nature (e.g. *Myriophyllum* leaves) that determination of average surface areas by the usual procedure of mathematical approximations produces only rough estimates, at best.

Results expressed in terms of dry weights must be interpreted with caution, however, if comparisons between different types of macrophytes are to be made since surface area to weight ratios may vary. In this study, for example, *Nuphar* petioles probably have a much different surface area to weight ratio than the finely divided leaves of *Myriophyllum,* thus making direct comparisons between the aufwuchs population densities of potentially limited value. Regardless of how the results

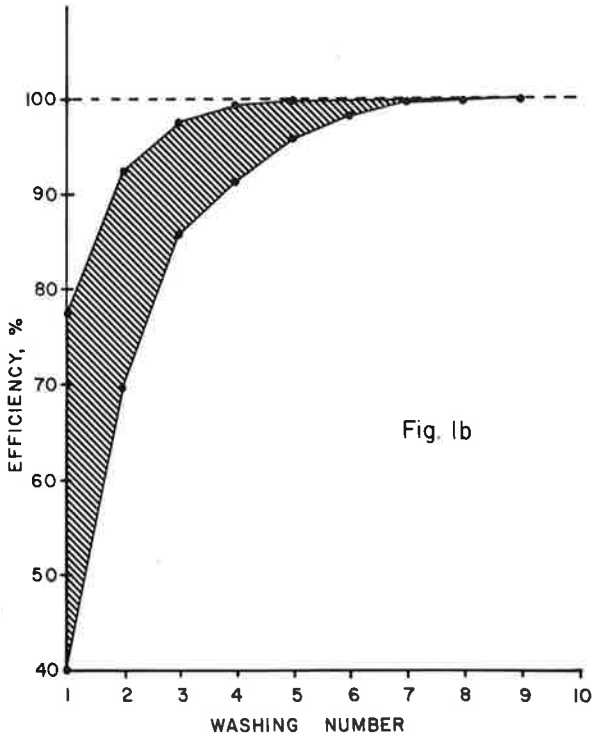

Fig. 1b. 95% confidence belt for removal efficiency based on the five macrophytes.

are to be expressed, however, the aufwuchs removal procedure is applicable.

The proposed procedure assumes that all aufwuchs will be removed after an infinite number of washings; i.e., there are no forms which are entirely resistant to removal. Microscopic examination of the macrophyte material after five washings revealed very few remaining organisms, thereby supporting this assumption. Finally, the force applied in the agitation cycle may not be completely uniform and a machine (e.g., a modified paint shaker) would probably have to be used to standardize the force. However, since removal of the aufwuchs by the procedure described here is nearly 100% after five washings for all of the hosts studied, the use of manual agitation appears justified.

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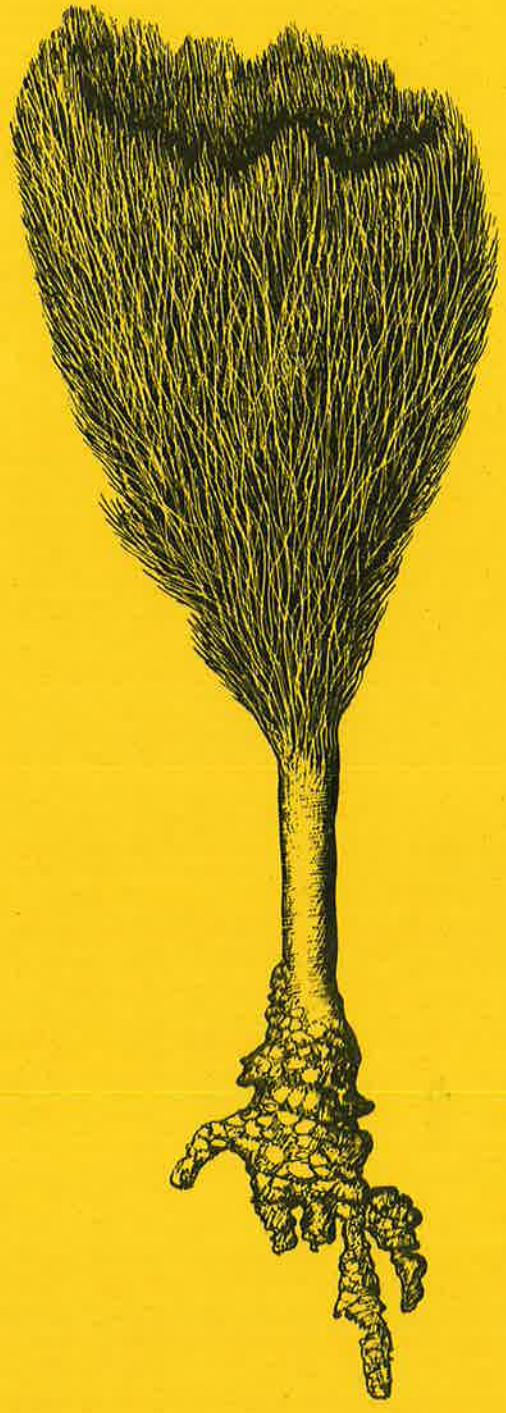

South Florida Benthic Marine Algae

Keys and Comments

by

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Division of
Marine Geology and Geophysics
Rosenstiel School of Marine
and Atmospheric Science
The University of Miami

1976

SOUTH FLORIDA BENTHIC MARINE ALGAE:
KEYS AND COMMENTS

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SEDIMENTA V

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CONTENTS

PREFACE

The luxuriance and bewildering variety of marine plants in shallow tropical seas is one of the strongest impressions of a first underwater experience off Southern Florida or in the West Indies. The more one looks, the more one finds: prairies of marine grasses and green algae; rock-making crusts of red corallines; sediment-trapping films of scum-like blue-greens; tiny filaments boring into every fragment of shell or coral; brilliant symbionts coloring nourishing reef corals. But to go beyond these first, arresting impressions has been difficult until now. To learn how to identify the elements of this varied flora one needs keys, descriptions, illustrations. Yet the existing keys and descriptions are so widely scattered in the botanical literature, written in such specialized language, and so often incomplete, that neophytes find them difficult if not impossible to use. This publication aims at filling the need for a relatively simple, yet comprehensive key to the marine algae of Southern Florida, which fortunately includes most of the Western Atlantic flora.

Appropriately, the compilation developed from Dr. Woelkerling's teaching visits to South Florida and therefore had the benefit of practical testing both in the field and laboratory. In hopes of still further refinements, Woelkerling solicits comments from users.

These well-illustrated keys, with the useful glossary and guide to the specialized literature will help newcomers to identify tropical algae, and learning the names and some anatomy opens the door to the challenging problems of zonation, ecology, and the relationship with invertebrates and sediments.

R. N. GINSBURG

I. GENERAL COMMENTS

Introduction

This document provides illustrated keys to the genera of green, brown, and red algae and to the genera and species of blue green algae commonly found in marine benthic communities of Florida. It has been designed primarily for student use in short courses and classroom situations, and in no way should it be considered a monographic treatment of Florida marine algae. Species keys have not been provided for the green, brown, and red algae because of their availability elsewhere (e.g. Dawes 1974 and Taylor 1960) and because species concepts in many genera still remain uncertain. The absence of clear cut species concepts coupled with the polymorphic behavior of many marine algae often frustrate inexperienced students who attempt to identify specimens to species, and generic concepts appear to be more readily grasped by individuals at the start. Species reference lists for the green, brown, and red algae recorded from Florida by Dawes (1974) and Taylor (1960) are provided in Tables following the respective generic keys.

In addition to the keys, this report also includes a glossary of morphological terms used in the keys and contains a bibliography of important references. The remainder of this general section considers briefly the literature of Florida marine algae, provides brief comments on marine algal habitats and communities, gives instructions for the collection, preservation, and examination of algal material, and makes suggestions for use of the keys.

Literature

Reference already has been made to two works (Dawes 1974, Taylor 1960) dealing with Florida marine algae, and both contain extensive bibliographies. Dawes' book includes comprehensive species keys and a glossary, avoids extensive use of technical terminology, and provides considerable ecological information, all of which make it an attractive volume for students. It deals, however, only with the Gulf of Mexico Coast of Florida and thus is of limited value for use in identifying material from the more floristicly diverse Atlantic Coast. Taylor's book, in contrast, includes the entire Florida region and contains an excellent series of illustrations. Most students, unfortunately, find Taylor's book difficult to use because of the extensive use of technical terminology and the absence of comprehensive generic keys. In addition, the work does not cover the blue-green algae. Nevertheless, individuals

interested in attempting identification of algae to species almost invariably must turn to one or both of these volumes.

Several other publications are of prime importance. Taylor (1928) provides an illustrated account of Florida algae which should be particularly helpful for work in the Florida Keys, although it is now somewhat dated. The papers of Boergesen (1913, 1914, 1915-1920) on Virgin Islands algae likewise are dated, but they include an excellent series of illustrations and provide species accounts with a minimum of technical language. Unfortunately, keys to species are given for relatively few genera. Beyond these works, one must turn to the periodical literature for detailed records.

Among the text books currently available, Dawson (1966) and Fritsch (1935, 1945) provide good accounts of algal morphology and systematics, while Hedgpeth (1957) and Moore (1959) provide more generalized ecological accounts of the marine environment. Stephenson and Stephenson (1950, 1952) present descriptive accounts of the rocky intertidal ecology of the Florida Keys and North Florida, and much of this material has been summarized in a recent book (Stephenson and Stephenson 1972). Calcareous algae also have been dealt with from the geological standpoint in several recent documents (Ginsburg et al. 1972, Ginsburg 1972).

Habitats and Communities

Dawes (1974) and Taylor (1960) provide good accounts of the various habitats present in Florida and the algal communities present in them. A comprehensive account of U. S. Coastal ecosystems (Odum et al. 1974) also contains valuable information on the Florida region and includes a detailed classification of habitat types.

For classroom purposes, it may be convenient to consider the habitats from the standpoints of exposure to wave action and to substrate. Thus one can examine and compare the algal communities of sheltered (e.g. lagoons, swamps) and exposed situations and look at the lithic (rocky and other solid substrata), pelic (sand, mud and other particulate substrata), and aufwuchs (epibiotic and endobiotic algae) components in each case.

Most students are apt to be impressed initially if introduced to the algal communities of sandy and muddy regions which usually harbor a variety of large green algae that are readily identifiable. Rocky substrates can be considered subsequently, and the aufwuchs community may best be considered last since it is here one commonly encounters a wealth of stunted or small plants which are more difficult to identify.

Collection, Processing and Examination of Marine Algae

Detailed information on the collection, processing, and examination of marine algae appears in a number of publications (e.g. Dawson 1956, 1966; Taylor 1960), but a few matters require emphasis:

1. Collection - Good collections of material can be obtained with or without the aid of snorkeling and/or scuba equipment, but the use of such gear markedly extends collection capabilities. For snorkelers and scuba divers, a fine mesh collecting bag which can be clamped or zippered shut will be needed, and a few Whirl-pak or similar sealable plastic bags should be taken along for housing smaller specimens. A scraping knife and/or geological pick often facilitate collection of material attached to rock. All of the safety rules for snorkelers and divers (e.g. see Ginsburg 1972) should, of course, be followed.

   When collecting inshore by means of wading, a plastic pail and a few small plastic bags will be needed for the specimens, and a scraping knife and geological pick will prove useful.

   PROTECTION FROM THE SUN IS OF VITAL IMPORTANCE. In the tropics one easily can become severely burned or be overcome with heat exhaustion or sunstroke suddenly. Even with an overcast sky, reflection from the water can cause problems. Long sleeve shirts, slacks, and hats are advised for waders and for snorkelers and divers when in boats. Use of good quality suntan creams is strongly recommended.

2. Processing - Preservation of material is NOT essential if specimens are examined upon return to shore or if they are placed in a holding tank with running sea water. Under other conditions preservation can be easily effected by using a solution of 1:10::formalin:sea water and storing material in the dark to avoid loss of color in the specimens. Excess fluids can be drained from the preserving containers after several hours, and the algae can be packed drip wet in plastic bags for transport. For information on herbarium processing, consult Dawson (1956, 1966) or Taylor (1960).

   For Cyanophyta (blue green algae), Drouet (1968) recommends that all material be air dried directly on paper rather than preserving first with formalin so as to avoid possible changes in cytological features utilized in taxon identification. Air dried specimens readily assume the form of living material when moistened with water.

3. Examination - Entire plants should be available for study, and plants bearing reproductive structures are of more value than sterile plants. For most work, a good quality dissecting

microscope and a compound microscope are essential. In addition, dissecting tools, a forceps, glass slides, cover slips, dropper bottles with water and 0.1N HCl, and a razor blade or scapel will be needed. With a little practice, good cross-sections of plants can be obtained in free hand fashion using a sharp, single edge razor blade. Fresh or liquid preserved material should be used whenever possible as dried herbarium specimens present problems of restoration (see Dawson 1956, 1966).

Keys for Identification

The taxonomic keys contained in this document are strictly dichotomous in organization and are presented in the progressive indentation format to facilitate use by students. Technical terminology has been minimized, but the glossary in Chapter 2 should be consulted when necessary. For many genera, reference is made in the keys to one or more illustrations (indicated in parentheses after the generic name) of Florida representatives. These drawings are numbered sequentially and are included in Chapter 8 at the end of this volume. Additional references to illustrations are provided in the species reference tables following each key.

Whenever possible, entire plants in good condition should be utilized for identification. Fragmentary specimens, young or markedly stunted plants, and damaged material often do not exhibit key characters clearly. In the vast majority of cases, sterile specimens can be used; in some cases, however, reproductive structures are needed for proper generic identification.

Most students quickly learn to sight recognize characters of the four algal divisions and can proceed directly to the appropriate generic key. (A key to the major groups of algae, however, is provided at the end of this section and should be consulted when necessary.) Similarly, the presence or absence of calcium carbonate (lime) incrustations soon becomes obvious. In cases where divisional status or calcification status present problems, the following tests can be utilized in conjunction with key characters:

1. Boiling water test - Because of variability in pigmentation, some red algae can appear brownish and greenish. Red-algae can readily be distinguished by boiling a bit of tissue in water. If the tissue changes color to a pale green or grass green (caused by the extraction of water soluble reddish pigments present), the alga belongs to the Rhodophyta. The absence of such a color change (due to the absence of these water soluble pigments) indicates that the specimen is not a red alga.

2. Starch test - Green algae normally are distinguishable from other algal groups dealt with here in that they usually store starch as a food reserve. To test for the presence of starch, add a drop of iodine solution (KI-2 gm; I_2-1 gm; water - 25 ml) to the tissue. If starch is present, the tissues will turn blue to blue-black.

3. Acid test for calcium carbonate (lime) - Calcareous algae can often be recognized by touch or by inspection with the dissecting microscope. In uncertain cases, several drops of dilute acid (e.g. 0.1N HCl) can be added to a bit of tissue. If bubbles (of CO_2) are released, calcareous deposits are present. This test should always be carried out with the aid of a dissecting microscope to make sure the bubbles are coming from tissue regions rather than from extraneous fragments of lime entrapped in the plant tissues from the sediments.

Although the keys presented here have been classroom and field tested in Florida, they should not be regarded as foolproof, and the author heartily welcomes any errors being called to his attention. Similarly, suggestions for improvements will be appreciated.

Key to Algal Divisions

1a. Plants procaryotic; cells lacking an apparent internal organization and pigments diffused throughout the cytoplasm. .Division Cyanophyta . . . . . (Blue-green Algae), Section 6, p. 67

1b. Plants eucaryotic; cells possessing an internal organization with pigments contained in plastids.

2a. Plants green; plastids more or less grass-green; starch present . . . . . .(Division Chlorophyta) . . . . . (Green Algae), Section 3, p. 14

2b. Plants reddish, brownish, whitish, red-olive; plastids not grass green; starch absent.

3a. Plastids brown and plants brown; pigments not soluble in boiling water . . . . . .Division Phaeophyta . . . . . .(Brown Algae), Section 4, p. 29

3b. Plastids red to purple to bluish to red-olive; pigments soluble in boiling water causing plant to become greenish when boiled . . . . . .Division Rhodophyta . . . . . .(Red Algae), Section 5, p. 39

II. MARINE ALGAE - GLOSSARY OF SELECTED TERMS

This glossary provides definitions of many of the more common terms used in keys to various groups of marine algae. It is by no means exhaustive, and for more comprehensive coverage, the glossaries of Jackson (1928) and Stearn (1966) should be consulted. In some cases reference is made to particular illustrations in Chapter 8 of this document.

acuminate - pointed

alternate - branching in which each cell of the axis bears a single later branch

anastomoses - cross connections (e.g. Fig. 60)

anticlinal - radiating outwards from the center (e.g. Fig. 151, 208a)

apical cell - the embryonic cell at the apex of a thallus, whose division in ancestral to all other cells of the thallus (e.g. Fig. 222)

apical depression - a pit-like cavity at the tip of a branch (e.g. Fig. 216, 263)

articulate - jointed (e.g. Fig. 259)

assimilators - erect, photosynthetic units of a thallus (e.g. Fig. 101)

attenuate - tapering

auxiliary cell - in most red algae, a cell of the carpogonial filament or a related filament which fuses with the carpogonium or an outgrowth of the carpogonium, and may subsequently give rise to the gonimoblasts

basipetal - growth toward the base

benthic - attached to a definite substrate or anchored in sand or mud

bipinnate - twice-branched, with both primary and secondary branches pinnately divided

biseriate - in two rows

bispore - one of two spores borne in pairs

bladder - a hollow, inflated, gas-filled tissue (e.g. Fig. 108)

caespitose - in tufts

calcareous - encrusted with lime (calcium or magnesium carbonate)

capitate - having a head-like end (with a neck-like constriction)

carpogonium - the female sex organ in the red algae

carposporophyte - a mass of tissue derived from a diploid zygote (fertilized carpogonium) and giving rise to carpospores (e.g. Fig. 259, 277)

cartilaginous - hard and tough, often shiny

central axis - the filament in the thallus of some red algae which gives rise to all other cells of the thallus - often visible in cross section as a single centrally located cell (e.g. Fig. 126, 127, 133, 14, 165)

clathrate - lattice-like, perforated

clavate - club-shaped

coenocytic - a type of thallus construction characterized by the absence of cross walls (e.g. Fig. 11-13)

conceptacle - a cavity (containing reproductive cells) with an opening to outside (e.g. Fig. 108)

constructed - narrowed or contracted (e.g. Fig. 150)

cordate - heart-shaped

coriaceous - leathery

cortex - the outer portion of a fleshy organ, assuming a central medulla is distinguishable (e.g. Fig. 208, 309-310)

cortication - filamentous or pseudoparenchymatous outgrowths which conjoin at least in part and form a new outer covering of the thallus or stipe

cruciate - having contents of a tetrasporangium divided in 2 or 3 planes at right angles to one another (e.g. Fig. 121, 228)

crustose - crust-like

cuneate - wedge-shaped

cystocarp - a reproductive structure in the red algae, bearing carpospores or tetraspores or formed after fertilization of the carpogonium

decumbent - lying flat, but with the summit ascending

dentate - toothed

determinate - having limited growth

dichotomous - branched by repeated forkings into two equivalent parts

dioecious - having distinct male and female plants

distichous - in two vertical ranks or rows

ditrichotomous - branching both in a dichotomous and a trichotomous manner

divaricate - extremely divergent

dorsiventral - having distinct dorsal and ventral surfaces (e.g. Fig. 254, 255)

ecortication - without cortication

endogenous - arising from internal tissues

epidermis - the surface layer of cells

eucaryotic - possessing membrane bound organelles such as a nucleus and chromoplasts

exogenous - arising from surface tissues

falcate - sickle-shaped

fasciculate - in tufts

filiform - thread-like

flabellate - fan-shaped (e.g. Fig. 4, 64, 93)

flaccid - limp, flabby

fountain type - multiaxial construction with numerous axial filaments forming the core of a thallus (e.g. Fig. 298)

fusiform - spindle-shaped

gelatinous - slippery and mucilaginous

gland cell - a secretory cell, often appearing opalescent (e.g. Fig. 121, 124, 179, 180)

gonimoblast - a short filament from the auxiliary cell or the carpogonium base, usually curving upwards and terminating in a carposporangium

hapteron - an attachment organ; in many red algae a unicellular or multicellular organ in which the tip is markedly flattened where it is in contact with the substrate (e.g. Fig. 177, 196, 279)

heterocyst - a cell which is conspicuously larger than and often thicker walled than adjacent vegetative cells

holdfast - a basal structure or cell specialized as an organ of attachment

hyaline - clear and colorless

indeterminate - having more or less unlimited growth

intercalary - within

internode - as applied to algae, the interval on a (stem-like) thallus between two joints or "nodes" (e.g. Fig. 159, 160, 181)

irregular - without a defined branching pattern

lamellate - made up of thin plates or sheets

lanceolate - shaped like a lance point

linear - narrow, ribbon-like

medulla - central core area of a massive thallus or stipe (e.g. Fig. 151, 189, 208, 219, 229)

midrib - a raised, usually cylindrical "nerve" of the thallus surface

moniliform - barrel-shaped or bead-like (e.g. Fig. 129)

moniecious - both sexes present in same individual

monosiphonous - uniseriate (e.g. Fig. 130, 313)

monospore - an asexual unicellular spore (e.g. Fig. 130-131)

mucronate - possessing a short, straight point (e.g. Fig. 157)

multiaxial - growth from a group or core of central filaments (e.g. Fig. 208, 266, 267, 297, 298)

multiseriate - in a number of rows

nemathecium - a wart-like projection bearing reproductive bodies

node - the point from which a branch arises; the junction of two cells; a joint between two levels or segments of the thallus

opposite - branching in which lateral branches regularly arise from a node in pairs

orbicular - like a disc, circular

ovate - having the outline of a longitudinal section of an egg (2 dimensional)

ovoid - shaped like an egg (3 dimensional)

papillate - covered with wart-like projections

paraphyses - sterile hairs (e.g. Fig. 106)

parenchymatous - a tissue resulting from cell divisions in more than one plane (e.g. Fig. 99-100)

parietal - appressed to the outer wall, or towards the outside

pericarp - the outer wall of an enclosed cystocarp

pericentral cells - cells arranged in regular tiers about the central axial cell in certain red algae

pinnate - having distichous branchlets arranged like the barbs of a feather

pit connection - a cytoplasmic strand connecting two adjoing cells through a pit in their respective walls

plumose - feather-like

plurilocular sporangium - a sporangium with numerous distinct walled cells, with walls which persist even after the spores have been shed

polysiphonous - in red algae, a type of construction in which the central axial cell is surrounded by 3 or more pericentral cells of similar length and arranged in regular tiers (e.g. Fig. 276, 279, 301)

procarp - a unit group of reproductive cells in some red algae consisting of carpogonium and the auxiliary cell as well as certain adjacent cells

procaryotic - without membrane bound organelles as the nucleus, chromoplast, etc.

procumbent - lying along the substrate

propagule - a few-celled branch of definite form which can break loose from the parent plant and form a new plant by vegetative means (e.g. Fig. 112-113)

prostrate - horizontal in relation to the substrate

pseudoparenchyma - tissue resulting from a compact arrangement of filaments in which the identity of individual filaments is more or less obscured

pulvinate - cushion-like or cushion-shaped (e.g. Fig. 45, 73)

pyrenoids - small, rounded, colorless, shiny structures embedded within the chromoplast

pyriform - pear-shaped

ramuli - branches

reniform - kidney-shaped

reticulate - netted or covered with a layer which is net-like

rhizines - slender, thick walled filaments

rhizoid - a slender, descending filament

scar cell - a small cell at the base of a trichoblast where it adjoins the thallus (e.g. Fig. 301)

secund - arranged in a single plane

septum - a partition or wall

seta - a hair or bristle

simple - unbranched

sinuate - with a deep wavy margin

siphon - a more or less tubular structure resembling a filament but without cell cross walls

sorus - a cluster, usually on the thallus surface, of sporangia or other reproductive bodies (e.g. Fig. 80, 81, 83)

spermatium - a non-motile male cell of the red algae

sporangium (sporangia) - a spore producing structure

stellate - star-shaped

stichidium - a specialized branch bearing reproductive organs

stipitate - having a stipe or stalk

stoloniferous - stolon-like; forming runners along the surface of the substrate from which the erect portions arise

sublittoral - the biological zone below the low tide mark

terete - cylindrical, in cross section circular

ternate - in threes

tetrad - in fours

tetrahedral - having the contents of a tetrasporangium divided triangularly so that only three of the tetraspores can be seen at once (e.g. Fig. 256, 313-315)

tetrasporangium - a spore producing organ whose contents divide into 4 parts

tetraspore - a meiospore in red algae

thallus - the entire plant body of an alga

torulose - beaded

trabeculae - simple or forked wall protuberances, often appearing as a meshwork (e.g. Fig. 21-22)

transversely divided - division in a plane perpendicular to the long axis

trichoblast - a simple or branched monosiphonous filament arising from or near the apex in the family Rhodomelaceae (Rhodophyta)

trichogyne - thread-like upper portion of a carpogonium

trichome - a hair (sometimes branched); in blue-green algae, the filament without its surrounding sheath

trichothallic - a form of growth involving the division of intercalary cells in a group of terminal filaments, with subsequent adhesion of the basal parts of the filaments

trichotomous - branched by repeated forkings into three equivalent parts

truncate - cut off

uniaxial - having only one axial filament in the thallus

unilocular - having only one cavity, i.e., not divided up by numerous persistent crosswalls as in a plurilocular structure

uniseriate - in a single row

urceolate - shaped like a pitcher with a protruding mouth

utricle - inflated ends of coenocytic filaments which are grouped to form an outer layer, as in Codium (Fig. 24, 25)

vesicular - sac-like, commonly more or less spherical

whorled - branching in which 3 or more lateral branches regularly arise from a node

zonate - having contents of a tetrasporangium lying in a row as a result of division in 3 parallel planes (e.g. Fig. 311b, 311c)

III. CHLOROPHYTA: KEY AND SPECIES REFERENCE LIST

Introductory Remarks

Although the Chlorophyta or green algae occur predominantly (in terms of species diversity) in fresh water environments, approximately 20% of the known taxa are marine, and 47 genera and 135 species have been recorded from Florida (Table 1, p.20) by Dawes (1974) and/or Taylor (1960). The most conspicuous developments of green algae in Florida waters usually occur in sublittoral muddy or sandy regions and most of the genera found in these substrates possess lime encrusted tissues. (A total of 9 genera and 28 species of calcified Chlorophyta occur in Florida.) Certain genera of the families Codiaceae (e.g. Halimeda, Penicillus, Udotea) and Dasycladaceae (e.g. Acetabularia, Cymopolia) commonly form extensive meadows, and their calcareous remains constitute an important element of the Florida marine sediments (see Ginsburg 1972, Ginsburg et al. 1972). Green algae also occur commonly on sublittoral rocks and can be found as members of the aufwuchs community. A few taxa (e.g. Enteromorpha, Ulva) also occur frequently in the intertidal zone.

Most genera of green algae found in Florida marine waters are distinctive and readily identifiable, but in some cases (e.g. Cladophora, Enteromorpha) species concepts require considerable refinement and present taxon limits are poorly defined.

Generic Key to the Chlorophyta

1a. Plants encrusted with lime (calcareous deposits react with dilute acid to release bubbles of CO_2; test on a clean piece of tissue and watch reaction with a dissecting microscope).

2a. Plants distinctly segmented, with flexible uncalcified joints.

3a. Apices bearing a tuft of uncalcified, branched filaments. . . . . .Cymopolia (Figs. 37-39)

3b. Apices lacking tufts of uncalcified, branched filaments. . . . . Halimeda (Figs. 50-52)

2b. Plants not segmented, lacking flexible uncalcified joints.

4a. Plants composed of a simple stalk bearing a disc at the apex.

5a. Spores not calcified. . . . . Acetabularia (Fig. 1)

5b. Spores calcified.

6a. Spores (borne in rays of the disc) embedded in a solid mass of lime. . . . . .Acicularia (Fig. 2)

6b. Spores individually calcified, not embedded in a solid mass of lime. . . . . .Chalmasia

4b. Plants lacking a terminal disc of cells on a simple stalk.

7a. Plants rarely over 3 cm tall; main axis bearing dense whorls of heavily calcified branches. . . . . .Neomeris (Fig. 59)

7b. Plants usually over 3 cm tall; main axis not bearing dense whorls of heavily calcified branches.

8a. Main axis terminated by a tuft of unconsolidated dichotomously branched filaments. . . . . Penicillus (Figs. 56-57)

8b. Main axis terminated by one or more blade-like expansions.

9a. Blades numerous, more or less radially arranged around the stalk and usually composed of a single layer of tissue. . . . . Rhipocephalus (Fig. 58)

9b. Blades usually single (sometimes with proliferations), composed of several layers of tissue. . . . . .Udotea (Fig. 64)

1b. Plants not encrusted with lime.

10a. Plants unicellular or composed of spherical cells irregularly embedded in a gelatinous maxtrix.

11a. Setae present. . . . . Diplochaete (Fig. 44)

11b. Setae absent

12a. Cells embedded in clusters in a gelatinous mat. . . . . .Pseudotetraspora

12b. Cells solitary, not embedded in clusters in a gelatinous matrix. . . . . .Halicystis (Fig. 49)

10b. Plants multicellular or coenocytic and of more complex morphology.

13a. Plants vesicular or forming erect foliar or netted sheet-like expanses of 1 - several cell layers.

14a. Plants vesicular, the sac-like structures occasionally rupturing and becoming saucer shaped.

15a. Plants composed of angular cells mostly 0.1-1.0 mm in diameter and much smaller lenticular cells interspersed between them; attached to substrate by several celled rhizoids . . . . . .Dictyosphaeria (Fig. 45)

15b. Plants composed of ovoid to angular cells mostly over 1 mm in diameter; lenticular cells usually absent; plant attached to substrate by small peg-like haptera cells or by irregular rhizoidal cells . Valonia (Fig. 65)

14b. Plants forming more or less erect foliar or net-like expanses.

16a. Plants parenchymatous, without any evidence of filamentous construction; cells of more or less uniform size and each containing 1-2 pyrenoids.

17a. Plants 1 cell thick . . . . . .Monostroma (Figs. 54-55)

17b. Plants 2 cells thick. . .Ulva (Fig. 67)

16b. Plants of evident filamentous construction, with vein-like series of cells forming a net or present in the foliar, sheet-like expanse; cells usually of variable size and lacking pyrenoids.

18a. Plants perforated or completely net-like

19a. Plants forming perforated, sheet-like expanses . . . . . Cystodictyon (Fig. 43)

19b. Plants forming net-like expanses without any solid parenchyma-like areas. . . . . .Microdictyon (Fig. 60)

18b. Plants forming a solid thallus without perforations or a net-like appearance. . . . . .Anadyomene (Fig. 3)

13b. Plants filamentous or forming small crustose discs or of more complex construction, but not vesicular or forming 1 - several layered foliar, or net-like expanses.

20a. Plants forming crustose discs.

21a. Discs of 1 cell layer throughout; cells each with one pyrenoid.

22a. Central cells enlarging to form sporangia. . . . . Pringsheimiella

22b. Central cells not developing into sporangia. . . . . .Protoderma

21b. Discs of more than 1 cell layer, at least in part; cells lacking pyrenoids.

23a. Plants 0.1-0.5 cm in diameter; marginal filaments 3-4 (-15) µm broad. . . . . .Ulvella (Fig. 66)

23b. Plants 2-6 cm in diameter; marginal filaments 300-850 µm broad. . . . . .Petrosiphon

20b. Plants filamentous or of more complex construction but not forming crustose discs.

24a. Plants forming branched or unbranched multicellular filaments.

25a. Filaments creeping upon or within the substrate, without an evident holdfast.

26a. Filaments bearing ovoid, thick-walled sporangia; plants usually perforating wood or shells. . . . . Gomontia

26b. Filaments lacking ovoid, thick-walled sporangia; plants usually epi- or endo-phytic.

27a. Cells bearing unicellular hairs. . . . . .Phaeophila

27b. Cells lacking unicellular hairs. . . . . .Entocladia

25b. Filaments more or less erect. [Go to 28a].

28a. Plants unbranched or bearing only short, rhizoidal branches.

29a. Cells commonly over 100 µm in diameter (except in one species); filaments unbranched, stiff, a mass not collapsing completely upon removal from water. . . . . Chaetomorpha (Figs. 31-34)

29b. Cells under 100 µm in diameter; filaments simple or with a few short branchlets, a mass completely collapsing upon removal from water.

30a. Cells with 1 pyrenoid; cells under 10 µm in diameter; plants usually under 1 mm tall. . . . . Stichococcus

30b. Cells with numerous pyrenoids; cells over 10 µm in diameter; plants usually over 1 mm tall. . . . . Rhizoclonium

28b. Plants moderately to profusely branched.

31a. Cells of axes divided locally in a parenchymatous fashion. . . . Siphonocladus (Fig. 61)

31b. Cells not dividing parenchymatously; filaments uniseriate.

32a. Plants forming a distinctive stalk-like main axis readily distinguished from the lateral branches.

33a. Branching whorled.

34a. Branching whorled throughout; each cell bearing an apical whorl of cells. . . . . Ernodesmis (Fig. 48)

34b. Branching of main axis whorled; main axial cell bearing a number of whorls of laterals which are further branched in a dichotomous or ditrichotomous manner.

35a. Whorled branches closely set; sporangia single and terminal on the basal cell of each branch cluster. . . Dasycladus (Figs. 40-42)

35b. Whorls of branches distant; sporangia several, clustered along the branch axes. . . . . Batophora (Figs. 5-8)

33b. Branching irregular, unilateral, opposite, but not regularly whorled.

36a. Main axis terminated by several more or less net-like expanses of branched filaments. . . . . .Struvea (Figs. 62-63)

36b. Main axis terminated by a tuft of branched brush-like filaments. . . . . .Chamaedoris (Fig. 29)

32b. Plants lacking a distinctive stalk-like main axis.

37a. Ultimate branches without cross walls at the base. . . . . Cladophoropsis (Figs. 35-36)

37b. Ultimate branches with cross walls at the base. . . . . Cladophora (Figs. 26-28)

24b. Plants parenchymatous or coenocytic (lacking cross walls) and of varying appearance.

38a. Plants parenchymatous; composed of numerous small cells compactly arranged; plant body tubular-hollow to flattened. . . . . Enteromorpha (Fig. 46)

38b. Plants coenocytic, without evidence of numerous cross walls; plant body various in form.

39a. Plants stoloniferous, composed of a distinct rhizome-like portion bearing the erect portions of the plant.

40a. Erect portions of various aspect; internal portions traversed by a series of trabeculae (simple or forked wall protuberances, often appearing as a meshwork). . . . . Caulerpa (Figs. 15-22)

40b. Erect portions appearing as tube-like filaments which may be simple or dichotomously forked; trabeculae absent . . . . . Derbesia

39b. Plants without a distinct differentiation into stoloniferous and erect portions.

41a. Branching plumose, feather-like. . . . . .Bryopsis (Figs. 9-14)

41b. Branching irregular, dichotomous, or not readily apparent, but not plumose.

42a. Surface of plant composed of a continuous layer of inflated utricles (terminal sac-like inflations of the tubular filaments). .

43a. Utricles laterally coherent. . . . . Pseudocodium

43b. Utricles contiguous but not adherent. . Codium (Figs. 23-25)

42b. Surface of plant not composed of a continuous layer of utricles.

44a. Plants prostrate, not organized into massive thalli with erect blade like portions.

45a. Siphons 4-10 (-40) µm in diameter, irregular in form and variable diameter; branches lacking regular basal construction; plants penetrating limestone or shells. . . . . Ostreobium (Fig. 53)

45b. Siphons (40-) 45-90 µm or more in diameter, more or less dichotomously branched; branches constricted at the base; plants generally in mud, not penetrating limestone or shells. . . Boodleopsis

44b. Plants erect, organized into massive thalli with blade-like erect portions.

46a. Erect portion differentiated into a distinct cortex and medulla. . . . . .Cladocephalus (Fig. 30)

46b. Erect portion without differentiation into cortex and medulla. . . . . .Avrainvillea (Fig. 4)

TABLE 1. Chlorophyta Species Reference List (Records of species occurrence in Florida as reported in Dawes 1974 and Taylor 1960).

Taxon	Dawes (1974)	Taylor (1960)
1. *Acetabularia crenulata* Lamouroux	p. 92 - fig. 41	p. 105 - pl. 4, fig. 5, pl. 6, fig. 12
2. *Acetabularia farlowii* Solms-Laubach	p. 93	p. 105
3. *Acetabularia pusilla* (Howe) Collins	----	p. 104 - pl. 6, fig. 13
4. *Acicularia shenckii* (Möbius) Solms-Laubach	p. 93	p. 107 - pl. 6, fig. 11
5. *Anadyomene menziesii* Harvey	p. 90	----
6. *Anadyomene stellata* (Wulfen) C. Agardh f. *prototypa* Howe	p. 91 - fig. 40	p. 125 - pl. 7, fig. 2, pl. 8, fig. 2
7. *Avrainvillea asarifolia* Børgesen	p. 78	p. 161
8. *Avrainvillea elliottii* A. et E. S. Gepp	p. 79	----
9. *Avrainvillea levis* Howe	p. 79	p. 162
10. *Avrainvillea nigricans* Decaisne f. *fulva* Howe	p. 79 - fig. 33	p. 160 - pl. 19, fig. 2, pl. 25, figs. 11, 12
11. *Batophora oerstedi* J. Agardh v. *occidentalis* (Harvey) Howe	p. 94 - fig. 42	p. 98 - pl. 4, figs. 3, 4, pl. 5, fig. 4, pl. 6, figs. 3, 9
12. *Boodleopsis pusilla* (Collins) Taylor, Joly et Bernatowicz	p. 79	----
13. *Bryopsis duchassaignii* J. Agardh v. *filicina* Collins and Hervey	----	p. 133
14. *Bryopsis hypnoides* Lamouroux f. *prolongata* J. Agardh	p. 72	p. 130
15. *Bryopsis pennata* Lamouroux	p. 72 - fig. 28	p. 132 - pl. 9, fig. 12

TABLE 1. con't.

Taxon	Dawes (1974)	Taylor (1960)
16. *Bryopsis plumosa* (Hudson) C. Agardh	p. 73	p. 131- pl. 9, fig. 11
17. *Bryopsis ramulosa* Montagne	----	p. 131
18. *Caulerpa ashmeadii* Harvey	p. 73 - fig. 29	p. 142 - pl. 11, fig. 4, pl. 18, fig. 9
19. *Caulerpa cupressoides* (West) C. Agardh	p. 74	p. 146 - pl. 14, figs. 3, 4, 6, pl. 15, figs. 1-4, pl. 18, figs. 11-13
20 *Caulerpa fastigiata* Montagne v. *confervoides* Crouan ex Weber-van Bosse	p. 74	p. 136 - pl. 10, fig. 12
21. *Caulerpa floridana* Taylor	----	p. 143 - pl. 11, figs. 5, 6, pl. 18, fig. 10
22. *Caulerpa lanuginosa* J. Agardh	p. 74	p. 145 - pl. 14, figs. 1-2
23. *Caulerpa mexicana* (Sonder) J. Agardh	p. 74 - fig. 30	p. 141 - pl. 12, figs. 2-5
24. *Caulerpa microphysa* (Weber-van Bosse) J. Feldman	----	p. 155 - pl. 17, fig. 5, pl. 18, fig. 6
25. *Caulerpa paspaloides* (Bory) Gerville	p. 75	p. 149 - pl. 16, figs. 1-4, pl. 18, figs. 8, 14, 15
26. *Caulerpa peltata* Lamouroux f. *imbricata* (Kjellman)	p. 75	p. 155 - pl. 17, fig. 2, pl. 18, fig. 1
27. *Caulerpa prolifera* (Forsskål) Lamouroux	p. 77 - fig. 31	p. 140 - pl. 11, figs. 1-3
28. *Caulerpa racemosa* (Forsskål) J. Agardh	p. 77 - fig. 32	p. 151 - pl. 17, figs. 1, 3, 4, 6, 7, pl. 18, figs. 2-5, 7
29. *Caulerpa sertularioides* (Gmelin) Howe	p. 77	p. 144 - pl. 13, fig. 1-7
30. *Caulerpa verticillata* J. Agardh f. *charoides* (Harvey) Weber-van Bosse	----	p. 138 - pl. 10, figs. 1, 2
31. *Caulerpa vickersiae* Børgesen	----	p. 137 - pl. 10, figs. 3-9

TABLE 1. con't.

Taxon	Dawes (1974)	Taylor (1960)
32. *Caulerpa webbiana* Montagne	----	p. 139 - pl. 10, fig. 10
33. *Chaetomorpha aerea* (Dillwyn) Kützing	p. 87	----
34. *Chaetomorpha brachygona* Harvey	p. 87	p. 70 - pl. 2, fig. 9
35. *Chaetomorpha clavata* (C. Agardh) Kützing	----	p. 73
36. *Chaetomorpha gracilis* Kützing	----	p. 70
37. *Chaetomorpha linum* (Müller) Kützing	p. 87	p. 71 - pl. 2, fig. 8
38. *Chaetomorpha minima* Collins et Hervey	p. 88	----
39. *Chalmasia antillana* Solms-Laubach	----	p. 103
40 *Chamaedoris peniculum* (Ellis and Solander) Kuntze	----	p. 115 - pl. 5, fig. 2
41. *Cladocephalus luteofuscus* (Crouan) Børgesen	----	p. 163 - pl. 29, figs. 8, 9
42. *Cladophora catenata* (Linneaus) Kützing	p. 88	----
43. *Cladophora deliculata* Montagne	p. 88	p. 87
44. *Cladophora fascicularis* (Mertens) Kützing	p. 88 - fig. 39	p. 91 - pl. 3, fig. 3
45. *Cladophora flexuosa* (Dillwyn) Harvey	----	p. 89
46. *Cladophora frascatii* Collins et Hervey	p. 88	----
47 *Cladophora fuliginosa* Kützing	----	p. 83 - pl. 2, fig. 3, pl. 3, fig. 4
48. *Cladaphora glaucescens* (Griffiths ex Harvey) Harvey	p. 88	p. 86
49. *Cladophora gracilis* (Griffiths ex Harvey) Kützing	p. 89	p. 90
50. *Cladophora hutchinsiae* (Dillwyn) Kützing	----	p. 90
51. *Cladophora longicellulata* van den Hoek	p. 89	----

TABLE 1. con't.

Taxon	Dawes (1974)	Taylor (1960)
52 *Cladophora luteola* Harvey	----	p. 88
53. *Cladophora polyacantha* Montagne	----	p. 86
54. *Cladophora prolifera* (Roth) Kützing	----	p. 91 - pl. 3, fig. 5
55. *Cladophora repens* (J. Agardh) Harvey	p. 90	p. 82
56. *Cladophora scitula* (Suhr) Kützing	----	p. 90
57. *Cladophoropsis macromeres* Taylor	----	p. 118 - pl. 2, fig. 2
58. *Cladophoropsis membranacea* (C. Agardh) Børgesen	p. 92	----
59. *Codium decorticatum* (Woodward) Howe	p. 80	p. 188 - pl. 26, figs. 1, 2
60. *Codium intertextum* Collins and Hervey	----	p. 185
61. *Codium isthmocladium* Vickers subspec. *clavatum* (Collins and Hervey) Silva	p. 80	p. 186 - pl. 26, fig. 3
62. *Codium repens* Crouan in Vickers	----	p. 186
63. *Codium taylori* Silva	p. 80 - fig. 34	p. 188 - pl. 26, fig. 4
64. *Cymopolia barbata* (Linnaeus) Lamouroux	----	p. 102 - pl. 4, fig. 1, pl. 6, fig. 1
65. *Cystodictyon pavonium* J. Agardh	p. 92	p. 124 - pl. 1, fig. 1, pl. 8, fig. 4
66. *Dasycladus vermicularis* (Scopoli) Krasser	----	p. 99 - pl. 4, fig. 2, pl. 6, figs. 2, 8
67. *Derbesia vaucheriaeformis* (Harvey) J. Agardh	p. 70	p. 128
68. *Dictyosphaeria cavernosa* (Forsskål) Børgesen	----	p. 116 - pl. 7, fig. 5
69. *Diplochaete solitaria* Collins	p. 65	----
70. *Enteromorpha chaetomorphoides* Børgesen	p. 67	----

TABLE 1. con't.

Taxon	Dawes (1974)	Taylor (1960)
71. *Enteromorpha clathrata* (Roth) J. Agardh	p. 67	p. 58
72. *Enteromorpha compressa* (Linnaeus) Greville	p. 67	p. 60
73. *Enteromorpha flexuosa* (Wulfen) J. Agardh f. *submarina* (Wulfen) J. Agardh	p. 67	p. 61
74. *Enteromorph intestinalis* (Linnaeus) Link	p. 67 - fig. 26	----
75. *Enteromorpha lingulata* J. Agardh	p. 68	p. 60 pl. 1, fig. 3
76. *Enteromorpha linza* (Linneaus) J. Agardh	p. 69	----
77. *Enteromorpha plumosa* Kützing	----	p. 58
78. *Enteromorpha prolifera* (Müller) J. Agardh	p. 69	p. 59
79. *Enteromorpha ramulosa* (J. E. Smith) Hooker	p. 69	p. 60
80. *Enteromorpha salina* Kützing v. *polyclados* Kützing	p. 69	p. 56
81. *Entocladia flustrae* (Reinke) Batters	p. 65	----
82. *Entocladia viridis* Reinke	p. 65	p. 50
83. *Ernodesmis verticillata* (Kützing) Børgesen	----	p. 113 - pl. 1, fig. 2, pl. 6, fig. 10
84. *Gomontia polyrhiza* (Lagerheim) Bornet and Flahault	p. 64	p. 53
85. *Halicystis osterhoutii* L. R. and A. H. Blinks	----	p. 109 - pl. 7, fig. 3
86. *Halimeda discoidea* Descaisne v. *platyloba* Børgesen	p. 81	p. 179 - pl. 24, fig. 2
87. *Halimeda gracilis* Harvey v. *opuntiodes* Børgesen	----	p. 177
88. *Halimeda incrassata* (Ellis) Lamouroux	p. 81 - fig. 35	p. 181 - pl. 23, figs. 1, 4

TABLE 1. con't.

Taxon	Dawes (1974)	Taylor (1960)
89. *Halimeda monile* (Ellis and Solander) Lamouroux	p. 82	p. 182 - pl. 23, fig. 2
90. *Halimeda opuntia* (Linnaeus) Lamouroux	p. 82	p. 176 - pl. 23, fig. 3, pl. 24, fig. 1
91. *Halimeda scabra* Howe	----	p. 180 - pl. 25, figs. 10, 13, 14
92. *Halimeda simulans* Howe	----	p. 180 - pl. 24, fig. 4
93. *Halimeda tuna* (Ellis and Solander) Lamouroux f. *platydisca* (Descaisne) Barton	----	p. 178 - pl. 24, fig. 5
94. *Microdictyon boergesenii* Setchell	----	p. 120 - pl. 8, fig. 1
95. *Microdictyon curtissiae* Taylor	----	p. 121
96. *Monostroma oxyspermum* (Kützing) Doty	p. 69	p. 64
97. *Neomeris annulata* Dickie	----	p. 101 - pl. 5, fig. 5, pl. 6, figs. 4-6
98. *Ostreobium quecketii* Bornet et Flahault	p. 87	----
99. *Penicillus capitatus* Lamarck	p. 83 - fig. 36	p. 171 - pl. 21, fig. 2, pl. 25, fig. 4
100. *Penicillus dumetosus* (Lamouroux) Blainville f. *expansus* Børgesen	p. 84	p. 172 - pl. 21, fig. 4, pl. 25, fig. 15
101. *Penicillus lamourouxii* Descaisne v. *gracilis* A. and E. S. Gepp	p. 84	p. 172 - pl. 21, fig. 1, pl. 25, fig. 2
102. *Penicillus pyriformis* A. and E. S. Gepp f. *explanatus* Børgesen	----	p. 170 - pl. 21, figs. 3, 5, pl. 25, fig. 1
103. *Petrosiphon adhaerens* Howe	----	p. 117
104. *Phaeophila dendroides* (Crouan) Batters	p. 65	p. 48 - pl. 2, fig. 4

TABLE 1. con't.

Taxon	Dawes (1974)	Taylor (1960)
105. *Pringsheimiella scutata* (Reinke) Schmidt et Petrak	p. 66	----
106. *Protoderma marinum* Reinke	p. 66	p. 52
107. *Pseudocodium floridanum* Dawes et Mathieson	p. 84 - fig. 37	----
108. *Pseudotetraspora antillarum* Howe	p. 64	----
109. *Rhipocephalus oblongus* (Decaisne) Kützing	----	p. 173 - pl. 22, fig. 1, pl. 25, fig. 7
110. *Rhipocephalus phoenix* (Ellis and Solander) Kützing	p. 84	p. 174 - pl. 22, figs. 2, 5
111. *Rhizoclonium hookeri* Kützing	p. 90	p. 77 - pl. 2, fig. 5
112. *Rhizoclonium kochianum* Kützing v. *kerneri* (Stockmayer) Hamel	p. 90	----
113. *Rhizoclonium riparium* (Roth) Harvey v. *implexum* (Dillwyn) Rosenvinge	p. 90	p. 76
114. *Siphonocladus rigidus* Howe	----	p. 114 - pl. 6, fig. 7
115. *Siphonocladus tropicus* (Crouan) J. Agardh	----	p. 114 - pl. 7, fig. 1
116. *Stichococcus marinus* (Wille) Hazen	p. 66	----
117. *Struvea anastomosans* (Harvey) Piccone v. *caracasana* (Grunow ex Murray and Boodle) Collins	----	p. 122 - pl. 5, fig. 1, pl. 9, fig. 2
118. *Struvea elegans* Børgesen	----	p. 123 - pl. 9, figs. 1, 8, 9
119. *Struvea pulcherrima* (J. E. Gray) Murray and Boodle	p. 92	p. 123
120. *Udotea conglutinata* (Ellis and Solander) Lamouroux	p. 84 - fig. 38	p. 165 - pl. 20, fig. 3, pl. 25, fig. 5

TABLE 1. con't.

Taxon	Dawes (1974)	Taylor (1960)
121. *Udotea cyathiformis* Decaisne	p. 86	p. 166 - pl. 22, fig. 4
122. *Udotea flabellum* (Ellis and Solander) Lamouroux	p. 86	p. 168 - pl. 20, figs. 4, 5, pl. 25, fig. 3
123. *Udotea occidentalis* A. and E. S. Gepp	----	p. 169
124. *Udotea spinulosa* Howe	----	p. 167 - pl. 20, fig. 2, pl. 25, figs. 6, 16, 17
125. *Udotea sublittoralis* Taylor	----	p. 165 - pl. 22, fig. 6
126. *Udotea wilsoni* Gepp and Howe	----	p. 167 - pl. 25, fig. 18
127. *Ulva fasciata* Delile	p. 70	p. 66 - pl. 1, fig. 4
128. *Ulva lactuca* Linnaeus	p. 70 - fig. 27	p. 65
129. *Ulva profunda* Taylor	----	p. 67 - pl. 8, fig. 3
130. *Ulvella lens* Crouan	p. 66	p. 52 - pl. 2, fig. 7
131. *Valonia aegagropila* C. Agardh	----	p. 111 - pl. 7, fig. 6
132. *Valonia macrophysa* Kützing	----	p. 110 - pl. 2, fig. 6, pl. 7, fig. 4
133. *Valonia ocellata* Howe	----	p. 111 - pl. 9, figs. 6, 7
134. *Valonia utricularis* C. Agardh	----	p. 112 - pl. 9, fig. 10
135. *Valonia ventricosa* J. Agardh	p. 92	p. 110 - pl. 9, figs. 4, 5

IV. PHAEOPHYTA: KEY AND SPECIES REFERENCE LIST

Introductory Remarks

The Phaeophyta are confined almost exclusively to marine environments, and in tropical waters they occur largely in the sublittoral zone. This contrasts markedly with the situation in temperate regions where certain brown algae dominate the intertidal vegetation. In Florida, 34 genera and 66 species (Table 2, p. 34) have been recorded by Dawes (1974) and/or Taylor (1960), but only one genus - Padina - is calcified. Thus, brown algae are inconsequential in terms of sediment contributors.

A number of brown algae occur mostly commonly on rock (e.g. Cystoseira, Sargassum, Dictyota, Sporochnus) while others develop primarily in the aufwuchs community (e.g. Herponema, Myriotrichia, Eudesme). Two species of Sargassum (S. fluitans and S. natans) are known only in the pelagic state and comprise the vast bulk of the vegetation of the so-called Sargasso Sea which borders the Atlantic Coast of Florida.

The state of our systematic knowledge of Florida Phaeophyta is extremely uneven, and species concepts in a number of groups remain unclear. Critical studies are needed in such taxa as Sargassum, the families Ectocarpaceae and Myrionemataceae, among others, and the current uncertain state therefore often causes problems with species identification.

In the following key, the suggestions of Cardinal (1964) have been adopted in delimiting genera within the Ectocarpaceae. This places the occurrence of Herponema in Florida in doubt since H. tortugensis (Taylor) Taylor reportedly (Taylor 1960, p. 204) has band shaped chromoplasts (characteristic of Ectocarpus) rather than discoid chromoplasts (characteristic of Herponema). Further study appears necessary to settle the matter.

Generic Key to the Phaeophyta

1a. Vegetative portions of plants 1 cell wide throughout; composed of branched filaments without cortication or pseudoparenchymatous organization.

2a. Reproductive organs intercalary (within) in vegetative branches. . . . . .Bachelotia

2b. Reproductive organs terminal.

3a. Chromoplasts 1- several; elongate, simple or forked bands each with several pyrenoids. . .Ectocarpus (Figs. 85-87)

3b. Chromoplasts numerous; discoid, or rod shaped with a single pyrenoid.

4a. Basal filaments endobiotic, penetrating at least beneath the surface layer of cells. . . . . Herponema

4b. Basal filaments not penetrating the substrate.

5a. One or several zones of intercalary growth clearly delimited; branches commonly arising at right angles to the main axis. . . . . .Acinetospora

5b. Zones of intercalary growth not usually clearly delimited; branches arising at acute angles from main axis. . . . . Giffordia (Figs. 89-92)

1b. Vegetative portions of plants more than one cell wide, at least in part; of various form and with cortication or pseudoparenchymatous or parenchymatous construction present.

6a. Plants either entirely hollow or with hollow stems, bladders or other structures.

7a. Plants more or less prostrate, varying from hollow spheres to expanded, convoluted partially hollow structures with a smooth to perforated surface.

8a. Plant surface entire. . . . . .Colpomenia (Fig. 73)

8b. Plant surface clathrate (appearing lattice-like or perforated). . . . . Hydroclathrus

7b. Plants more or less erect, with partially to entirely hollow stems or bearing hollow bladders or other strucures.

9a. Plants composed of cylindrical to compressed stem-like portions; not differentiated into stems and spine-like, leaf-like, or pyramid-like foliar organs.

10a. Plants branched.

11a. Plants locally hollow; a single central axis clearly visible in younger portions of branches . . . . . .Nemacystus

11b. Plants hollow throughout except near the base of branches; central axis not discernible. . . Rosenvingea (Figs. 103-106)

10b. Plants unbranched. . . . *Scytosiphon* (Fig. 109)

9b. Plants composed of stems and spine-like, leaf-like, or pyramid-like portions.

12a. Stems bearing spine-like foliar organs; smaller branches inflated into hollow, bladder-like parts. . . . . *Cystoseira*

12b. Stems bearing leaf-like or pyramid-like foliar organs; bladders not borne within the stem.

13a. Foliar organs leaf-like. . . . . *Sargassum* (Figs. 107-108)

13b. Foliar organs pyramid-like. . . . . *Turbinaria* (Figs. 117)

6b. Plants without distinctly hollow structures.

14a. Plants forming thin, firm, more or less woody-appearing crusts. . . . . *Ralfsia* (Figs. 101-102)

14b. Plants erect or forming pulvinate (cushion-like) or tufted thalli which do not resemble thin woody-appearing crusts.

15a. Plants parenchymatous, without evidence of filamentous construction (examine in cross section) or of uniseriate branch tips; thalli more or less compressed, linear-strap shaped to broadly fan-shaped.

16a. Plants forming entire or lobed fan-shaped segments or consisting of a series of 1- several unbranched strap-like erect portions.

17a. Plants more or less fan-shaped.

18a. Plants usually calcified; growing margin inrolled. . . . . *Padina* (Figs. 93-98)

18b. Plants not calcified; margins not inrolled. . . . . *Lobophora* (Syn. *Pocockiella*) (Figs. 99-100)

17b. Plants composed of 1- several unbranched strap-like portions. . . . . *Petalonia*

16b. Plants branched or split into a number of distinct segments which may be linear to foliar or somewhat fan-shaped.

19a. Growth at branch tips from a single apical cell.

20a. Thallus structure throughout of one layer of large medullary cells and a single smaller celled cortical layer. . . *Dictyota* (Figs. 77-81)

20b. Medulla of more than one cell layer, at least near the margins. . . . . .Dilophus (Figs. 82-84)

19b. Growth at branch tips from a marginal row of many apical cells.

21a. Plants with a prominent midrib. . . . . Dictyopteris (Figs. 74-76)

21b. Plants lacking a midrib.

22a. Plants with conspicuous concentric zones of hairs and sporangia; commonly iridescent when submerged in living state.Stypopodium . . . . . .(Fig. 116)

22b. Plants lacking concentric zones of hairs and sporangia; not iridescent.Spatoglossum . . . . . .(Fig. 110)

15b. Plants with evidence of filamentous construction and/or with uniseriate branch tips; plants more or less cylindrical erect or forming tufts or pulvinate expanses.

23a. Plants forming pulvinate (cushion-like) or tufted thalli which rarely exceed 5 cm in extent.

24a. Growth from a conspicuous apical cell; branches largely covered with cells arranged in regular tiers. . . . . Sphacelaria (Figs. 111-113)

24b. Growth from the base of hair-like filaments (look for small cells at base); branches not covered with cells arranged in regular tiers.

25a. Erect filaments usually over 1.0 mm long. . . . . .Myriotrichia

25b. Erect filaments, if present, usually under 0.5 mm long.

26a. Plants prostrate, discoid and pulvinate; base distinctly discoid.

27a. Plants bearing elongate, hyaline paraphyses. . Ascocyclus (Figs. 71-72)

27b. Plants lacking elongate, hyaline paraphyses.

28a. Basal disc of 1 cell layer throughout. .Myrionema

28b. Basal disc of 2 cell layers, at least in part. . . .Hecatonema

26b. Plants tufted, more or less erect; base irregular, of congested filaments. . . . . Elachista

23b. Plants forming erect or spreading more or less cylindrical thalli which usually exceed 10 cm in length (reportedly 3-8 cm. in Stictyosiphon).

29a. Tips of branches with conspicuous tufts of free (separated) filaments.

30a. Sporangia confined to swollen portions of branch tips just below the tufts of filaments; holdfast fibrous. . . . . Sporochnus (Fig. 114)

30b. Sporangia scattered over the branches; holdfast discoid. . . . . Nereia

29b. Tips of branches lacking conspicuous tufts of free filaments.

31a. Branch tips composed of numerous axial filaments.

32a. Filaments of medulla firmly joined into a pseudoparenchymatous core. . . . . Cladosiphon (Figs. 68-70)

32b. Filaments of medulla easily separated from one another. . . . . Eudesme (Fig. 88)

31b. Branch tips composed of a single or only several (up to 4-5) axial filaments.

33a. Cross section showing a medulla of 4 large cells surrounded by a cortex of smaller cells.Stictyosiphon

33b. Cross section showing a medulla of numerous cells not markedly larger than the cortex.

34a. Branch tips with a single axial filament; plants slimy and soft. . . . . .Nemacystus

34b. Branch tips with several axial filaments; plants stiff and relatively brittle. . . . . Stilophora (Fig. 115)

TABLE 2. Phaeophyta Species Reference List (Records of species occurrence in Florida as reported in Dawes 1974 and Taylor 1960).

Taxon	Dawes (1974)	Taylor (1960)
1. *Acinetospora crinita* (Carmichael) Kornmann	p. 96	----
2. *Ascocyclus orbicularis* (J. Agardh) Magnus	p. 106	----
3. *Bachelotia antillarum* (Grunow) Gerloff	p. 96	p. 197, as *Pylaiella* (Syn.: *Bachelotia fulvescens*, p. 198)
4. *Cladosiphon occidentalis* Kylin	p. 105 - fig. 47	p. 248
5. *Colpomenia sinuosa* Derbès and Solier	p. 110	p. 260 - pl. 36, fig. 1
6. *Cystoseira myrica* Gmelin) J. Agardh	----	p. 267
7. *Dictyopteris delicatula* Lamouroux	p. 100	p. 227 - pl. 33, fig. 3
8. *Dictyopteris justii*	----	p. 226 - pl. 33, fig. 1
9. *Dictyopteris plagiogramma* (Montagne) Vickers	----	p. 229 - pl. 33, fig. 2
10. *Dictyota bartayresii* Lamouroux	----	p. 219 - pl. 30, fig. 2
11. *Dictyota cervicornis* Kützing	p. 100	p. 22 - pl. 31, fig. 2
12. *Dictyota ciliolata* Kutzing v. *bermudensis* Taylor	p. 100	p. 223 - pl. 32, fig. 3, pl. 59, fig. 1
13. *Dictyota dentata* Lamouroux	p. 100	p. 224 - pl. 30, figs. 4, 5
14. *Dictyota dichotoma* (Hudson) Lamouroux v. *menstrualis* Hoyt	p. 101 - fig. 43	p. 218 pl. 31, fig. 5
15. *Dictyota divaricata* Lamouroux	p. 101 - fig. 44	p. 221 - pl. 31, figs. 3, 4
16. *Dictyota indica* Sonder in Kützing	----	p. 221 - pl. 31, fig. 1
17. *Dictyota linearis* (C. Agardh) Greville	p. 102	----

TABLE 2 con't.

Taxon	Dawes (1974)	Taylor (1960)
18. *Dilophus alternans* J. Agardh	p. 102	p. 216 - pl. 30, fig. 3
19. *Dilophus guineensis* (Kützing) J. Agardh	----	p. 216 - pl. 30, fig. 1
20. *Ectocarpus dasycarpus* Kuckuck	p. 97	----
21. *Ectocarpus elachistaeformis* Heydrich	p. 97	p. 202
22. *Ectocarpus intermedius* Kützing	p. 97	p. 200 as *E. confervoides*
23. *Ectocarpus siliculosus* (Dillwyn) Lyngbye	p. 98	p. 199
24. *Elachistea minutissima* Taylor	----	p. 245 - pl. 29, fig. 11
25. *Eudesme zosterae* (J. Agardh) Kylin	p. 106, as *Cladosiphon*	p. 247
26. *Giffordia conifera* (Børgesen) Taylor	p. 98	----
27. *Giffordia indica* (Sonder) Papenfuss et Chihara	p. 98	p. 207 - pl. 29, fig. 10 as *G. duchassaigniana*
28. *Giffordia mitchellae* (Harvey) Hamel	p. 98	p. 206 - pl. 29, figs. 1, 2
29. *Giffordia rallsiae* (Vickers) Taylor	p. 99	----
30. *Hecatonema floridana* (Taylor)	----	p. 241
31. *Herponema tortugensis* (Taylor)	----	p. 204
32. *Hydroclathrus clathratus* (Bory) Howe	----	p. 261 - pl. 36, fig. 5
33. *Lobophora variegata* (Lamouroux) Womersley	p. 102	p. 231 - pl. 33, fig. 4 (as *Pocockiella*)
34. *Myrionema strangulans* Greville	p. 106	p. 240

TABLE 2 con't.

Taxon	Dawes (1974)	Taylor (1960)
35. *Myriotrichia occidentalis* Børgesen	p. 110	----
36. *Myriotrichia subcorymbosa* (Holden) Bomquist	p. 111	----
37. *Nemacystus howei* (Taylor) Kylin	p. 107	p. 249 - pl. 29, figs. 12-14
38. *Nereia tropica* (Taylor) Taylor	----	p. 252 - pl. 29, fig. 1
39. *Padina gymnospora* (Kützing) Vickers	----	p. 237
40. *Padina pavonica* (Linnaeus) Thivy	----	p. 234
41. *Padina sanctae - crucis* Børgesen	----	p. 237 - pl. 34, fig. 2
42. *Padina vickersiae* Hoyt	p. 103 - fig. 45	p. 236 - pl. 34, fig. 1
43. *Petalonia fascia* v. *caespitosa* (J. Agardh) Taylor	----	p. 258
44. *Ralfsia expansa* J. Agardh	----	p. 243
45. *Rosenvingea floridana* (Taylor) Taylor	----	p. 262 - pl. 29, figs. 7, 8
46. *Rosenvingea intricata* (J. Agardh) Børgesen	p. 111 - fig. 50	p. 262 - pl. 36, fig. 2
47. *Rosenvingea sanctae - crucis* Børgesen	----	p. 263
48. *Sargassum acinarium* (Linnaeus) C. Agardh	----	p. 271
49. *Sargassum cymosum* C. Agardh	----	p. 278 - pl. 38, fig. 4
50. *Sargassum filipendula* C. Agardh	p. 112 - fig. 51	p. 270 - pl. 37, fig. 3, pl. 40 fig. 2
51. *Sargassum fluitans* Børgesen	p. 112	p. 281 - pl. 39, fig. 2, pl. 40, fig. 7
52. *Sargassum hystrix* J. Agardh	p. 114	p. 279 - pl. 37, fig. 1, pl. 38, fig. 2, pl. 40, fig. 6
53. *Sargassum natans* (Linnaeus) J. Meyen	p. 114	p. 281 - pl. 37, fig. 2, pl. 40, figs. 3, 8

TABLE 2 con't.

Taxon	Dawes (1974)	Taylor (1960)
54. *Sargassum polyceratium* Montagne v. *ovatum* (Collins) Taylor	p. 114	p. 276 - pl. 40, fig. 1
55. *Sargassum pteropleuron* Grunow	p. 115 - fig. 52	p. 274 - pl. 39, fig. 1, pl. 40, figs. 4, 9
56. *Sargassum vulgare* C. Agardh v. *foliosissimum* (Lamouroux) J. Agardh	----	p. 273 - pl. 38, fig. 1, pl. 40, fig. 5
57. *Scytosiphon lomentaria* (Lyngbye) C. Agardh	----	p. 259
58. *Spatoglossum schroederi* (Mertens) Kützing	p. 104 - fig. 46	p. 225 - pl. 33, fig. 5
59. *Sphacelaria furcigera* Kützing	p. 99	p. 210 - pl. 29, fig. 5
60. *Sphacelaria tribuloides* Meneghini	p. 99	p. 211 - pl. 29, fig. 6
61. *Sporochnus bolleanus* Montagne	p. 108	p. 253 - pl. 35, figs. 2, 3
62. *Sporochnus pedunculatus* (Hudson) C. Agardh	p. 109 - fig. 49	p. 253 - pl. 35, figs. 4, 5
63. *Stictyosiphon subsimplex* Holden	p. 110	----
64. *Stilophora rhizoides* (Ehrhart) J. Agardh	p. 107 - fig. 48	p. 250
65. *Stypopodium zonale* (Lamouroux) Papenfuss	----	p. 232 - pl. 28, fig. 1
66. *Turbinaria turbinata* (Linnaeus) Kuntze	----	p. 285 - pl. 39, figs. 3-5

V. RHODOPHYTA: KEY AND SPECIES REFERENCE LIST

Introductory Remarks

The vast majority of Rhodophyta occur only in marine environments, and in tropical and subtropical regions, red algae grow both in the intertidal and sublittoral zones. A total of 93 genera and 248 species (Table 3, p. 53) have been reported for Florida waters by Dawes (1974) and/or Taylor (1960). Although relatively few red algae are calcified, members of the family Corallinaceae (see Kylin 1956) are of considerable geological significance (see Ginsburg et al. 1972, Hedgpeth 1957) in terms of coral reef building. In present day reefs, coralline algae function as the chief cementing agents, binding coral skeletons and other debris into a consolidated reef.

The state of systematic knowledge of red algae, like that of brown algae, is very uneven, and critical studies are needed on a number of taxa with representatives in Florida waters. In the following key, the suggestions of Wynne and Taylor (1973) have been incorporated regarding the use of the generic names Agardhiella, Neoagardhiella, and Soleria. Similarly, following Taylor (1960, p. 449), the generic name Gracilariopsis is referred to Gracilaria. Finally, taxa of the Acrochaetiaceae have not been dealt with at the generic level since several recent studies (Woelkerling 1971, 1973) indicate that Florida representatives of the group must be examined critically before generic realignment of these taxa is effected. Older generic names for the Acrochaetiaceae, however, have been used in Table 3.

Rhodophyta: Key to Genera

1a. Plants calcified (i.e., encrusted with lime; if in doubt test tissue with dilute acid; if lime is present CO_2 bubbles will be released).

2a. Plants crustose, forming prostrate expanses on the substratum.

3a. Plants more or less loosely attached to substrate by rhizoids growing from ventral surface; sporangia on surface of thallus. . . . . Peyssonnelia

3b. Plants firmly attached to substrate, ventral rhizoids absent; sporangia sunken in conceptacles.

4a. Roof of sporangial conceptacles perforated by numerous pores.

5a. Vegetative portion of thallus largely or entirely 1 cell thick. . . . . .Melobesia

5b. Vegetative portion of thallus more than 1 cell thick. . . . . Lithothamnium

4b. Roof of sporangial conceptacles perforated by a single pore.

6a. Vegetative portions 1-3 cells thick (rarely to 10 cells thick. . . . . .Fosliella

6b. Vegetative portions of numerous cell layers.

7a. Heterocysts (cells which are conspicuously larger and often thicker walled than ordinary vegetative cells) present. . . . . Goniolithon

7b. Heterocysts absent. . . . . .Lithophyllum

2b. Plants erect, upright or ascending.

8a. Plant body distinctly segmented; joints articulate, uncalcified.

9a. Conceptacles scattered over the surface of the segments. . . . . .Amphiroa

9b. Conceptacles marginal or terminal.

10a. Branching strictly dichotomous. . . . . Jania (Figs. 257-259)

10b. Branching opposite, alternate, or irregular. . . . . Corallina (Figs. 181-183)

8b. Plant body not differentiated into calcified segments and uncalcified joints.

11a. Branches with apical depressions. . . . . .Galaxaura (Figs. 216-218)

11b. Branches lacking apical depressions.

12a. Plants stony, rigid.

13a. Sporangial conceptacles perforated by numerous pores. . . . . .Lithothamnium

13b. Sporangial conceptacles perforated by single pore.

14a. Heterocysts present. . Goniolithon

14b. Heterocysts absent. . Lithophyllum

12b. Plants soft, flexible.

15a. Outer cortex filamentous; gland cells absent. . . . . .Liagora (Figs. 265-269)

15b. Outer cortex parenchymatous; gland cells present. . . . . Titanophora

1b. Plants not calcified; without encrustations of lime.

16a. Plants crustose, forming a thin expanse on the substrate.

17a. Thallus mostly 1 cell thick, usually epiphytic. . . . . .Erythrocladia

17b. Thallus more than 1 cell thick, usually on rock.

18a. Plants firmly adherent; tetrasporangia irregularly zonate and borne in conceptacles. . .Hildenbrandia

18b. Plants attached by rhizoids on underside; tetrasporangia cruciate and borne in a superficial layer. . . . . .Peyssonnelia

16b. Plants generally erect, not forming a crustose expanse of cells.

19a. Plants composed of uniseriate filaments; never bearing groups of cells about the nodes, but sometimes with older cells corticated by rhizoids.

20a. Pit connections between cells absent.

21a. Filaments simple. . . . . Erythrotrichia

21b. Filaments branched.

22a. Filaments procumbent, creeping horizontally on the substrate. . . . . .Erythrocladia

22b. Filaments erect.

23a. Cells longer than broad, greenish gray in color. . . . . .Asterocytis (Fig. 128)

23b. Cells more or less isodiametric or shorter than broad, usually reddish in color. . . . . Goniotrichum (Figs. 223-226)

20b. Pit connections between cells present.

24a. Plants attached to substrate by means of single cells or by multicellular filaments which may or may not become congested; without special hapteral cells; cells with 1 - several chromoplasts. . . . . Audouinella-Colaconema complex (Family Acrochaetiaceae) (Figs. 129-131)

24b. Plants attached to substrate by means of special hapteral cells; cells of filaments with numerous discoid chromoplasts.

25a. Plants showing a clear distinction between larger indeterminate branch axes and shorter determinate branches arranged in a whorled fashion.

26a. Whorl-branches in groups of 3. . . . . Crouania (Figs. 194-196)

26b. Whorl-branches in groups of 4-5. . Wrangelia (Figs. 322-325)

25b. Plants without a clear distinction between indeterminate axes and determinate branchlets.

27a. Branching opposite and/or secund.

28a. Ultimate branches arranged in a secund series. . . . . .Gymnothamnion

28b. Ultimate branches not secund.

29a. Gland cells present; tetrasporangia curciate. . . . . Antithamnion . . (Figs. 121-124)

29b. Gland cells absent; tetrasporangia tetrahedral. . . . . Spermothamnion (Figs. 312-315)

27b. Branching alternate, dichotomous, trichotomous, or irregular.

30a. Cells macroscopic, commonly over 800 µm long. . . . . Griffithsia (Figs. 234-236)

30b. Cells microscopic, rarely over 600 µm long.

31a. Asexual reproductive spores borne in chains. . Seirospora . . .(Figs. 304-305)

31b. Asexual reproductive spores borne singly.

32a. Branching regularly alternate, with a branch arising from each cell of the main axis, at least above. .Callithamnion (Figs. 143-145)

32b. Branching not regularly alternate. . . . . Spermothamnion (Figs. 312-315)

19b. Plants more than one cell broad; minimally bearing parenchyma-like whorls of cells about the nodes.

33a. Thallus hollow throughout or with hollow structures or parts.

34a. Thallus differentiated into solid, wiry axes and inflated grape-like branches. . . . . .Botryocladia (Figs. 135-137)

34b. Thallus of more or less uniform structure throughout.

35a. Plants entirely hollow; without evidence of internal septations at the base of branches or elsewhere.

36a. Plants forming densely branched cushions up to 5 cm tall; branches firm, almost wiry. . . . . Coelothrix (Figs. 178-180)

36b. Plants 5-30 cm tall, not forming densely branched cushions; branches soft, almost gelatinous.

37a. Upper portions of plant plumose (feather-like). . . . . Falkenbergia . . .(Asparagopsis stage) (Figs. 125-127)

37b. Upper portions of plant not plumose. . . . . Chrysymenia (Figs. 166-168)

35b. Plants septate, at least at the base of branches.

38a. Plants regularly constricted into series of more or less moniliform segments by regular internal septation. . . . . Champia

38b. Plants not constricted into moniliform segments; septae mostly at the base of branches. . . . . . Lomentaria (Figs. 270-274)

33b. Thallus solid; without a distinctly hollow internal structure.

39a. Branch tips with apical depressions.

40a. Plants showing (in cross section) a distinct central axis surrounded by 5 pericentral cells. . . . . Chondria (Figs. 162-165)

40b. Plants in cross section without a distinct central axis and without pericentral cells. . . . . Laurencia (Figs. 263-264)

39b. Branch tips without apical depressions.

41a. Vegetative portions of plants predominantly cylindrical or only very slightly compressed or only locally flattened such as at points of branching; axes more or less circular in cross section. [41b is on page 48].

42a. Plants polysiphonous; pericentral cells externally visible or evident in cross sections of at least the younger portions of branches. [42b is on page 45].

43a. Ultimate branches anastomosing to form a mesh-like network.

44a. Network supported by a distinct axis with 4 pericentral cells. . . . . Dictyurus (Figs. 198-202)

44b. Network without a central supporting axis; polysiphonous structure evident only in branches bearing reproductive structures. . . . . Halodictyon

43b. Ultimate branches not anastomosing to form a mesh-like network.

45a. Plants bearing monosiphonous, pigmented branchlets or bearing polysiphonous branchlets which grade into monosiphonous, pigmented multicellular segments near the tips.

46a. Younger branches with externally visible, transversely divided pericentral cells. . .Bostrychia (Figs. 132-134)

46b. Younger branches corticated or with externally visible non-transversely divided pericentral cells.

47a. Pericentral cells 4.

48a. Plants without cortication. . . . . Murrayella (Figs. 289-294)

48b. Plants more or less corticated.

49a. Trichoblasts absent. . . . . .Cottoniella (Figs. 169-177)

49b. Trichoblasts or their scar cells present.

50a. Trichoblasts distichous, laterally branched; tetrasporangial branches lacking trichoblasts. . . . . .Lophocladia (Figs. 275-279)

50b. Trichoblasts spirally branched; tetrasporangial branches with long, unbranched trichoblasts. . . . .Wrightiella (Figs. 326-328)

47b. Pericentral cells 5 or more.

51a. Apices of monosiphonous filaments mucronate. . . . . Brongniartella

51b. Apices of monosiphonous filaments rounded to acute.

52a. Entire plants densely beset with monosiphonous branches on all sides. . . . . Dasya (Fig. 197)

52b. Monosiphonous branches largely confined to younger portions of the plants. . . . . Heterosiphonia (Figs. 245-251)

45b. Plants polysiphonous throughout except for apical cells; with or without colorless monosiphonous trichoblasts.

53a. Plants entirely or almost entirely corticated in a parenchymatous fashion; filamentous nature of cortication completely obscured.

54a. Pericentral cells visible only in the shorter lateral branches. . . . .Digenia (Figs. 203-205)

54b. Pericentral cells visible throughout the plant.

55a. Pericentral cells 7-9; branchlets primarily in 2-4 ranks. . Bryothamnion (Figs. 138-142)

55b. Pericentral cells 5; branching more or less radial.

56a. Axes bearing wart-like branchlets. . . . . Acanthophora (Figs. 118-120)

56b. Axes bearing cylindrical branchlets. . . . . Chondria (Figs. 163-165)

53b. Plants ecorticate or corticated to a greater or lesser extent in a rhizoidal fashion; filamentous nature of cortication evident.

57a. Plants with 3 pericentral cells. . . . . Falkenbergia (Figs. 209-213)

57b. Plants with 4 or more pericentral cells.

58a. Plants with a dorsiventral organization; erect axes unbranched or sparingly branched and sharply determinate.

59a. Branching endogenous; erect axes occasionally bearing lateral branches. . . . . .Lophosiphonia (Figs. 280-283)

59b. Branching exogenous; erect axes unbranched.Herposiphonia (Figs. 241-244)

58b. Plants with a radial organization; erect axes branched and not all determinate.

60a. Main axes bearing numerous short more or less determinate axes. . . . . Bryocladia (Figs. 135-137)

60b. Main axes gradually giving rise to laterals without sharp distinctions. . . . . Polysiphonia (Figs. 300-302)

42b. Plants without external or internal evidence of polysiphonous construction.

61a. Central axis clearly visible throughout the plant, at least in cross section.

62a. Branches with whorls of spines at the nodes. . . . . .Centroceras (Figs. 153-157)

62b. Branches lacking whorls of spines.

63a. Central axis surrounded by a cortex of branched monosiphonous filaments which are often whorled.

64a. Cortex very loosely organized; outer cortical cells without unicellular hairs. . . . . Acrosymphyton

64b. Cortex densely compact; outer cortical cells commonly bearing unicellular hairs. . . . Naccaria

63b. Central axis corticated by groups of parenchyma-like cells.

65a. Sporangia borne in marginal stichidia; cortication not arising at the nodes. Cyclospora

65b. Sporangia not in stichidia; cortication arising from the nodes.

66a. Main axes completely corticated; ultimate branches corticated only by bands of cells about the nodes. . . . . Spyridia (Figs. 316-318)

66b. Main axes and lateral branches more or less uniformly corticated with the cortication in most cases restricted to the nodes. . . . . Ceramium (Figs. 158-161)

61b. Central axis not clearly visible throughout the plant.

67a. Medulla clearly filamentous.

68a. Plants clavate (club-shaped) or irregularly constricted.

69a. Erect axes simple or rarely forked; plants clavate. . . . . Corynomorpha (Figs. 184-187)

69b. Erect axes branched; plants irregularly constricted. Catenella (Figs. 149-152)

68b. Plants more or less cylindrical; erect axis usually repeatedly branched.

70a. Plants very soft and gelatinous.

71a. Cortex filamentous. . . . . Helminthocladia

71b. Cortex parenchymatous.

72a. Epidermis composed solely of tightly compacted, enlarged cells. . . . . Scinaia (Figs. 306-307)

72b. Epidermis composed of loosely compacted cells which are not noticeably enlarged. . . Gloiopholea

70b. Plants firm to cartilaginous.

73a. Tetrasporangia cruciate . . . . . Gigartina

73b. Tetrasporangia zonate.

74a. Branches constricted at the base, never bearing spines; cystocarps immersed in thallus . . . Soliera (syn:Agardhiella) . . . . . (Figs. 308-311)

74b. Branches not constricted at the base, but commonly bearing spines; cystocarps in stalk-like papillar. . . . .Eucheuma . . . . . (Figs. 206-208)

67b. Medulla composed of mixed filaments and parenchyma or entirely parenchymatous.

75a. Branches beset with monosiphonous ramuli. . . . . Dasyopsis

75b. Branches lacking monosiphonous ramuli.

76a. Plants fleshy to cartilaginous; main axes generally 5 mm or more in diameter.

77a. Tetrasporangia zonate . . . . . .Hypnea (Figs. 252-253)

77b. Tetrasporangia cruciate . . . . Gracilaria (incl. Gracilariopsis) . . . . . (Figs. 227-230)

76b. Plants wiry; main axes generally under 5 mm in diameter.

78a. Rhizines (slender thick-walled filaments) present.

79a. Rhizines mostly in inner medulla; cystocarps with a single cavity . . . . . .Pterocladia

79b. Rhizines mostly in outer medulla; cystocarps with two cavities. . .Gelidium

78b. Rhizines absent.

80a. Branch tips multiaxial.

81a. Sporangia zonate; cells of central medulla thin-walled. . . . . .Wurdemannia . . .(Figs. 329-332)

81b. Sporangia cruciate or irregular; cells of central medulla somewhat thick-walled. . . . . .Gelidiopsis

80b. Branch tips with a single apical cell. . . . . .Gelidiella (Figs. 219-222)

41b. Vegetative portions of plants predominantly compressed or flattened, commonly forming strap-like or blade-like expanses.

82a. Plants with blades which are largely 1-2 cells thick.

83a. Blades with an evident midrib or veins.

84a. Blade apices terminated in a monosiphonous hair; basal creeping portions of plant polysiphonous. . . . . Taenioma (Figs. 319-320)

84b. Blade apices not ending in a monosiphonous hair; basal portions not polysiphonous.

85a. Blades unbranched foliar expanses. . . . . Grinnellia (Fig. 237)

85b. Blades branched, strap-like to foliar.

86a. Blades with veins but without a raised midrib; branching lateral.Cryptopleura

86b. Blades with a raised midrib in part at least; branching from the midrib.

87a. Tetrasporangia developing on or along the midrib. . . . . .Hypoglossum (Figs. 254-256)

87b. Tetrasporangia formed on the lateral part of the blade. . . Caloglossa (Figs. 146-148)

83b. Blades without an evident midrib.

88a. Pit connections present between cells.

89a. Blades forming partially net-like grids and partially entire expanses. . Martensia (Figs. 284-285)

89b. Blades entire throughout. . . Nitophyllum (Fig. 299)

88b. Pit connections absent. . . . . .Porphyra (Fig. 303)

82b. Blades mostly more than 2 cells thick.

90a. Blades in cross section showing a distinct midrib bearing a central axis surrounded by 5 pericentral cells.

91a. Branching opposite. . . . . Enantiocladia

91b. Branching alternate.

92a. Blades corticated throughout; margins toothed. . . . . Vidalia (Fig. 321)

92b. Blades corticated only along the midrib; margins not toothed. . . . Amansia

90b. Blades in cross section without a midrib bearing a central axis surrounded by 5 pericentral cells.

93a. Blades showing a distinct central axis (no midrib); sporangia in marginal stichidia. . . . . .Cyclospora

93b. Blades without a distinct central axis; sporangia, where known, not in marginal stichidia.

94a. Medulla parenchymatous throughout.

95a. Medulla composed entirely of large, more or less isodiametric cells.

96a. Sporangia in nemathecial sori; cortex with distinct anticlinal organization. . . . Fauchea

96b. Sporangia scattered over the thallus; cortex without an obvious anticlinal organization. . . . . Gracilaria and Gracilariopsis (Figs. 227-230)

95b. Medulla composed of large cells interspersed with small cells. . Agardhinula

94b. Medulla filamentous or a mixture of cells and filaments or partly hollow.

97a. Epidermis composed in part of enlarged cells (i.e., cells much larger in size than those of subepidermal layers). . . . . .Scinaia . . .(Figs. 306-307)

97b. Epidermis composed of cells not noticeably larger than those of the subepidermal layers.

98a. Cells of outer cortex arranged in more or less anticlinal (radiating from the center) rows.

99a. Central axis visible in younger parts of plant. . .*Catenella* (Figs. 149-152)

99b. Central axis absent.

100a. Sporangia zonate.

101a. Plants repeatedly branched; branches strap-like. *Eucheuma*

101b. Plants foliose, at most cleft or lobed. . . . . *Meristotheca* (Figs. 286-288)

100b. Sporangia cruciate; cystocarps immersed in the thallus. . . . . *Grateloupia* . . (Figs. 231-233)

98b. Cells of outer cortex not arranged in anticlinal rows.

102a. Medulla containing some or less star shaped cells.

103a. Tetrasporangia scattered over the thallus; medulla of scattered filaments with few stellate cells. . . . . *Halymenia* . . (Figs. 238-240)

103b. Tetrasporangia largely confined to special marginal leaflets; medulla congested, with numerous stellate cells. *Cryptonemia* . . . . (Fig. 193)

102b. Medulla lacking star-shaped cells.

104a. Gland cells present in inner cortex; cells of outer cortex 1-3 layers, abruptly and distinctly smaller than those of inner cortex. . . . . *Cryptarachne* . . (Figs. 188-192)

104b. Gland cells absent; cells of outer cortex small, gradually giving way to a large-celled inner cortex.

105a. Sporangia zonate; medulla composed of loosely organized filaments. . *Neoagardhiella* (Figs. 294-298)

105b. Sporangia cruciate; medulla of firmly compact filaments or a mixture of cells and filaments. . *Kallymenia* (Figs. 260-262)

TABLE 3. Rhodophyta Species Reference List (Records of species occurrence in Florida as reported by Dawes 1974 and Taylor 1960).

Taxon	Dawes (1974)	Taylor (1960)
1. *Acanthophora muscoides* (Linnaeus) Bory	p. 151	p. 619 - pl. 72, fig. 3
2. *Acantophora spicifera* (Vahl) Børgesen	p. 151 - fig. 74	p. 620 - pl. 71, fig. 3, pl. 72, figs. 1, 2
3. *Acrochaetium avrainvilleae* Børgesen	p. 118	----
4. *Acrochaetium leptonema* (Rosenvinge) Børgesen	----	p. 308
5. *Acrochaetium sargassi* Børgesen	p. 118	p. 306
6. *Acrochaetium seriatum* Børgesen	p. 118	----
7. *Acrochaetium thuretii* (Bornet) Collins et Hervey	p. 118	----
8. *Acrosymphyton caribaeum* (J. Agardh) Sjostedt	----	p. 366
9. *Agardhinula browneae* (J. Agardh) Detoni	----	p. 482
10. *Amansia multifida* Lamouroux	----	p. 608 - pl. 70, fig. 5
11. *Amphiroa brasiliana* Decaisne	----	p. 405 - pl. 48, fig. 2
12. *Amphiroa fragilissima* (Linnaeus) Lamouroux	p. 122 - fig. 54	p. 403 - pl. 47, figs. 1, 2
13. *Amphiroa rigida* Lamouroux v. *antillana* Børgesen	p. 122	p. 404 - pl. 47, fig. 3, pl. 48, fig. 1
14. *Amphiroa tribulus* (Ellis and Solander) Lamouroux	----	p. 406 - pl. 47, figs. 4, 5
15. *Antithamnion plumula* (Ellis) Thuret	----	p. 500
16. *Asterocytis ramosa* (Thwaites) Gobi	p. 117	p. 287
17. *Bostrychia binderi* Harvey	p. 152 - fig. 75	p. 598
18. *Bostrychia calliptera* Montagne	p. 152	----

TABLE 3 con't.

Taxon	Dawes (1974)	Taylor (1960)
19. *Bostrychia montagnei* Harvey	----	p. 598 - pl. 74, fig. 1
20. *Bostrychia moritziana* (Sonder) J. Agardh	p. 153	p. 596
21. *Bostrychia radicans* Montagne f. *moniliforme* Post.	p. 153	p. 595
22. *Bostrychia rivularis* Harvey	----	p. 595
23. *Bostrychia scorpioides* (Gmelin) Montagne	p. 153	p. 597
24. *Bostrychia tenella* (Vahl) J. Agardh	p. 154	p. 599
25. *Botryocladia occidentalis* (Børgesen) Kylin	p. 141 - fig. 66	p. 483 - pl. 64, fig. 1
26. *Botryocladia pyriformis* (Børgesen) Kylin	----	p. 483 - pl. 64, fig. 2
27. *Brongniartella mucronata* (Harvey) Schmitz	p. 154	p. 590 - pl. 66, figs. 11, 12
28. *Bryocladia cuspidata* (J. Agardh) DeToni	p. 154	p. 586
29 *Bryocladia thyrsigera* (J. Agardh) Schmitz	----	p. 585
30. *Bryothamnion seaforthii* (Turner) Kützing f. *imbricata* J. Agardh	----	p. 587 - pl. 73, fig. 3
31. *Bryothamnion triquetrum* (Gmelin) Howe	----	p. 587 - pl. 72, fig. 6, pl. 73, fig. 4
32. *Callithamnion byssoides* Arnott ex Hooker	p. 143	----
33. *Callithamnion cordatum* Børgesen	p. 143	----
34. *Callithamnion halliae* Collins	----	p. 505
35. *Callithamnion roseum* (Roth) Harvey	p. 143	----
36. *Caloglossa leprieurii* (Montagne) J. Agardh v. *hookeri* (Harvey) Post.	p. 149 - fig. 72	p. 544 - pl. 68, fig. 1
37. *Catenella repens* (Lightfoot) Batters	p. 133 - fig. 61	p. 462 - pl. 66, fig. 13

TABLE 3. con't.

Taxon	Dawes (1974)	Taylor (1960)
38. *Centroceras clavulatum* (C. Agardh) Montagne	p. 143 - fig. 68	p. 537
39. *Ceramium brevizonatum* H. E. Petersen v. *caraibica* Petersen and Børgesen	----	p. 527 - pl. 67, figs. 7-9
40. *Ceramium byssoideum* Harvey	p. 143 - fig. 69	p. 528 - pl. 67, figs. 1-3
41. *Ceramium codii* (Richards) Feldmann - Mazoyer	p. 145	----
42. *Ceramium corniculatum* Montagne	p. 145	p. 530
43. *Ceramium diaphanum* (Lightfoot) Roth f. *strictoides* H. E. Petersen	----	p. 532
44. *Ceramium fastigiatum* (Roth) Harvey f. *flaccida* H. E. Petersen	p. 145	p. 526 - pl. 67, figs. 4-6
45. *Ceramium floridanum* J. Agardh	p. 145	p. 534
46. *Ceramium nitens* (C. Agardh) J. Agardh	----	p. 535 - pl. 66, fig. 14
47. *Ceramium strictum* (Kützing) Harvey	p. 146	p. 530
48. *Ceramium subtile* J. Agardh	p. 146	p. 527 - pl. 65, figs. 5, 6
49. *Ceramium tenuissimum* (Lyngbye) J. Agardh	----	p. 531
50. *Champia parvula* (C. Agardh) Harvey	p. 139 - fig. 65	p. 490 - pl. 61, fig. 4
51. *Champia salicornoides* Harvey	----	p. 491 - pl. 61, fig. 5
52. *Chondria atropurpurea* Harvey	----	p. 613
53. *Chondria baileyana* (Montagne) Harvey	----	p. 614
54. *Chondria cnicophylla* (Melvill) DeToni	p. 154	p. 614 - pl. 74, fig. 3
55. *Chondria collinsiana* Howe	p. 154	p. 617
56. *Chondria dasyphylla* (Woodward) C. Agardh	p. 155	p. 616

TABLE 3. con't.

Taxon	Dawes (1974)	Taylor (1960)
57. *Chondria floridana* (Collins) Howe	p. 155	p. 616 - pl. 74, fig. 4
58. *Chondria leptacremon* (Melvill) DeToni	p. 155	p. 615
59. *Chondria littoralis* Harvey	p. 155	p. 612
60. *Chondria polyrhiza* Collins and Hervey	----	p. 617
61. *Chondria sedifolia* Harvey	p. 155	p. 615
62. *Chondria tenuissima* (Goodenough and Woodward) C. Agardh	p. 156 - fig. 76	p. 613
63. *Chrysymenia enteromorpha* Harvey	p. 141	p. 479 - pl. 62, fig. 2
64. *Chrysymenia halymenioides* Harvey	----	p. 479 - pl. 62, fig. 1
65. *Coelothrix irregularis* (Harvey) Børgesen	----	p. 488 - pl. 45, fig3, pl. 46, fig. 4
66. *Compsopogon caeruleus* (Balbis) Montagne	----	p. 296
67. *Corallina cubensis* (Montagne) Kützing	p. 122	p. 409 - pl. 50, figs. 3, 4
68. *Corynomorpha clavata* (Harvey) J. Agardh	----	p. 429 - pl. 64, fig. 3
69. *Cottoniella filamentosa* (Howe) Børgesen	----	p. 550
70. *Crouania attenuata* (Bonnemaison) J. Agardh	p. 146	p. 495
71. *Crouania pleonospora* Taylor	----	p. 496
72. *Cryptarachne agardhii* (Harvey) Kylin	----	p. 480 - pl. 63, fig. 2
73. *Cryptarachne planifrons* (Melvill) Kylin	----	p. 481 - pl. 63, fig. 1
74. *Cryptonemia crenulata* J. Agardh	----	p. 427 - pl. 58, fig. 4
75. *Cryptonemia luxurians* (Mertens) J. Agardh	----	p. 428 - pl. 58, fig. 3
76. *Cryptopleura fimbriata* (Greville) Kützing	p. 150	----
77. *Cyclospora curtissiae* J. Agardh	----	p. 546

TABLE 3. con't.

Taxon	Dawes (1974)	Taylor (1960)
78. *Dasya caraibica* Børgesen	----	p. 560
79. *Dasya collinsiana* Howe	----	p. 558
80. *Dasya corymbifera* J. Agardh	p. 164	p. 559
81. *Dasya crouaniana* J. Agardh	----	p. 561 - pl. 71, fig. 1
82. *Dasya harveyi* Ashmead	----	p. 561
83. *Dasya mollis* Harvey	----	p. 562
84. *Dasya pedicellata* (C. Agardh) C. Agardh	p. 165 - fig. 80	p. 562
85. *Dasya ramosissima* Harvey	----	p. 561
86. *Dasya rigidula* (Kützing) Ardissone	----	p. 558 - pl. 72, fig. 4
87. *Dasyopsis antillarum* Howe	p. 165	p. 564
88. *Dictyurus occidentalis* J. Agardh	----	p. 567 - pl. 70, figs. 1, 2
89. *Digenia simplex* (Wulfen) C. Agardh	p. 156 - fig. 77	p. 589
90. *Enantiocladia duperreyi* (C. Agardh) Falkenberg	----	p. 610
91. *Erythrocladia subintegra* Rosenvinge	p. 117	p. 290 - pl. 41, fig. 1
92. *Erythrotrichia carnea* (Dillwyn) J. Agardh	p. 117	p. 292
93. *Eucheuma acanthocladum* (Harvey) J. Agardh	p. 135	p. 458 - pl. 50, fig. 5
94. *Eucheuma echinocarpum* Areschoug	----	p. 458
95. *Eucheuma gelidium* (J. Agardh) J. Agardh	----	p. 459
96. *Eucheuma isiforme* (C. Agardh) J. Agardh	p. 135 - fig. 63A	p. 459 - pl. 45, fig. 11, pl. 50, figs. 6, 7
97. *Eucheuma nudum* J. Agardh	p. 137 - figs. 63 B, C	----
98. *Falkenbergia hillebrandii* (Bornet) Falkenberg	p. 157	p. 571 - pl. 72, fig. 8
99. *Fauchea hassleri* Howe and Taylor	p. 142 - fig. 67	----

TABLE 3. con't.

Taxon	Dawes (1974)	Taylor (1960)
100. *Fauchea peltata* Taylor	p. 142	----
101. *Fosliella atlantica* (Foslie) Taylor	p. 123 - fig. 55	----
102. *Fosliella farinosa* (Lamouroux) Howe	p. 123	p. 388
103. *Fosliella lejolisii* (Rosanoff) Howe	p. 124	p. 387
104. *Galaxaura cylindrica* (Ellis and Solander) Lamouroux	----	p. 341 - pl. 44, fig. 1
105. *Galaxaura flagelliformis* Kjellman	----	p. 338
106. *Galaxaura lapidenscens* (Ellis and Solander) Lamouroux	----	p. 337
107. *Galaxaura marginata* (Ellis and Solander) Lamouroux	----	p. 343 - pl. 44, fig. 2, pl. 45, figs. 7, 8
108. *Galaxaura oblongata* (Ellis and Solander) Lamouroux	----	p. 341
109. *Galaxaura obtusata* (Ellis and Solander) Lamouroux v. *major* Taylor	p. 119	p. 342 - pl. 44, figs. 4, 5, pl. 45, fig. 5
110. *Galaxaura rugosa* (Ellis and Solander) Lamouroux	----	p. 340
111. *Galaxaura squalida* Kjellman	----	p. 339 - pl. 44, fig. 3, pl. 45, fig. 6
112. *Galaxaura subverticillata* Kjellman	----	p. 339 - pl. 44, fig. 6, pl. 45, fig. 9
113. *Gelidiella acerosa* (Forsskål) Feldmann and Hamel	p. 119	p. 351 - pl. 46, fig. 5
114. *Gelidiopsis intricata* (C. Agardh) Vickers	----	p. 353
115. *Gelidium corneum* (Hudson) Lamouroux	----	p. 356
116. *Gelidium crinale* (Turner) Lamouroux v. *platycladum* Taylor	p. 120	p. 355

TABLE 3. con't.

Taxon	Dawes (1974)	Taylor (1960)
117. *Gelidium floridanum* Taylor	----	p. 357
118. *Gelidium pusillum* (Stackhouse) LeJolis v. *conchicola* Piccone and Grunow	p. 120	p. 354 - pl. 45, fig. 4
119. *Gigartina acicularis* (Wulfen) Lamouroux	----	p. 473 - pl. 60, fig. 6
120. *Gloiophlaea halliae* Setchell	----	p. 332
121. *Goniolithon accretum* Foslie and Howe	----	p. 396
122. *Goniolithon boergesenii* Foslie	----	p. 397 - pl. 76, fig. 2
123. *Goniolithon decutescens* (Heydrich) Foslie	p. 124	p. 398
124. *Goniolithon mamillare* (Harvey) Foslie	----	p. 397
125. *Goniolithon solubile* Foslie and Howe	----	p. 396 - pl. 76, fig. 3
126. *Goniolithon spectabile* Foslie	----	p. 399 - pl. 78, fig. 1
127. *Goniolithon strictum* Foslie v. *nanum* Foslie and Howe	----	p. 399 - pl. 48, fig. 4, pl. 77, figs. 1, 2
128. *Goniotrichum alsidii* (Zanardini) Howe	p. 118	----
129. *Gracilaria armata* (C. Agardh) J. Agardh	p. 128	p. 441
130. *Gracilaria blodgettii* Harvey	p. 128	p. 449 - pl. 56, fig. 1
131. *Gracilaria cervicornis* (Turner) J. Agardh	p. 129	p. 445
132. *Gracilaria compressa* (C. Agardh) Greville	p. 129	p. 444
133. *Gracilaria crassissima* Crouan ex J. Agardh	----	p. 443 - pl. 55, fig. 4, pl. 57, fig. 4
134. *Gracilaria curtissiae* J. Agardh	----	p. 449 - pl. 54, fig. 1
135. *Gracilaria cylindrica* Børgesen	p. 129	p. 450 - pl. 56, fig. 3
136. *Gracilaria damaecornis* J. Agardh	p. 129	p. 443 - pl. 55, fig. 2

TABLE 3. con't.

Taxon	Dawes (1974)	Taylor (1960)
137. *Gracilaria debilis* (Forsskål) Børgesen	p. 129	p. 442 - pl. 45, fig. 10, pl. 57, fig. 3
138. *Gracilaria ferox* J. Agardh	----	p. 444 - pl. 56, fig. 4
139. *Gracilaria foliifera* (Forsskål) Børgesen v. *angustissima* (Harvey) Taylor	p. 130 - fig. 58	p. 446 - pl. 55, fig. 1
140. *Gracilaria mammillaris* (Montagne) Howe	p. 131 - fig. 59	p. 447 - pl. 59, fig. 4
141. *Gracilaria sjoestedtii* Kylin	p. 132 as *Gracilariopsis*	p. 449
142. *Gracilaria verrucosa* (Hudson) Papenfuss	p. 132 - fig. 60	p. 441 - pl. 56, fig. 2
143. *Grateloupia filicina* (Wulfen) C. Agardh	p. 126	p. 424 - pl. 54, figs. 2, 3
144. *Grateloupia gibbesii* Harvey	----	p. 425
145. *Griffithsia globulifera* Harvey	p. 146 - fig. 70	p. 517
146. *Griffithsia tenuis* C. Agardh	p. 146	p. 516
147. *Grinnellia americana* (C. Agardh) Harvey	p. 150 - fig. 73	----
148. *Gymnothamnion elegans* (Schousboe) J. Agardh	----	p. 522 - pl. 66, figs. 1-4
149. *Halodictyon mirabile* Zanardini	----	p. 567 - pl. 72, fig. 5
150. *Halymenia agardhii* DeToni	p. 126	p. 417 - pl. 51, figs. 1, 2
151. *Halymenia bermudensis* Collins and Howe	----	p. 419 - pl. 53, fig. 1
152. *Halymenia floresia* (Clemente) C. Agardh	p. 126 - fig. 57	p. 418 - pl. 45, fig. 12, pl. 51, fig. 3
153. *Halymenia floridana* J. Agardh	----	p. 420 - pl. 53, fig. 2
154. *Halymenia gelinaria* Collins and Howe	p. 127	p. 420
155. *Halymenia pseudofloresia* Collins et Howe	p. 127	----
156. *Helmintocladia calvadosii* (Lamouroux) Setchell	----	p. 324 - pl. 43, fig. 5

TABLE 3. con't.

Taxon	Dawes (1974)	Taylor (1960)
157. *Herposiphonia pecten - veneris* (Harvey) Falkenberg v. *laxa* Taylor	----	p. 603
158. *Herposiphonia secunda* (C. Agardh) Ambronn	p. 157	p. 604 - pl. 72, figs. 10, 11
159. *Herposiphonia tenella* (C. Agardh) Ambronn	p. 158	p. 604 - pl. 72, fig. 12
160. *Heterosiphonia gibbesii* (Harvey) Falkenberg	----	p. 566 - pl. 72, fig. 7, pl. 73, fig. 5
161. *Heterosiphonia wurdemanni* (Bailey ex Harvey) Falkenberg v. *laxa* Børgesen	----	p. 565 - pl. 72, fig. 9
162. *Hildenbrandia prototypus* Nardo	p. 122	p. 369
163. *Hypoglossum involvens* (Harvey) J. Agardh	----	p. 545 - pl. 68, fig. 4
164. *Hypoglossum tenuifolium* (Harvey) J. Agardh v. *carolinianum* Williams	p. 151	p. 545 - pl. 68, fig. 2
165. *Hypnea cervicornis* J. Agardh	p. 138	p. 466 - pl. 73, fig. 2
166. *Hypnea cornuta* (Lamouroux) J. Agardh	p. 138	p. 467
167. *Hypnea musciformis* (Wulfen) Lamouroux	p. 138 - fig. 64	----
168. *Hypnea spinella* (C. Agardh) Kützing	p. 138	----
169. *Jania adherens* Lamouroux	p. 124	p. 413 - pl. 49, figs. 1, 2
170. *Jania capillacea* Harvey	p. 125 - fig. 56	p. 412 - pl. 49, fig. 4
171. *Jania pumila* Lamouroux	p. 125	p. 414 - pl. 49, fig. 5
172. *Jania rubens* (Linnaeus) Lamouroux	----	p. 413 - pl. 49, fig. 3
173. *Kallymenia limminghii* Montagne	p. 128	p. 432 - pl. 80, fig. 2
174. *Kallymenia perforata* J. Agardh	p. 128	p. 432 - pl. 60, fig. 3

TABLE 3. con't.

Taxon	Dawes (1974)	Taylor (1960)
175. *Kylinia crassipes* (Børgesen) Kylin	p. 119	p. 300
176. *Kylinia liagoriae* (Børgesen) Papenfuss	----	p. 301
177. *Laurencia corallopsis* (Montagne) Howe	----	p. 623
178. *Laurencia gemmifera* Harvey	p. 158	p. 624
179. *Laurencia intricata* Lamouroux	p. 158	p. 626
180. *Laurencia microcladia* Kützing	p. 158	p. 627
181. *Laurencia obtusa* (Hudson) Lamouroux	p. 158	p. 626
182. *Laurencia papillosa* (Forsskål) Greville	p. 159	p. 623 - pl. 74, fig. 2
183. *Laurencia poitei* (Lamouroux) Howe	p. 159 - fig. 78	p. 625
184. *Liagora ceranoides* Lamouroux	----	p. 326 - pl. 43, fig. 1, pl. 45, fig. 1
185. *Liagora farinosa* Lamouroux	----	p. 326 - pl. 43, fig. 3, pl. 45, fig. 2
186. *Liagora mucosa* Howe	----	p. 328
187. *Liagora pedicellata* Howe	----	p. 329
188. *Liagora pinnata* Harvey	----	p. 329
189. *Liagora valida* Harvey	----	p. 327 - pl. 43, fig. 2
190. *Lithophyllum bermudense* Foslie and Howe	----	p. 393
191. *Lithophyllum intermedium* (Foslie) Foslie	----	p. 391
192. *Lithophyllum prototypum* Foslie	----	p. 392
193. *Lithophyllum pustulatum* (Lamouroux) Foslie	----	p. 392
194. *Lithothamnium floridanum* Foslie	----	p. 383
195. *Lithothamnium heteromorphum* (Foslie) Foslie	----	p. 383

TABLE 3. con't.

Taxon	Dawes (1974)	Taylor (1960)
196. *Lithothamnium incertum* Foslie	----	p. 384 - pl. 78, fig. 2
197. *Lithothamnium mesomorphum* Foslie v. *ornatum* Foslie and Howe	----	p. 382
198. *Lithothamnium occidentale* Foslie v. *effusa* (Foslie) Foslie	p. 126	p. 385 - pl. 79, fig. 2
199. *Lithothamnium syntrophicum* Foslie	p. 126	p. 381
200. *Lomentaria baileyana* (Harvey) Farlow	p. 140	p. 487
201. *Lomentaria rawitscheri* Joly	p. 140	----
202. *Lophocladia trichoclados* (Mertens in C. Agardh) Schmitz	----	p. 590
203. *Lophosiphonia cristata* Falkenberg	p. 160	----
204. *Lophosiphonia saccorhiza* Collins et Hervey	p. 160	----
205. *Martensia pavonia* (J. Agardh) J. Agardh	----	p. 555 - pl. 68, fig. 3
206. *Melobesia membranacea* (Esper) Lamouroux	----	p. 379
207. *Meristotheca floridana* Kylin	p. 138	p. 460
208. *Murrayella periclados* (C. Agardh) Schmitz	p. 160	p. 593
209. *Naccaria corymbosa* J. Agardh	----	p. 347
210. *Neoagradhiella ramosissima* (Harvey ex Kützing) Wynne and Taylor	p. 133, as *Agardhiella*	p. 457 - pl. 58, fig. 5, as *Agardhiella*
211. *Nitophyllum punctatum* (Stackhouse) Greville v. *ocellatum* (Lamouroux) J. Agardh	----	p. 551 - pl. 69, fig. 2
212. *Peyssonnelia rosenvingii* Schmitz	----	p. 373
213. *Peyssonnelia rubra* (Greville) J. Agardh	p. 122	p. 371
214. *Polysiphonia binneyi* Harvey	----	p. 577

TABLE 3. con't.

Taxon	Dawes (1974)	Taylor (1960)
215. *Polysiphonia denudata* (Dillwyn) Kützing	p. 160	----
216. *Polysiphonia echinata* Harvey	p. 161	p. 579
217. *Polysiphonia exilis* Harvey	----	p. 581
218. *Polysiphonia ferulacea* Suhr	p. 161	p. 578
219. *Polysiphonia fracta* Harvey	----	p. 576
220. *Polysiphonia gorgoniae* Harvey	p. 161	p. 576
221. *Polysiphonia hapalacantha* Harvey	p. 161	p. 579
222. *Polysiphonia havanensis* Montagne v. *mucosa* J. Agardh	p. 161	p. 577
223. *Polysiphonia howei* Hollenberg	p. 161	p. 582
224. *Polysiphonia macrocarpa* Harvey	p. 162	p. 578
225. *Polysiphonia opaca* (C. Agardh) Moris and De Notaris	p. 162	p. 583
226. *Polysiphonia ramentacea* Harvey	p. 162	p. 580
227. *Polysiphonia subtilissima* Montagne	p. 162 - fig. 79	p. 575
228. *Polysiphonia tepida* Hollenberg	p. 162	----
229. *Porphyra leucosticta* Thuret	----	p. 295
230. *Porphyra umbilicalis* (Linnaeus) J. Agardh	----	p. 295
231. *Pterocladia americana* Taylor	p. 120 - fig. 53	p. 360 - pl. 46, fig. 3
232. *Scinaia complanata* (Collins) Cotton v. *intermedia* Børgesen	p. 119	p. 334 - pl. 42, fig. 3
233. *Seirospora occidentalis* Børgesen	p. 147	p. 510
234. *Soleria tenera* (J. Agardh) Wynne and Taylor	p. 135 - fig. 62, as *Agardhiella*	p. 456, as *Agardhiella*

TABLE 3. con't.

Taxon	Dawes (1974)	Taylor (1960)
235. *Spermothamnion gorgoneum* (Montagne) Bornet	----	p. 521 - pl. 65, fig. 2
236. *Spermothamnion turneri* (Mertens) Areschoug v. *variabile* (C. Agardh) Ardissone	p. 148	p. 519
237. *Spyridia aculeata* (Schimper) Kützing	----	p. 541 - pl. 66, fig. 16, pl. 71, fig. 5
238. *Spyridia clavata* Kützing	----	p. 541
239. *Spyridia filamentosa* (Wulfen) Harvey v. *refracta* (Wulfen) Harvey	p. 148 - fig. 71	p. 539 - pl. 66, fig. 15
240. *Taenioma nanum* (Kützing) Papenfuss	p. 151	p. 548, as *T. macrourum*
241. *Titanophora incrustans* (J. Agardh) Børgesen	----	p. 437
242. *Vidalia obtusiloba* (Mertens) J. Agardh	----	p. 609 - pl. 70, figs. 3, 4
243. *Wrangelia argus* Montagne	----	p. 502 - pl. 66, figs. 7, 8
244. *Wrangelia bicuspidata* Børgesen	----	p. 503 - pl. 66, figs. 9, 10
245. *Wrangelia penicillata* C. Agardh	----	p. 503 - pl. 66, figs. 5, 6, pl. 74, fig. 5
246. *Wrightiella blodgettii* (Harvey) Schmitz	----	p. 591
247. *Wrightiella tumanowiczi* (Gatty) Schmitz	p. 163	p. 592
248. *Wurdemannia miniata* (Draparnaud) Feldmann and Hamel	p. 120	p. 361

VI. CYANOPHYTA: KEY AND NAME REVISIONS LIST

Introductory Remarks

The Cyanophyta or blue green algae are ubiquitous, and many taxa occur both in marine and freshwater environments. Dawes (1974) records 34 taxa from Florida marine waters, but Taylor (1960) does not provide an account of this group. Blue greens grow in muds and sands, on rocks, and in the aufwuchs. In some localities, certain taxa form extensive blackish coatings on rocks in the littoral and supralittoral zones, and they usually crop up in most collections.

The taxonomy of blue green algae is currently in a state of flux, and considerable controversy exists (see discussions Carr and Whitton 1973, Desikachary 1972) over the merits of the drastic reduction of taxa to synonomy by Drouet (1968, 1973) and Drouet and Daily (1956). The recent account of Dawes (1974) for the Florida Gulf Coast incorporates the proposals of Drouet (1968) and Drouet and Daily (1956), but apparently it had gone to press before the revision (Drouet 1973) of the families Scytonemataceae and Rivulariaceae (placed by Drouet in the Nostocaceae) became available.

The series of keys presented below differs from those to the Chlorophyta, Phaeophyta and Rhodophyta in several respects. First, a series of keys is given - to orders and families and then a second series is presented for the genera and species of each family. The entire series of keys, however, are coordinated through sequential numbering. Wherever possible, the revisions of Drouet (1968, 1973) and Drouet and Daily (1956) have been incorporated as indicated in notes at the beginning of the generic and specific keys. All species recognized by Drouet have been included in the keys and those recorded from Florida have been noted with an asterisk. For groups not yet dealt with by Drouet, older literature sources (especially Dawes 1974, Desikachary 1959, and Taylor 1928) have been used, and only Florida taxa have been included. Table 4 summarizes name revisions for taxa reported from Florida by Dawes (1974) and Taylor (1928).

Considerable study will be needed before the proposals of Drouet can be fully evaluated, and for those who prefer not to accept them until further evidence supporting their soundness becomes available, the more "conservative" account of Desikachary (1959) can be consulted for taxon identification. Similarly, the Drouet revisions and Desikachary (1959) should be utilized for illustrations.

The Cyanophyta:

Key to Orders and Families

1a Plants unicellular or forming non-filamentous colonies. . . . . Order Chroococcales . . 2

2a Cells of the colonies not separated from each other by sheath materials . . . . . .Family Clastidiaceae . . 10

2b Cells separated from one another by sheath materials

3a Cell divisions resulting in daughter cells of equal size . . . . . Family Chroococcaceae . . 11

3b Cell divisions giving rise to daughter cells of unequal size and further developing into cushions of radial structure . . . . . Family Chamaesiphonaceae . . 6

1b Plants filamentous. . . . . .Order Nostocales . . 4

4a Trichomes (filaments minus the sheaths) unbranched (not exhibiting true branching)

5a Heterocysts absent. . . . . Family Oscillatoriaceae . . 28

5b Heterocysts usually present (if absent, trichomes moniliform or torulose). . . . . Family Nostocaceae . . 51

4b Trichomes branched (i.e. true branching). . . . . .Family Stigonemataceae . . 57

Family Chamaesiphonaceae

One Genus: Entophysalis

Key to Species

This key is based on the taxonomic revision of Drouet and Daily (1956). Taxa marked with an asterisk [*] are reported from Florida marine waters.

6a Marine taxa

7a On rocks, wood, and shells. . . . . E. deusta*

7b On larger algae and living animals

8a Cells 1-2 µm in diameter, yellowish in color . . . . . .E. endophytica*

8b Cells larger, blue-green, violet, or red in color . . . . . .E. conferta*

6b Freshwater taxa

9a On rocks, wood, and shells. . . . . .E. rivularis

9b On larger plants. . . . . E. lemaniae

Family Clastidiaceae:

Key to Genera and Species

This key is based on the taxonomic revision of Drouet (1956). Taxa marked with an asterisk [*] are reported from Florida marine waters.

10a Plants terminating above in a hair-like extension of the sheath. . . . . Genus Clastidium - one species, C. setigerum

10b Plants smooth at the apex . . . . . .Genus Stichosiphon - one species, S. sansibaricus

Family Chroococcaceae:

Key to Genera and Species

This key is based on the taxonomic revision of Drouet and Daily (1956). Taxa marked with an asterisk [*] are reported from Florida marine waters.

11a Cells before division ovoid to cylindrical, longer than broad, each dividing in a plane perpendicular to the long axis. . . . . Genus Coccochloris

12a Cells before division ovoid to cylindrico-elliptic, up to 3 times as long as broad

13a Cells 7-45 µm broad. . . . . .C. aeruginosa

13b Cells (3-) 4-8 µm broad. . . . . C. stagnina*

12b Cells before division cylindrical, up to 8-12 times as long as broad

14a Cells straight, usually quasi truncate at the ends, 2-6 µm broad . . . . . .C. elabens*

14b Cells commonly curved, rotund or tapering at the ends, 1-3 µm broad. . . . . C. peniocystis

11b Cells before division spherical, ovoid, discoid, cylindrical, or pyriform, never dividing in planes perpendicular to the long axis

15a Cell division confined to a single plane; cells arranged in a single linear series within a gelatinous matrix. . . . . Genus Johannesbaptista - one species, J. pellucida*

15b Cells dividing in more than one plane; cells forming flat or curved sheets or irregularly distributed in a gelatinous matrix.

16a Cell division occurring in three planes; cells distributed in a three dimensional gelatinous matrix in an irregular manner or in a series of rows in 3 planes .Genus Anacystis

17a Cells containing pseudovacuoles, forming water blooms

18a Cells 0.5-2.0 µm in diameter. . . . . A. incerta

18b Cells (2.5-) 3-7 (-10) µm in diameter .A. cyanea

17b Cells lacking pseudovacuoles, not developing as water blooms

19a Cells 0.5-2.0 µm in diameter. . . . . .A. marina

19b Cells larger

20a Cells up to 6 µm in diameter (larger when parasitized by fungi; gelatinous matrix variously pigmented in aerial and subaerial habitats . . . . . .A. montana*

20b Cells 6 µm or more in diameter; gelatinous matrix hyaline

21a Cells (8-) 12-50 µm in diameter, usually remaining angular after division. . . . . .A. dimidiata*

21b Cells chiefly 6-12 µm in diameter, soon becoming spherical after division

22a Plants marine, usually macroscopic . . . . . .A. aeruginosa*

22b Plants of fresh water, usually microscopic . . . . A. thermalis*

16b Cell division occurring in two planes; cells distributed through a flat or curved surface

23a Plants spherical or ovoid. . . . Genus Gomphosphaeria

24a Cells containing pseudovacuoles, 3-5 µm in diameter; plants developing as water blooms in fresh water . . . . . .G. wichurae

24b Cells lacking pseudovacuoles, 2-15 µm in diameter; plants not developing as water blooms

25a Cells 2-4 µm in diameter . . . G. lacustris

25b Cells 4-15 µm in diameter. . . .G. aponina*

23b Plants forming flat on curved plates

26a Cells regularly arranged in series of rows perpendicular to each other . . Genus Agmenellum

27a Cells 1-3.5 µm in diameter; plants 1-256 celled . . . . . A. quadruplicatum*

27b Cells 4-10 µm in diameter; plants larger and often foliose. . . . . A. thermale*

26b Cells irregularly arranged. . . . . . Genus Microcrocis - one species, M. geminata

Family Oscillatoriaceae:

Key to Genera and Species

This key is based on the taxonomic revision of Drouet (1968). Taxa marked by an asterisk [*] are reported from Florida marine waters.

28a Trichomes appearing unicellular; cross walls apparently absent. . . . . Genus Spirulina - one Species, S. subsala*

28b Trichomes multicellular; cross walls present

29a A layer of granules present on either side of each cross wall

30a Outer wall of terminal cell thin, never beocming thickened . . . . . .Genus Arthrospira

31a Terminal cell conical; cells mostly 3 or more times as broad as long . . . . . A. brevis*

31b Terminal cell hemispherical; cells about as long as broad. . . . . A. jenneri

30b Outer wall of terminal cell becoming thickened. . . . . .Genus Microcoleus

32a Dense protoplasm and granules present along both side walls and cross walls. . . . . .M. lyngbyaceus*

32b Dense protoplasm and granules present only along cross walls

33a Trichomes conspicuously attenuated at the tips . . . . . M. vaginatus*

33b Trichomes not or at most slightly attenuated at the tips. . . . . M. irriguus*

29b No (or at most 2) granules present on either side of each cross wall

34a Outer wall of the terminal cell becoming thickened. . . . . Genus Oscillatoria

35a Cells at least 1/3 as long as broad

36a Cells with numerous, conspicuous pseudovacuoles. . . . . .O. erythraea*

36b Cells lacking or occasionally with isolated pseudovacuoles

37a Outer wall of terminal cell low conical or hemispherical. . . . . .O. submembranacea*

37b Outer wall of terminal cell slightly convex

38a Cells broader than long, the terminal cell short truncate conical or short-cylindrical . . . . . .O. lutea*

38b Cells usually as long as or longer than broad, the terminal cell long-truncate-conical . . . . . .O. retzii

35b Cells less than 1/3 as long as broad

39a Trichomes becoming conspicuously attentuated near the tips. . . . . O. princeps*

39b Trichomes not or only slightly attenuated near the tips. . . . . O. lutea*

34b Outer wall of terminal cell thin, never becoming thickened

40a Trichomes not attenuate except for the terminal cell . . . . . Genus Schizothrix

41a Terminal cell becoming rotund, at least at the tip, and very slightly if at all attenuate

42a Terminal cell hemispherical or almost spherical

43a Trichomes up to 3.5 µm in diameter. . . . . S. calcicola *

43b Trichomes 4-60 µm in diameter . . . . . S. mexicana*

42b Terminal cell becoming cylindrical and rotund at the tip . . . . . S. friesii

41b Terminal cell becoming conical

44a Terminal cell becoming blunt or acute conical

45a Trichomes becoming constricted at the cross walls . . . . . S. arenaria*

45b Trichomes not constricted at the cross walls . . . . . .S. rubella

44b Terminal cell becoming acuminate conical

46a Terminal cell short-acuminate . . . . . S. monticulosa

46b Terminal cell long acuminate. . . . . .S. tenerrima*

40b Trichomes attenuate, the attenuation involving several to many cells. . . . . Genus Porphyrosiphon

47a Trichome becoming capitate at the tips

48a Terminal cell several times longer than broad. . . . . .P. splendidus

48b Terminal cell about as long as broad . . . . . P. miniatus*

47b Trichome becoming attenuate conical at the tips

49a Terminal cell rotund to acute conical

50a Cells mostly less than 1/3 as long as broad . . . . . .P. kurzii*

50b Cells mostly 1/3 as long as broad or longer. . . . . .P. notarisii *

49b Terminal cell acuminate conical. P. animalis

Family Nostocaceae:

Key to Genera and Species

This key incorporates the recent revision of Drouet (1973) of those Nostocaceae with cylindrical trichomes (formerly constituting the Syctonemataceae and Rivulariaceae) and includes all taxa recognized by Drouet. Taxa marked with an asterisk are reported from Florida. The portion of the key dealing with the moniliform or torulose members of the Nostocaceae is based on older sources and includes only those taxa recorded from Florida marine waters. See Desikachary (1959) for more detailed keys to these groups.

51a Trichomes normally cylindrical

- 52a Terminal vegetative cells (not heterocysts) becoming almost spherical. . . . . Genus Scytonema - one species, S. hofmannii*
- 52b Terminal vegetative cells conical or cylindrical
  - 53a Terminal vegetative cells becoming blunt-conical or cylindrical with rotund tips. . . . . .Genus Calothrix
    - 54a Trichocomes gradually attenuated towards the tips; fresh water plants . . . . . .C. parietina*
    - 54b Trichomes abruptly attenuated near the tips; marine plants . . . . . .C. crustacea*
  - 53b Terminal vegetative cells becoming more or less acute-conical . . . Genus Raphidiopsis - one species, R. curvata

51b Trichomes normally moniliform or torulose

- 55a Trichomes without a firm sheath; sheath if present watery . . . . . .Genus Anabaena, A. fertilissima
- 55b Trichomes with a firm sheath
  - 56a Trichomes single within a sheath . . . . . .Genus Nodularia, N. spumigera
  - 56b Trichomes in parts of the thallus more than one in a sheath. . . . . Genus Hormothamnion, H. enteromorphoides

Family Stigonemataceae:

Key to Genera and Species

Recorded from Florida Marine Waters

57a Trichomes uniseriate throughout; heterocysts terminal . . . . . .
. . . . . .Genus Mastigocoleus, M. testarum*

57b Trichomes in part biseriate or multiseriate; heterocysts intercalary. . . . . .Genus Stigonema, S. aerugineum*

Note: Drouet (1973) regards Scytonema ocellatum as a species of Stigonema.

Table 4. Name Revisions for Marine Florida Cyanophyta. Recent monographic work by Drouet has resulted ina drastic reduction of taxa to synonomy. The following list includes older names used for taxa reported from Florida marine waters and the revised names used in the keys and in the Drouet papers.

OLDER NAME		REVISED NAME
Calothrix aeruginea	=	*Calothrix crustacea*
Calothrix confervicola	=	*Calothrix crustacea*
Calothrix longifila	=	*Calothrix crustacea*
Calothrix parasitica	=	*Calothrix crustacea*
Calothrix pilosa	=	*Scytonema hofmannii*
Calothrix rosea	=	*Calothrix crustacea*
Calothrix scopulorum	=	*Calothrix crustacea*
Chroococcus membraninus	=	*Anacystis thermalis*
Chroococcus turgidis	=	*Anacystis dimidiata*
Dermocarpa prasina	=	*Entophysalis conferta*
Dermocarpa solitaria	=	*Entophysalis conferta*
Dichothrix fucicola	=	*Calothrix crustacea*
Dichothrix olivacea	=	*Scytonema hofmannii*
Dichothrix penicillata	=	*Calothrix crustacea*
Gloeocapsa fuscolutea	=	*Coccochloris stagnina*
Hydrocoleum lyngbyaceum	=	*Microcoleus lyngbyaceus*
Hyella caespitosa	=	*Entophysalis deusta*
Lyngbya confervoides	=	*Microcoleus lyngbyaceus*
Lyngbya hyalina	=	*Oscillatoria lutea*
Lyngbya rosea	=	*Schizothrix mexicana*

Lyngbya semiplena	=	*Microcoleus irregularus*
Lyngbya versicolor	=	*Schizothrix calcicola*
Merismopedia convoluta	=	*Agmenellum thermale*
Microcoleus chthonoplastes	=	*Schizothrix arenaria*
Microcoleus tenerrimus	=	*Schizothrix tenerrima*
Oscillatoria corallinae	=	*Microcoleus lyngbyaceus*
Oscillatoria laetevirens	=	*Schizothrix arenaria*
Phormidium calothrichoides	=	*Schizothrix calcicola*
Phormidium fragile	=	*Schizothrix calcicola*
Phormidium nostochoides	=	*Schizothrix calcicola*
Phormidium persicinum	=	*Schizothrix calcicola*
Phormidium terebrans	=	*Schizothrix calcicola*
Phormidium valderianum	=	*Schizothrix calcicola*
Polythrix corymbosa	=	*Calothrix crustacea*
Rivularia atra	=	*Calothrix crustacea*
Rivularia nitida	=	*Calothrix crustacea*
Rivularia polyotis	=	*Calothrix crustacea*
Schizothrix longiarticulata	=	*Schizothrix arenaria*
Schizothrix taylorii	=	*Porphyrosiphon notarisii*
Spirulina rosea	=	*Spirulina subsalsa*
Spirulina subtilissima	=	*Spirulina subsalsa*
Symploca laete-virides	=	*Schizothrix arenaria*
Symploca profunda	=	*Schizothrix mexicana*
Trichodesmium thiebautii	=	*Oscillatoria erythraea*
Xenococcus schousboei	=	*Entophysalis conferta*

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VIII. ILLUSTRATIONS

Most of the following 332 illustrations have been redrawn from earlier publications and due acknowledgment is provided in the accompanying figure legends. The figures are designed to assist in identification at the generic level and thus only selected species have been included. Data on size, range and habitat are provided for most genera in the legends, and a scale of approximate magnification factors appears at the bottom of each page containing figure legend data. For purposes of habitat data, the term lithos refers to rocky niches, the term pelos refers to sandy and muddy niches, and the term aufwuchs refers to epibiotic and endobiotic niches.

Sincere thanks are due Ms. Jan MacKenzie for drawing Figs. 1-117, 125, 147, 148, 162-164, 166-168, 241-244, 260, 280, 284, 285, 299, and 322-325 and Ms. Briony Foy for drawing the remaining 193 figures. Without their assistance, these illustrations could not have been included in the manual.

A generic index to the illustrations follows Fig. 332. The Chlorophyta are depicted in Figs. 1-67; the Phaeophyta in Figs. 68-117, and the Rhodophyta in Figs. 118-332. Within each group, genera are dealt with in alphabetical order.

FIG. 1. ACETABULARIA CRENULATA LAMOUROUX

(After Boergesen 1913). Habit.
Species of Acetabularia reach heights of 1-70 mm and bear discs 1-8 mm broad. Plants most commonly occur on rock, coral or shell fragments in lagoons and other areas sheltered from wave action.

FIG. 2. ACICULARIA SCHENCKII (MÖBIUS) SOLMS-LAUBACH

(After Boergesen 1913). Habit.
Acicularia plants seldom exceed heights of 2 mm, and they bear 3-8 mm broad discs. Specimens occur in niches similar to those of Acetabularia.

FIG. 3. ANADYOMENE STELLATA (WULFEN) C. AGARDH

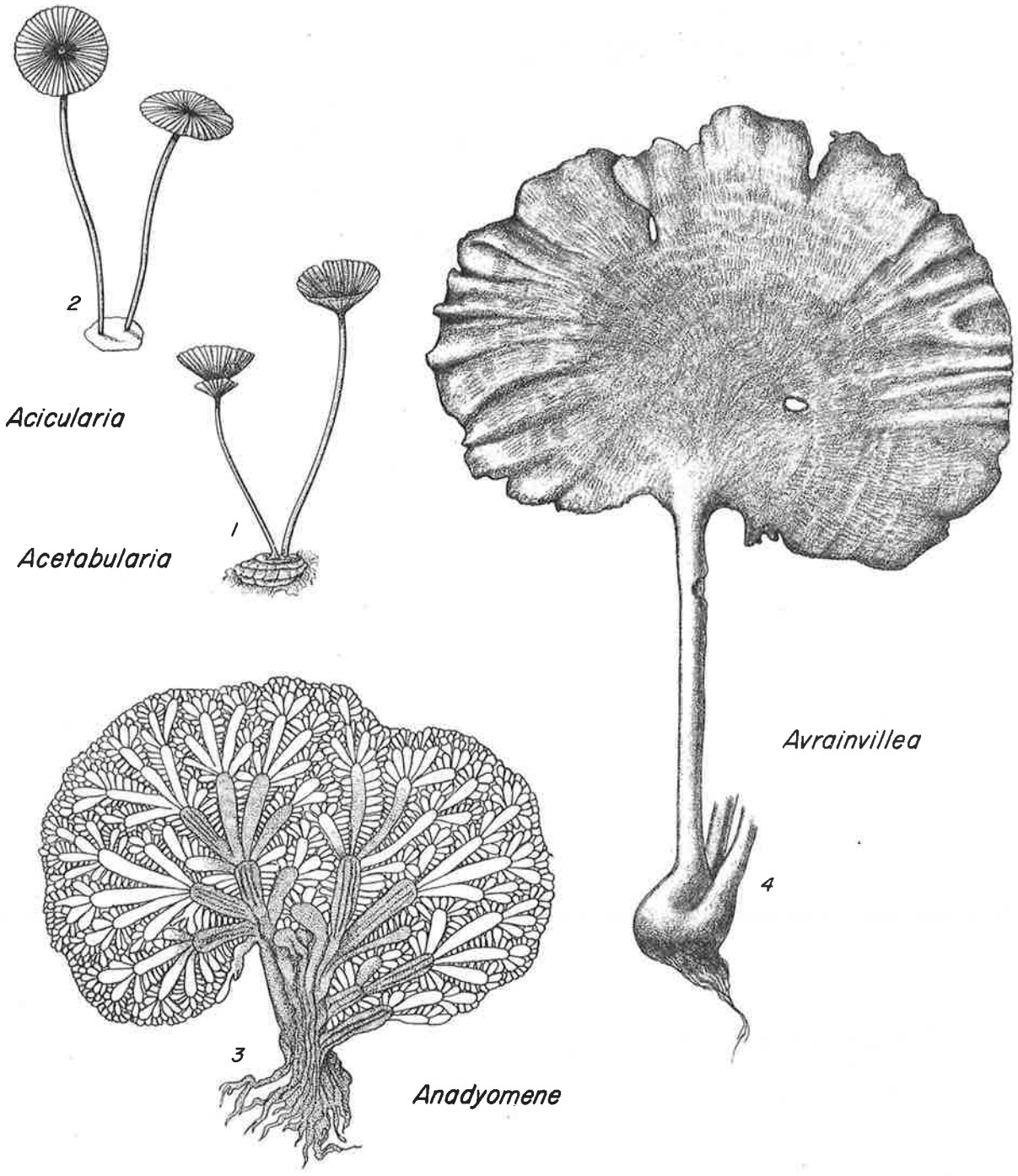
(After Oltmanns 1922). Habit.
Fan shaped plants can reach diameters of 10 cm and occur most commonly on shaded rocks or mangrove roots in both sheltered and exposed localities.

FIG. 4. AVRAINVILLEA NIGRICANS DECAISNE

(Original). Habit.
Avrainvillea species reach maximum heights of 10-30 cm and are usually found in sand or muddy areas of slight to moderate wave action.

MAGNIFICATION FACTORS:

Fig. 1: 1.2×; Fig. 2: 2.5×; Fig. 3: 0.9×; Fig. 4: 0.7×.


2
Acicularia
1
Acetabularia
Avrainvillea
4
3
Anadyomene

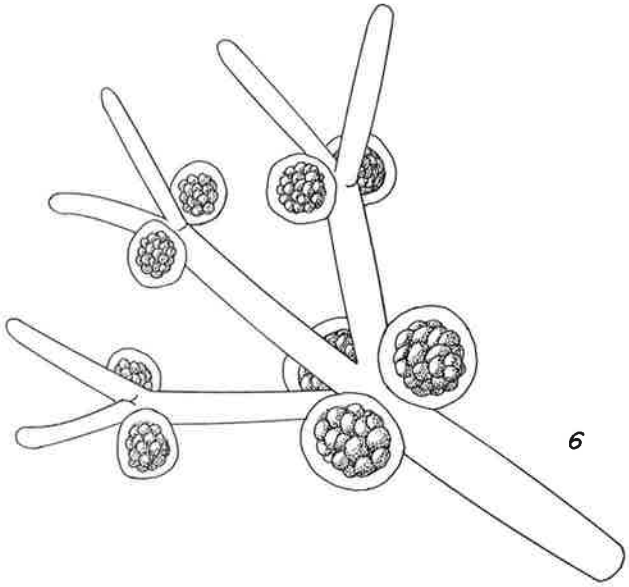
FIGS. 5-8. BATOPHORA OERSTEDI J. AGARDH

(After Boergesen 1913 [Fig. 5] and Harvey 1858 [Figs. 6-8] as Dasycladus occidentalis). Habit showing sterile and fertile axes (5); sporangia on fertile branchlets (6-7); cross section of main axis showing branching pattern (8).

Plants of Batophora commonly grow to 3-10 cm and are found in greatest abundance in protected lagoons and mangrove thickets. They can occur on small stones, shell fragments, mangrove roots, etc.

MAGNIFICATION FACTORS:

Fig. 5: 0.7×; Fig. 6: 50×; Fig. 7: 75×; Fig. 8: 20×.



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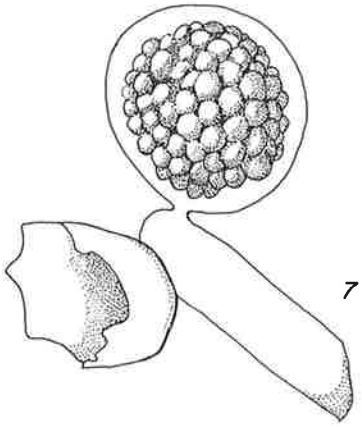
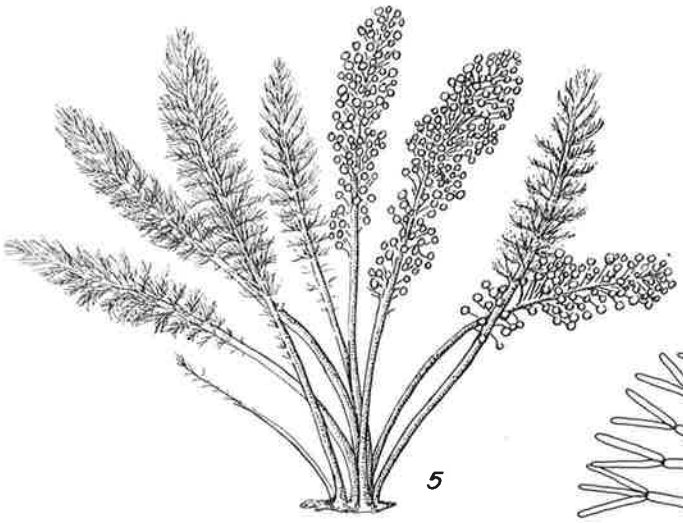
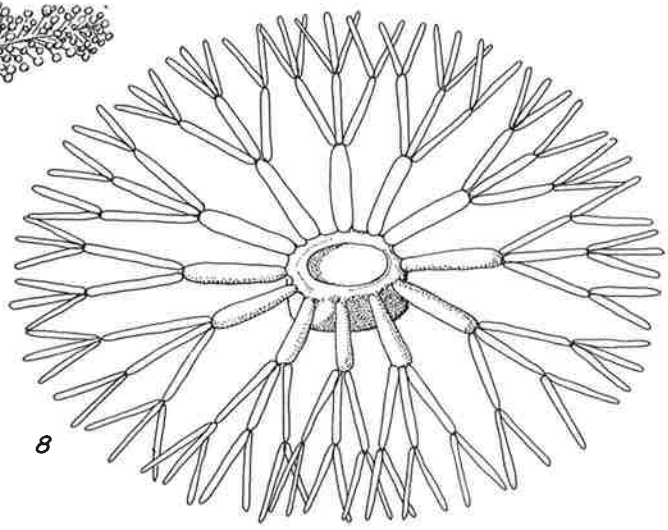


7



5

Batophora

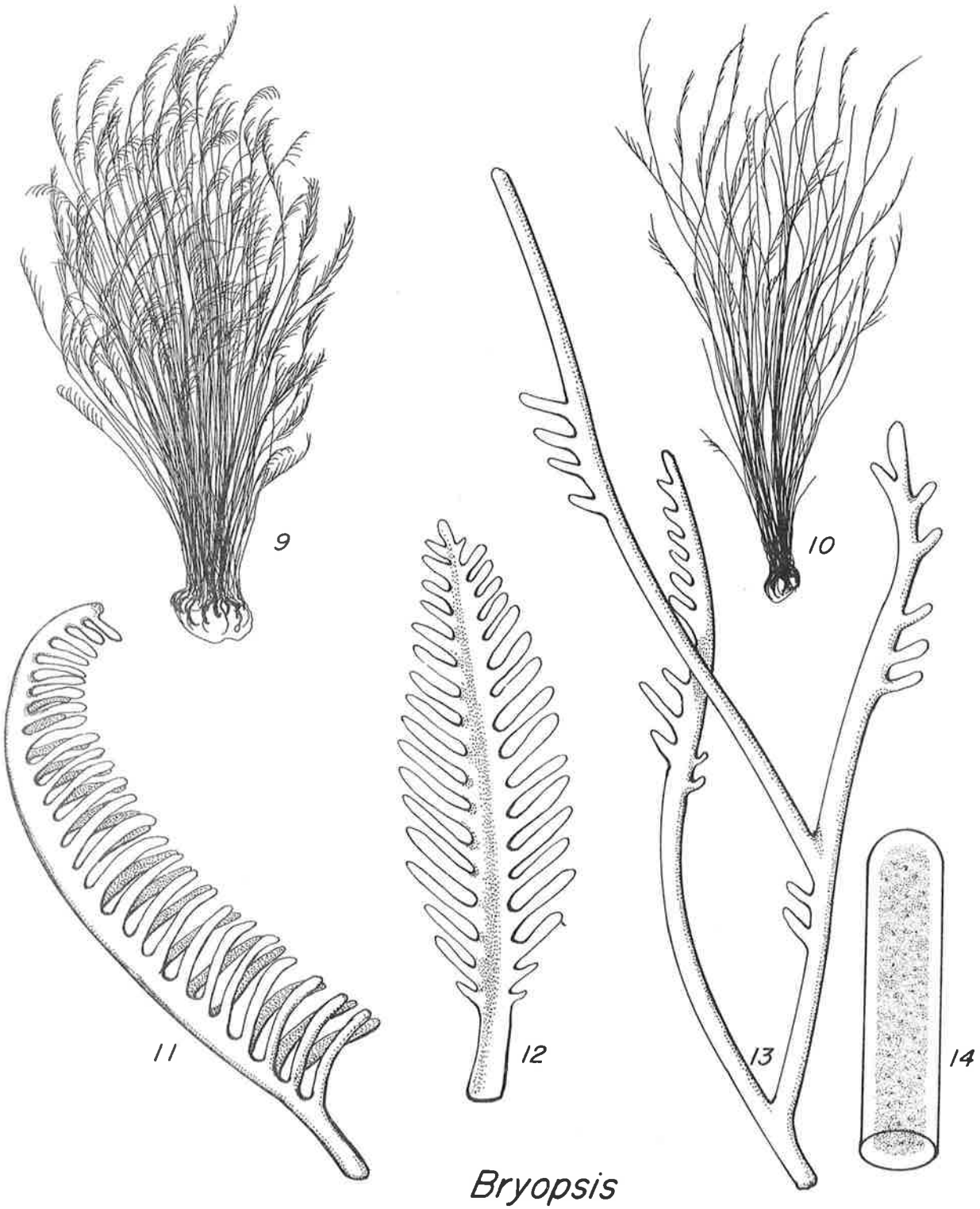


8

FIGS. 9-14. BRYOPSIS PLUMOSA (HUDSON) C. AGARDH (After Harvey 1858). Habits of pinnately (9) and irregularly branched specimens; branch tips of pinnately (11-12) and irregularly (13) branched specimens; greatly enlarged segment of a siphon (14).
Bryopsis plants attain heights of 5-12 cm. Most species occur in lagoons and very sheltered waters, but B. plumosa occasionally occurs in moderate surf. In most cases, plants are components of the lithos community.

MAGNIFICATION FACTORS:

Fig. 9: 1.0×; Fig. 10: 1.0×; Fig. 11: 25×; Fig. 12: 25×; Fig. 13: 25×; Fig. 14: 60×.



Bryopsis

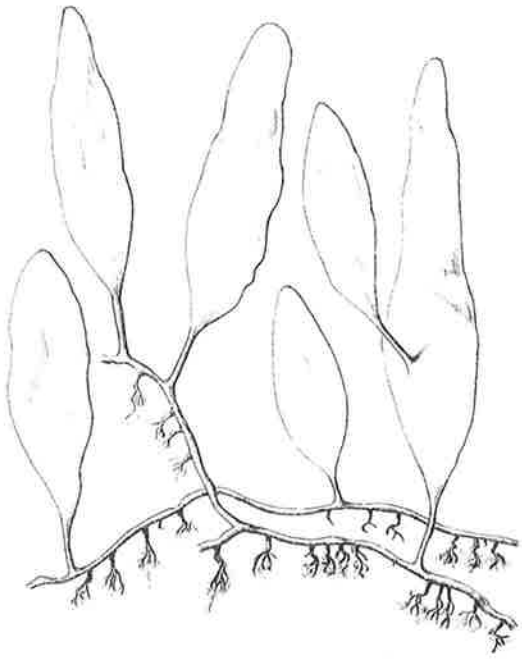
FIG. 15. CAULERPA PROLIFERA (FORSSKÅL) LAMOUROUX
(After Harvey 1858). Habit.

FIG. 16. CAULERPA LANUGINOSA J. AGARDH
(After Harvey 1858, as C. lycopodium).

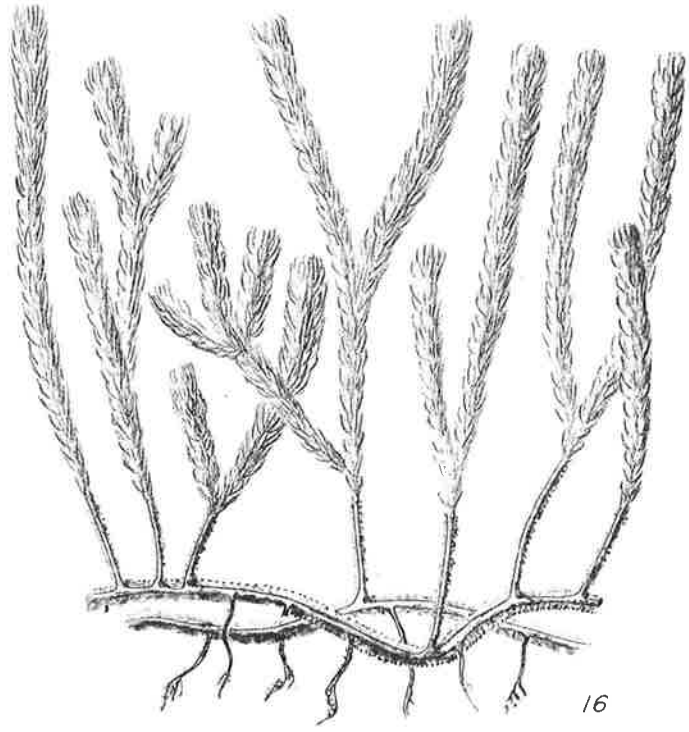
FIG. 17. CAULERPA MEXICANA (SONDER) J. AGARDH
(After Harvey 1858).
Species of Caulerpa occur in both the lithos and pelos and grow both under sheltered and exposed wave conditions. In general a greater diversity of species occurs in quiet waters with sandy or muddy substrates, and plants growing under these conditions appear more luxuriant and reach a greater size than do those found under the more harsh conditions of wave washed areas. Plants of some species commonly attain heights of 20 cm while those of other species rarely exceed 5 cm.

MAGNIFICATION FACTORS:

Fig. 15: 0.75×; Fig. 16: 0.6×; Fig. 17: 0.6×.

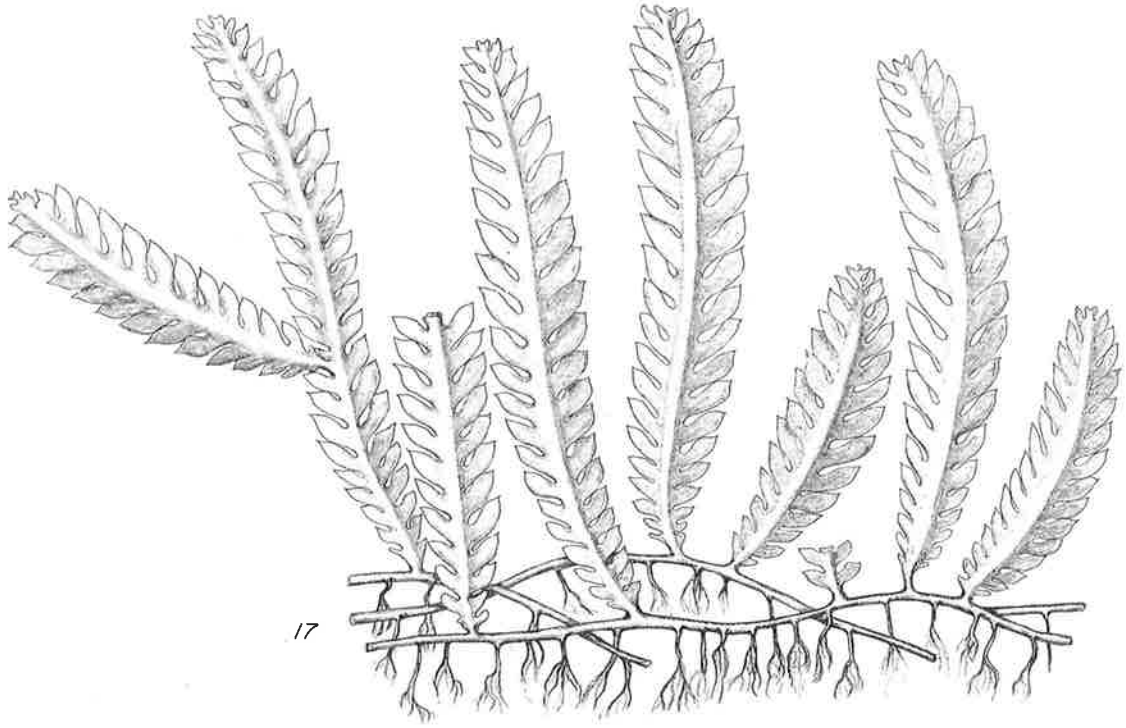


15



16

Caulerpa



17

FIG. 18. CAULERPA CUPRESSOIDES (WEST) C. AGARDH VAR. ERICIFOLIA (CROUAN) WEBER VAN BOSSE (After Harvey 1858). Habit.

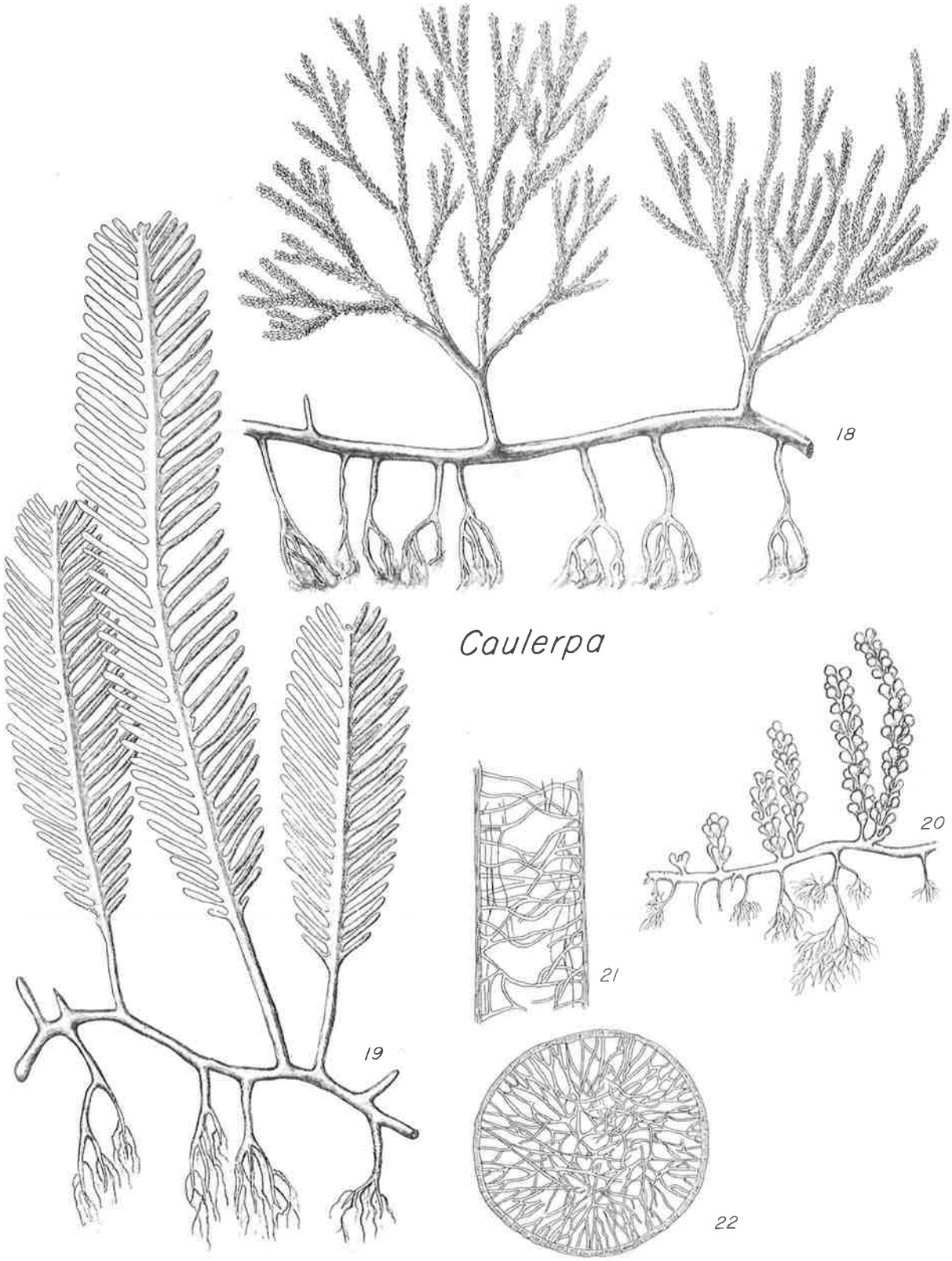
FIG. 19. CAULERPA ASHMEADII HARVEY (After Harvey 1858). Habit.

FIG. 20. CAULERPA RACEMOSA (FORSSKÅL) J. AGARDH (After Boergesen 1913). This is an extremely variable species both as to size and appearance.

FIGS. 21-22. LONGITUDINAL (21) AND CROSS (22) SECTION OF CAULERPA SIPHONS SHOWING MESH WORK OF TRABECULAE. (After Oltmanns 1922).
Habitat and size information on Caulerpa is provided in the legend for Figs. 15-17. Of the various species of Caulerpa, C. racemosa is found under a greater variety of conditions than other species and exhibits greater morphological variation than almost all other Caulerpa species.

MAGNIFICATION FACTORS:

Fig. 18: 0-6×; Fig. 19: 1.0×; Fig. 20: 0.75×; Fig. 21: 7×; Fig. 22: 10×.


18
Caulerpa
19
20
21
22

FIGS. 23-25. CODIUM SP.

(After Oltmanns 1922). Habit of plant (23); utricles bearing sporangia and hairs (24-25).
Codium occurs in rocky situations both in deep and shallow waters of exposed coasts. Some species form mats; others are erect and reach heights of 50 cm.

FIGS. 26-28. CLADOPHORA SP.

(After Harvey 1858). Habit (26); branches (27-28).
Species of Cladophora are poorly defined in Florida waters. Plants occur mostly on rocks and grow both in the intertidal and sublittoral zones.

FIG. 29. CHAMEDORIS PENICULUM (ELLIS & SOLANDER) KUNTZE. (After Harvey 1858). Habit of plant.
This species occurs primarily in deep waters but occasionally grows under shallow water rock ledges; plants attain heights of up to 20 cm.

FIG. 30. CLADOCEPHALUS LUTEOFUSCUS (CROUAN) BOERGESEN

(After Boergesen 1913). Habit of plant.
Known only from deeper waters in Florida; specimens grow to 10 cm.

FIGS. 31-34. CHAETOMORPHA SP.

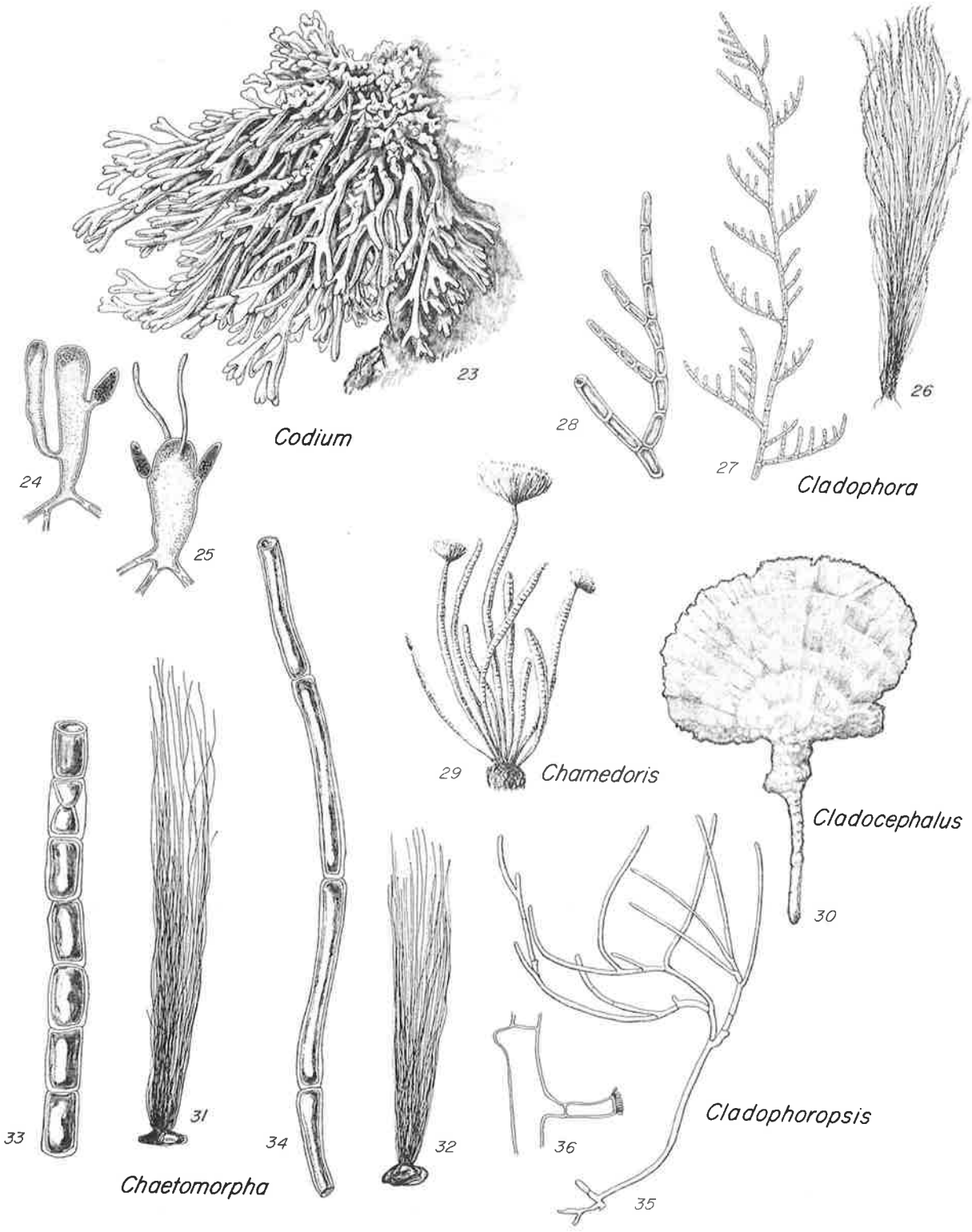
(After Harvey 1858). Habit of plants (31-32); enlargement of filaments (33-34).
Various species occur on rocks or in the aufwuchs of tidepools and localities of moderate wave exposure.

FIGS. 35-36. CLADOPHOROPSIS SP.

(After Oltmanns 1922). Habit of plant (35); enlarged cell (36).
Cladophoropsis occurs in very sheltered situations on mud or stones or woodwork. Plants can reach heights of 15 cm.

MAGNIFICATION FACTORS:

Fig. 23: 0.25×; Figs. 24-25: 2.5×; Fig. 26: 0.3×; Fig. 27: 10×; Fig. 28: 15×; Fig. 29: 0.5×; Fig. 30: 0.6×; Figs. 31-32: 0.75×; Fig. 33: 40×; Fig. 34: 40×; Fig. 35: 3×; Fig. 36: 20×.


23
Codium
24
25
28
27
26
Cladophora
29
Chamedoris
Cladocephalus
30
33
31
34
32
Chaetomorpha
36
35
Cladophoropsis

FIGS. 37-39. CYMOPOLIA BARBATA (LINNEAUS) LAMOUROUX

(After Harvey 1858). Habit (37); branch tip (38); cross section (39) with sporangia.
Cymopolia plants grow to 25 cm and occur primarily on stones in warm waters just below the low tide mark. They are known primarily from the lower Florida Keys.

FIGS. 40-42. DASYCLADUS VERMICULARIS (SCOPOLI) KRASSER

(After Oltmanns 1922). Habit of group of plants (40); plants with sporangia (41); branches bearing sporangia (42).
Plants reach heights of 2-4 cm and grow on rocks in areas of moderate wave action.

FIG. 43. CYSTODICTYON PAVONIUM J. AGARDH

(After Collins 1909). Habit of portion of plant.
Plants up to 14 cm across occur in deep waters, but seldom are found.

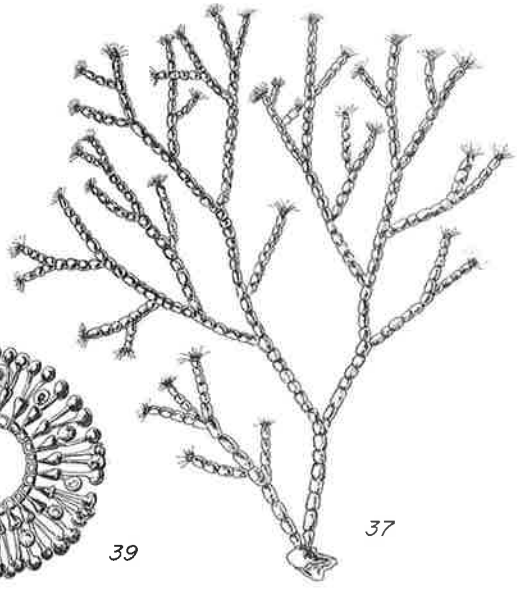
FIG. 44. DIPLOCHAETE SOLITARIA COLLINS

(After Collins 1909). Habit.
Specimens are known exclusively as epiphytes on other algae growing in shallow water; cells are mostly 30 μm or less broad.

MAGNIFICATION FACTORS:

Fig. 37: 0.3×; Fig. 38: 3×; Fig. 39: 25×; Fig. 40: 0.4×; Fig. 41: 1×; Fig. 42: 16×; Fig. 43: 7×; Fig. 44: 270×.

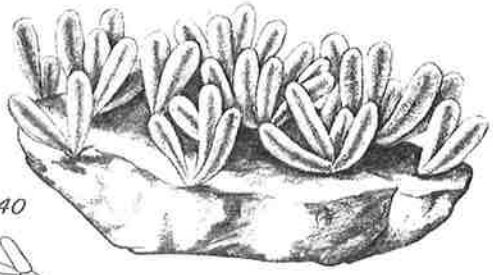
38



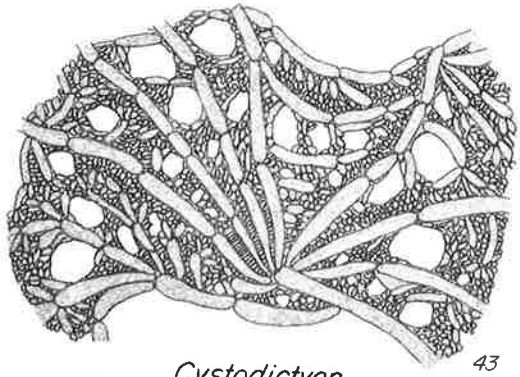
37

Cymopolia

39

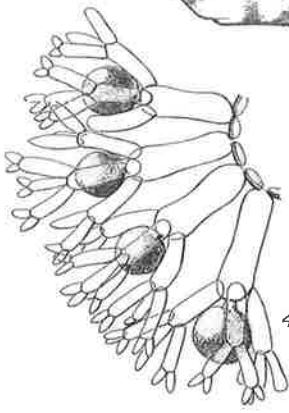


40

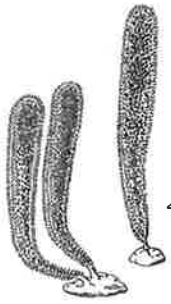


Cystodictyon

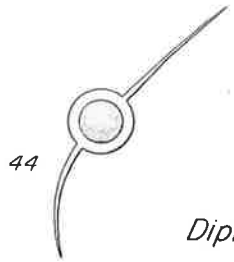
43



42



41



44

Diplochaete

Dasycladus

FIG. 45. DICTYOSPHAERIA CAVERNOSA (FORSSKÅL) BOERGESEN
(After Boergesen 1913).
Plants up to 12 cm across develop in shallow water rocky situations.

FIG. 46. ENTEROMORPHA LINGULATA J. AGARDH
(Original).
Plants usually occur in the intertidal zone on rocks and can reach lengths of over 30 cm.

FIG. 47. DICTYOSPHAERIA VAN BOSSEAE BOERGESEN
(After Boergesen 1913). This species occurs in Jamaica and the Virgin Islands and can be expected in the Florida Keys.

FIG. 48. ERNODESMIS VERTICILLATA (KÜTZING) BOERGESEN
(After Boergesen 1913).
Plants grow to 6 cm tall and occur primarily in shallow, sheltered, shaded lagoons.

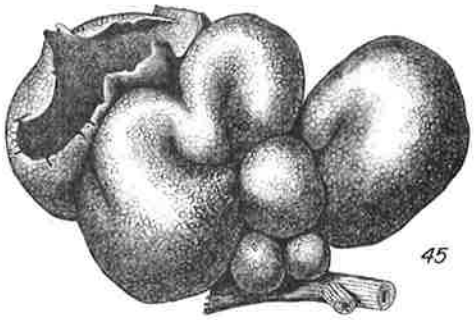
FIG. 49. HALICYSTIS OVALIS (LYNGBYE) ARESCHOUG
(After Oltmanns 1922). Figure included to show form of plants; material of Florida species has not been available.
Florida plants reportedly are 4-7 mm broad and occur on shaded rocks.

FIGS. 50-51. HALIMEDA SIMULANS HOWE
(Original and after Boergesen 1913, as H. incrassata var. simulans).

FIG. 52. HALIMEDA INCRASSATA (ELLIS) LAMOUROUX
(After Boergesen 1913).
Various Halimeda species occur on rocks or in the pelos and can reach heights of 25 cm or more. Halimeda is among the more common algae of southern Florida.

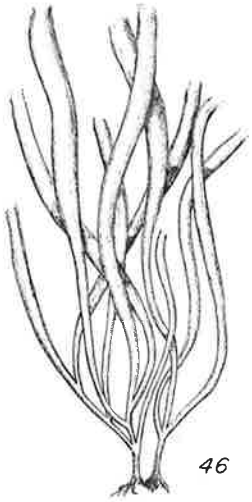
MAGNIFICATION FACTORS:

Fig. 45: 0.9×; Fig. 46: 0.75×; Fig. 47: 6×; Fig. 48: 4×; Fig. 49: 1.2×; Fig. 50: 0.5×; Fig. 51: 0.35×; Fig. 52: 0.5×.



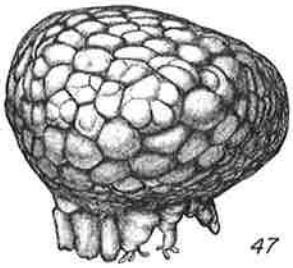
45

Dictyosphaeria



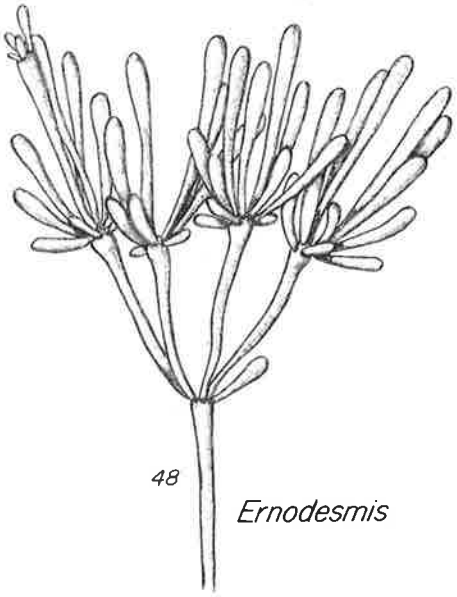
46

Enteromorpha



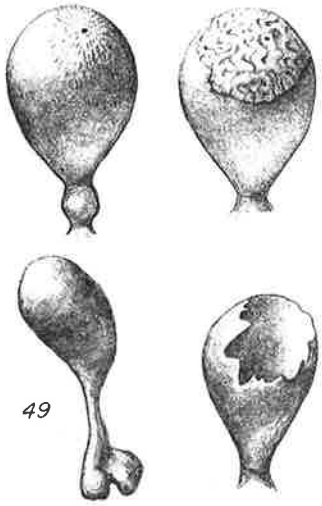
47

Dictyosphaeria



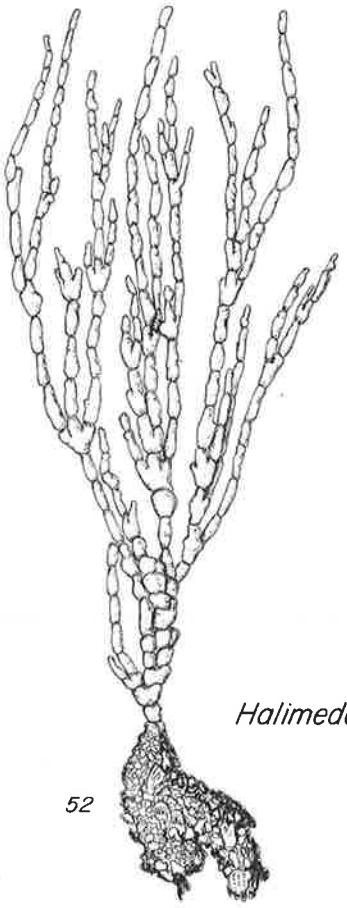
48

Ernodesmis



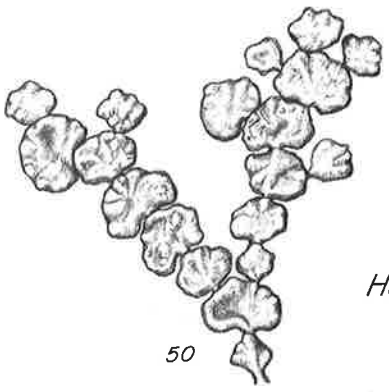
49

Halicystis



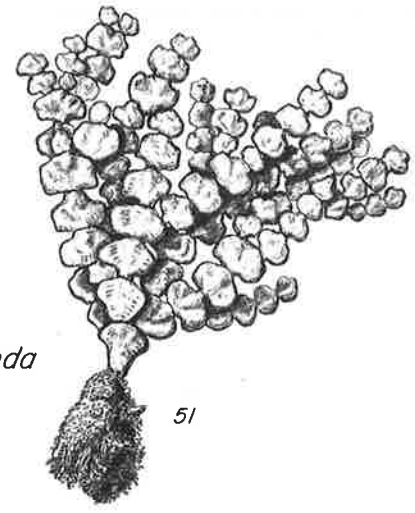
52

Halimeda



50

Halimeda



51

FIG. 53. OSTREOBIUM QUEKETTII BORNET AND FLAHAULT
(After Collins 1909).
Microscopic plants grow within old or dead shells.

FIGS. 54-55. MONOSTROMA SP.
(After Oltmanns 1922). Note blade-like habit and monostromatic construction.
Plants usually up to 10 cm tall occur on various objects in shallow water and tidepools.

FIG. 56. PENICILLUS PYRIFORMIS A. AND E. S. GEPP
(After Boergesen 1913).
Penicillus plants occur commonly in sand and mud and can reach heights of 15 cm.

FIG. 57. PENICILLUS CAPITATUS LAMARC
(After Boergesen 1913).

FIG. 58. RHIPOCEPHALUS PHOENIX (ELLIS AND SOLANDER) KUTZING. (After A. and E. S. Gepp 1911).
Plants rarely exceed 6 cm in length and occur in sand or mud.

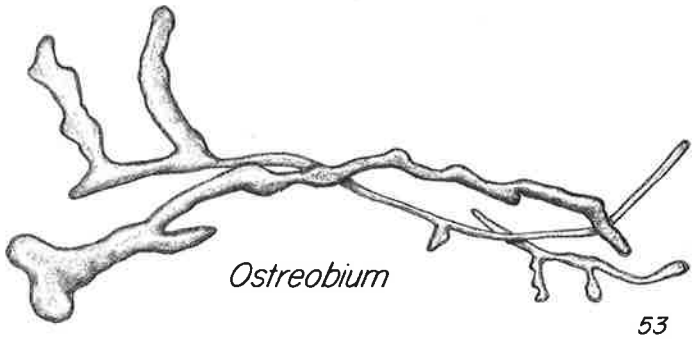
FIG. 59. NEOMERIS ANNULATA DICKIE
(Original).
Plants generally grow to 1-2 cm tall and occur on stones in shallow water; they can stand moderate wave action.

FIG. 60. MICRODICTYON BOERGESENII SETCHELL
(After Setchell 1925). Portion of a plant showing netlike habit.
Plants of indefinite size and shape occur on stones or in the aufwuchs, usually in deeper water.

FIG. 61. SIPHONOCLADUS TROPICUS (CROUAN) J. AGARDH
(After Boergesen 1918). Habit of plant.
Plants usually do not grow over seven cm tall and occur in the aufwuchs or in loose lying clumps in very sheltered localities.

MAGNIFICATION FACTORS:

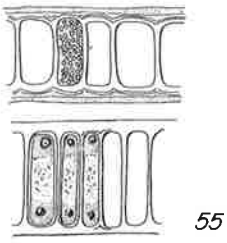
Fig. 53: 250×; Fig. 54: 0.7×; Fig. 55: 375×; Fig. 56: 0.5×; Fig. 57: 0.5×; Fig. 58: 1.0×; Fig. 59: 4×; Fig. 60: 6×; Fig. 61: 2×.



Ostreobium

53

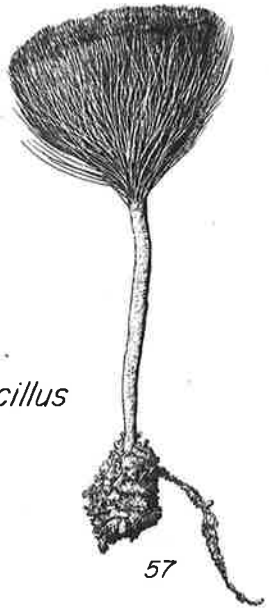
54



55

Monostroma

56



Penicillus

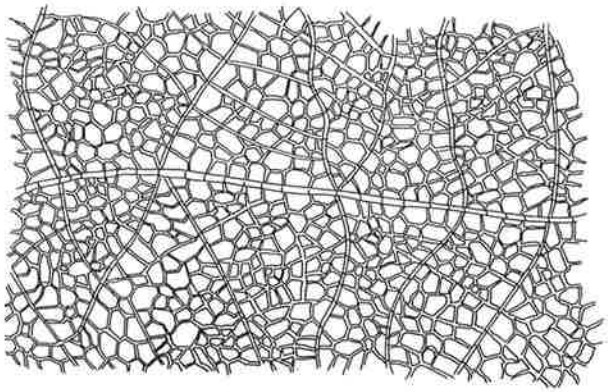
57

Rhipocephalus

58

59

Neomeris



60

Microdictyon

Siphonocladus

61

FIGS. 62-63. STRUVEA SP.

(After Oltmanns 1922). Habit of young and reasonably mature individuals.
Plants grow to 15 cm and occur on rocks, often in deeper waters.

FIG. 64. UDOTEA FLABELLUM (ELLIS AND SOLANDER) LAMOUROUX. (Original). Habit.
Plants reach heights of over 20 cm and occur in the pelos of both sheltered and exposed habitats. Large plants are common in lagoons.

FIG. 65. VALONIA VENTRICOSA J. AGARDH

(After Boergesen 1913). Habit of young plant.
Most species are less than 4 cm across and can occur in the lithos or aufwuchs in both sheltered and exposed localities. They are common on vertical rock faces just below the low tide mark.

FIG. 66. ULVELLA LENS CROUAN

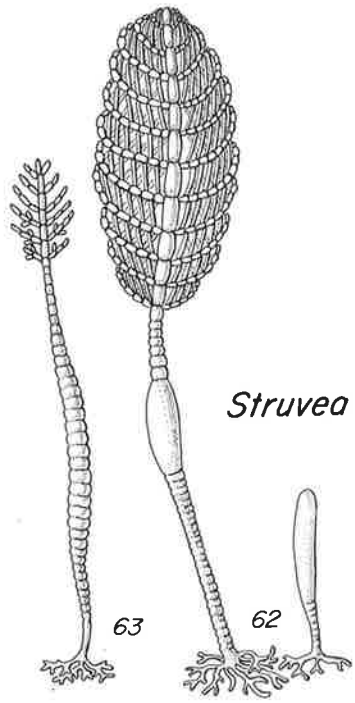
(After Collins 1909). Habit.
Plants form colonies 1-5 mm broad on stones or other algae.

FIG. 67. ULVA LACTUCA LINNEAUS

(After Oltmanns 1922). Habit.
Plants can attain lengths of over 1 mm and occur on stones, coral fragments, mangrove roots and other objects most commonly in the intertidal zone both in sheltered and exposed localities.

MAGNIFICATION FACTORS:

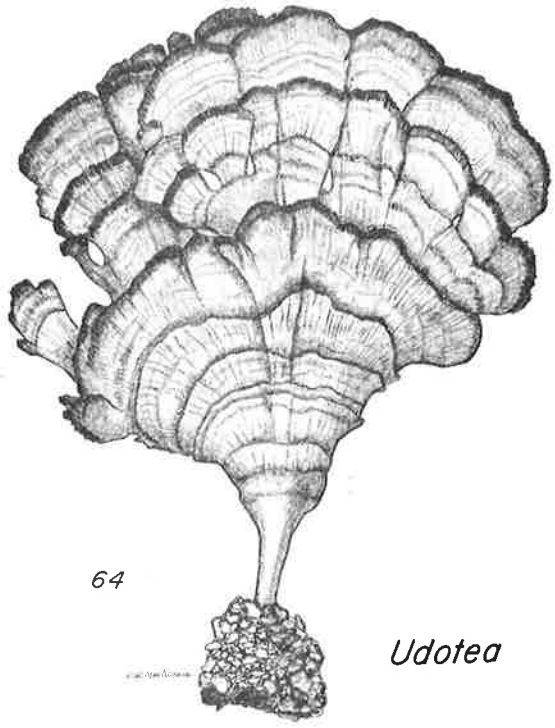
Fig. 62: 0.9×; Fig. 63: 0.9×; Fig. 64: 0.3×; Fig. 65: 50×; Fig. 66: 300×; Fig. 67: 0.2×.



Struvea

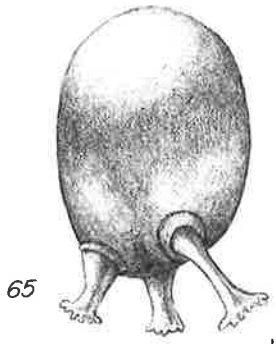
63

62



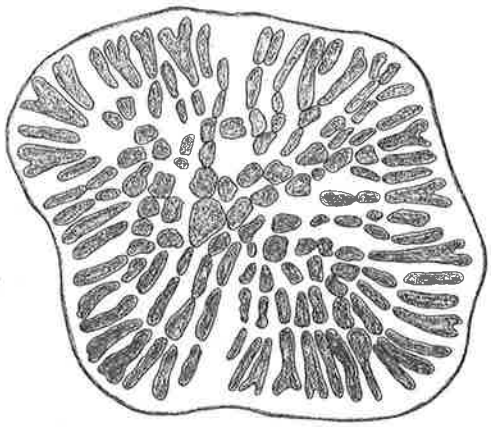
64

Udotea



65

Valonia



66

Ulvella

67

Ulva

FIGS. 68-70. CLADOSIPHON OCCIDENTALIS KYLIN

(After Boergesen 1914 as Castagnea zosterae). Assimilators and plurilocular sporangia (68); Longitudinal section of plant (69); unilocular sporangium (70).
Plants attain heights of 15-20 cm and usually occur in the aufwuchs on sea grasses or other algae in shallow water.

FIGS. 71-72. ASCOCYCLUS ORBICULARIS (J. AGARDH) MAGNUS

(Original). Habit on a sea grass (71); portion of thallus (72) showing erect filaments.
Plants rarely exceed 3 mm in diameter and usually occur on sea grasses or algae in shallow water.

FIG. 73. COLPOMENIA SINUOSA (ROTH) DERBÈS AND SOLIER

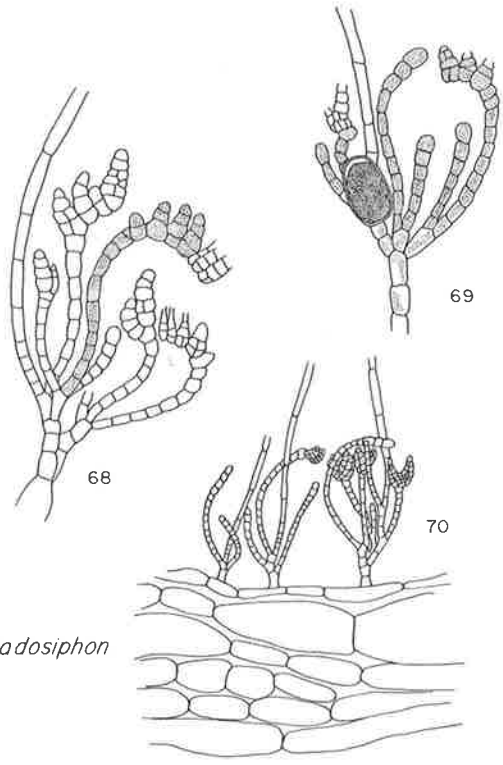
(After Oltmanns 1923). Habit.
Colpomenia plants grow to 12 cm across and are most common on intertidal rocks in exposed habitats.

FIGS. 74-76. DICTYOPTERIS DELICATULA LAMOUROUX

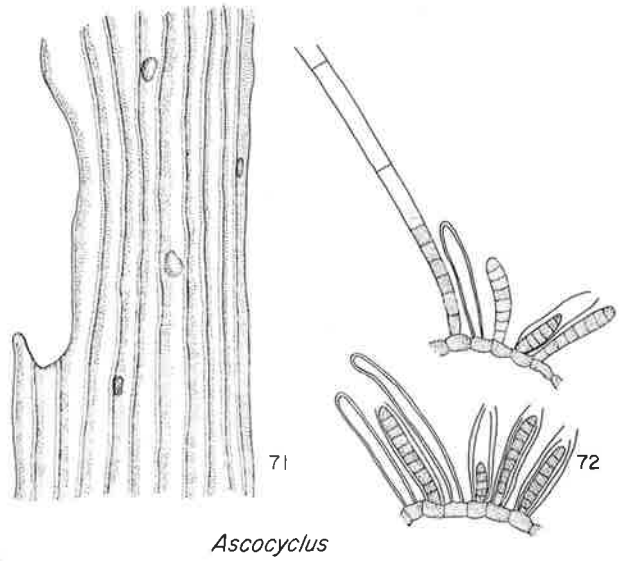
(After Boergesen 1914). Habit, part of thallus (74); cross sections of thallus (75-76). Note hairs (75).
Species of Dictyopteris range from 5 to over 40 cm tall. Certain species grow on rocks in areas of moderate wave action; others occur as epiphytes on larger algae.

MAGNIFICATION FACTORS:

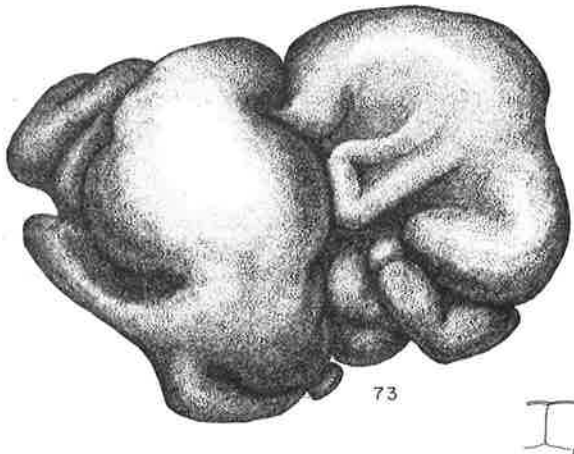
Fig. 68: 200×; Fig. 69: 170×; Fig. 70: 60×; Fig. 71: 1×; Fig. 72: 140×; Fig. 73: 1.2×; Fig. 74: 2.8×; Figs. 75: 12×; Fig. 76: 15×.



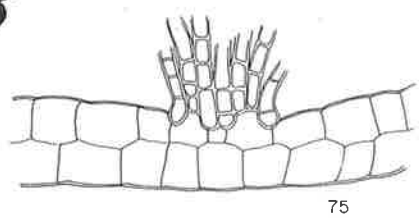
Cladosiphon

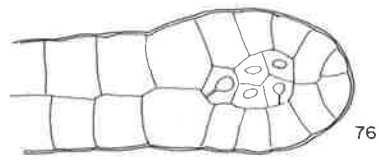


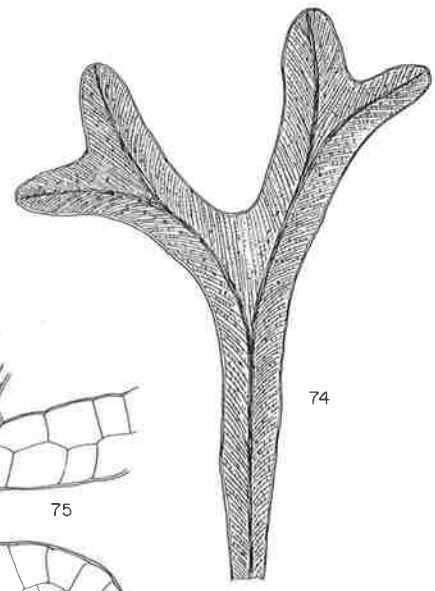
Ascocyclus



Colpomenia







Dictyopteris

FIGS. 77-79. DICTYOTA DICHOTOMA (HUDSON) LAMOUROUX

(After Oltmanns 1922). Habit of portion of plant (77). Branch tips (78-79). Note apical cells.

Plants of Dictyota vary from 5-35 cm or more tall and generally occur on rocks in shallow water in the upper sublittoral zone. Certain species seem to do better in more exposed habitats; others prefer more sheltered localities.

FIGS. 80-81. DICTYOTA CRENULATA J. AGARDH

(After Boergesen 1914). Cross section (80) showing female reproductive organs; cross section (81) showing male reproductive organs. Note: This taxon occurs in the neighboring Virgin Islands.

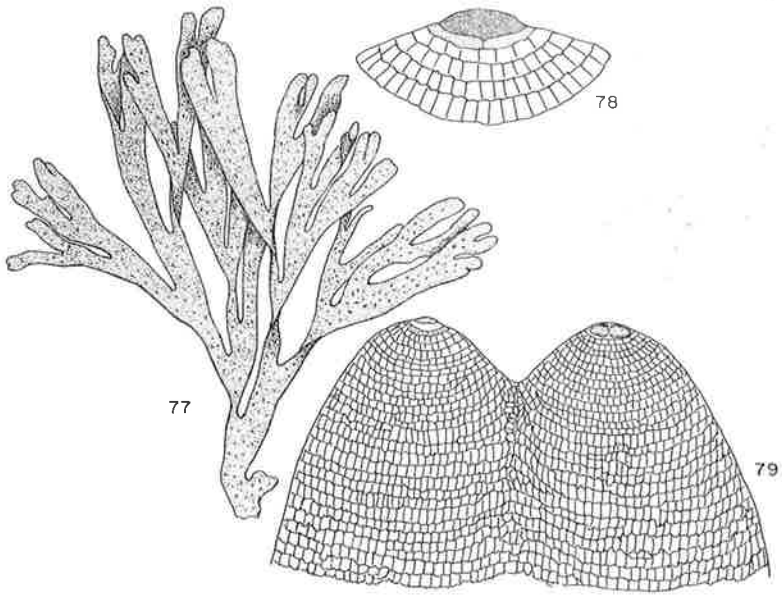
FIGS. 82-84. DILOPHUS QUINEENSIS (KUTZING) J. AGARDH

(After Boergesen 1914). Cross section (82) near tip showing sporangia and hairs; branch tip (83) with sporangia; cross section of older part of thallus (84).

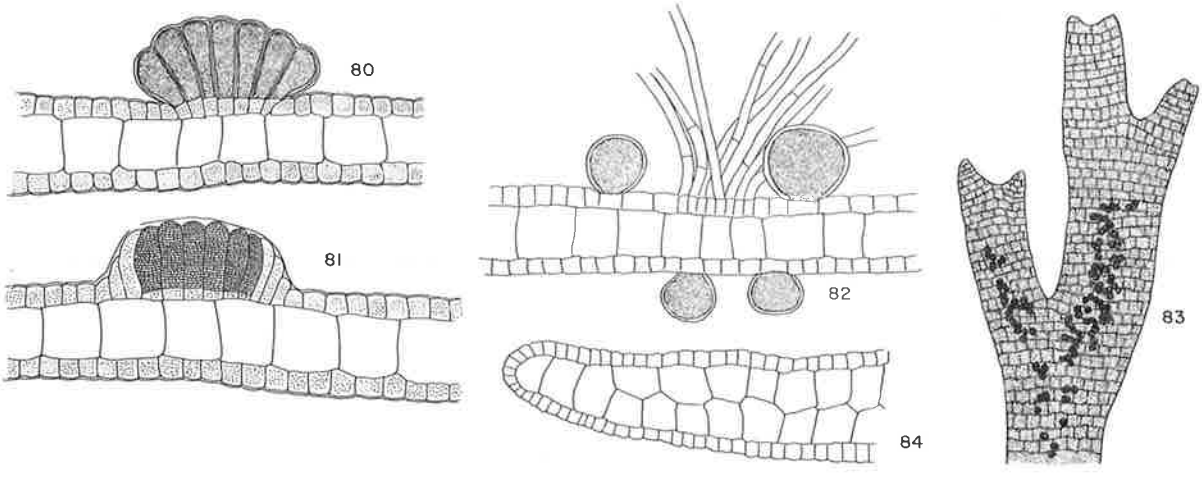
Plants rarely reach 15 cm in length and most commonly occur on upper sublittoral rocks on open coasts. Deeper water collections (to 26 m) are also known.

MAGNIFICATION FACTORS:

Fig. 77: 0.6×; Fig. 78: 30×; Fig. 79: 8×; Fig. 80: 75×; Fig. 81: 75×; Fig. 82: 80×; Fig. 839×; Fig. 84: 80×.



Dictyota



Dilophus

FIGS. 85-87. ECTOCARPUS SILICULOSUS (DILLWYN) LYNGBYE

(Original). Habit (85); branches bearing sporangia (86-87).

Some species of Ectocarpus rarely grow over 1.5 mm tall; others attain heights of 60 cm. The plants occur in a variety of habitats and are common in both the aufwuchs and lithos communities. Sporangia occur on most plants throughout the year and may be one celled or many celled.

FIG. 88. EUDESME ZOSTERAE (J. AGARDH) KYLIN

(After Boergesen 1914). Erect filaments showing trichothallic growth.

Plants of Eudesme consist of numerous filaments more or less firmly united in a common mucilage to form a more or less cylindrical thallus up to 10 (-30) cm tall. Specimens most commonly occur as epiphytes in shallow, sheltered habitats.

FIGS. 89-92. GIFFORDIA MITCHELLAE (HARVEY) HAMEL

(After Boergesen, as Ectocarpus). Erect branches (89, 92) with sporangia (89); cells with chromoplasts (90, 91).

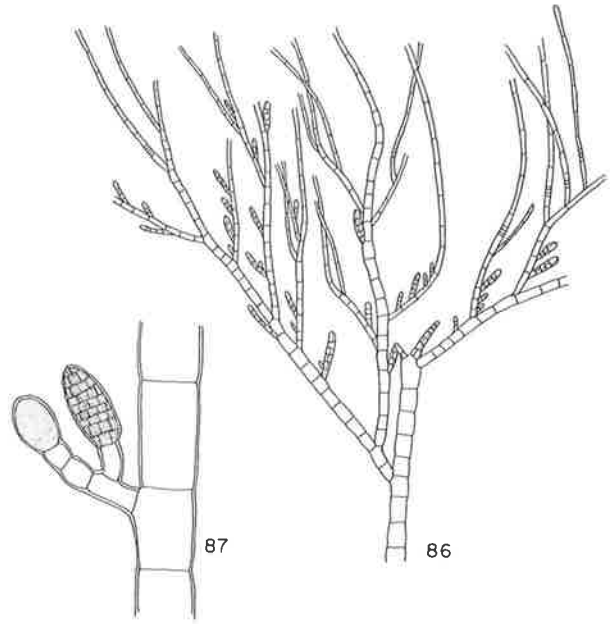
Giffordia plants show the same size range, habitat distribution and reproductive cycles as do species of Ectocarpus (see above).

MAGNIFICATION FACTORS:

Fig. 85: 0.5×; Fig. 86: 70×; Fig. 87: 250×; Fig. 88: 125×; Fig. 89: 70×; Figs. 90-91: 70×; Fig. 92: 155×.

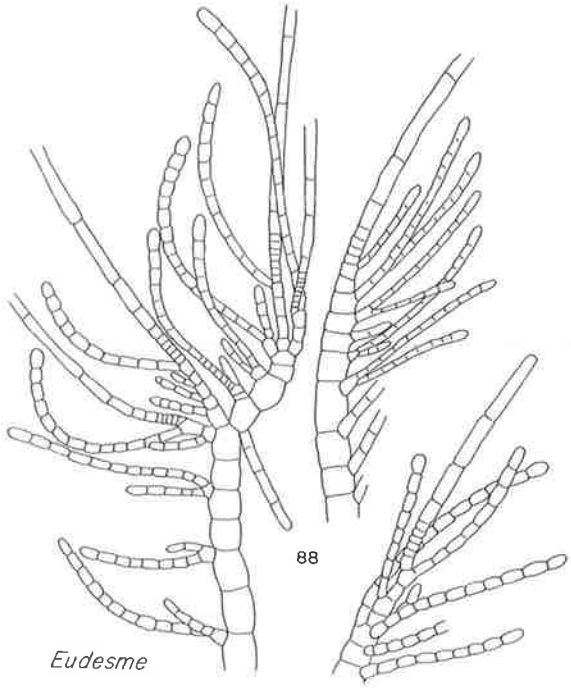
85

Ectocarpus



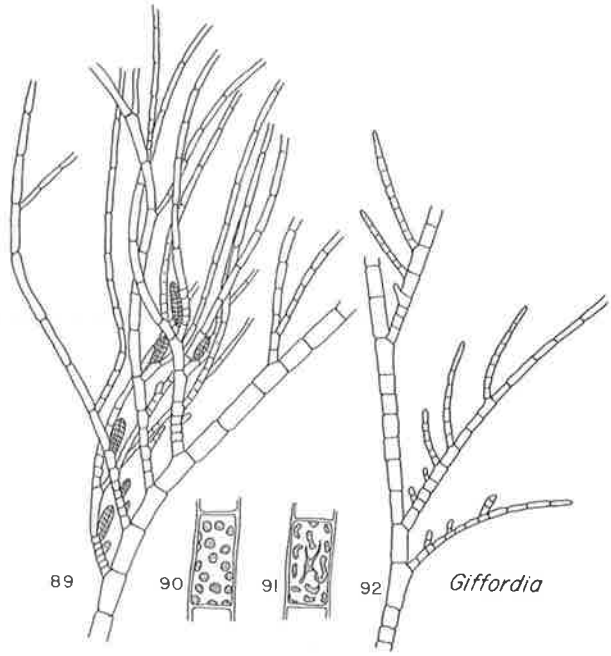
87

86



88

Eudesme



89

90

91

92

Giffordia

FIGS. 93-98. PADINA PAVONICA (LINNEAUS) THIVY IN TAYLOR

(After Harvey 1852, as P. pavonis). Habit of plant (93); surface of blade (94); close up of a sorus (95) and spores (97); close up of surface hairs (96, 98). Figs. 97, 98 also show thallus cross sections.

Padina is the only brown alga in Florida with a calcified thallus. Blades up to 10 cm across occur on rocks, usually in shallow water with slight to moderate wave action.

FIGS. 99-100. LOBOPHORA VARIEGATA (LAMOUROUX) WOMERSLEY

(After Boergesen 1914, as Zonaria variegata). Cross section (99) of thallus with sporangia in a sorus (top) and empty sori (bottom); cross section of young thallus (100).

Fan shaped blades up to 8 cm tall occur most commonly on intertidal rocks of exposed coasts.

FIGS. 101-102. RALFSIA EXPANSA J. AGARDH

(After Boergesen 1914). Cross section showing sporangia (101); cross section near edge of thallus (102).

Ralfsia plants form tar-like crusts on rocks and other hard objects in shallow water, mostly in areas of moderate wave action.

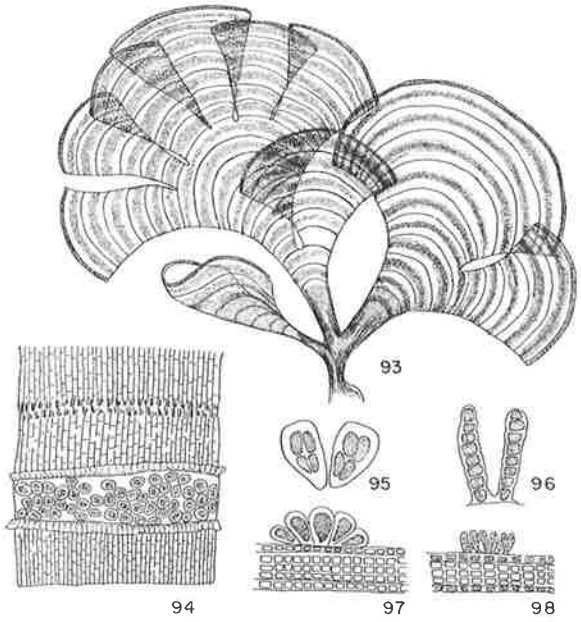
FIGS. 103-106. ROSENVINGEA SANCTAE-CRUSIS BOERGESEN

(After Boergesen 1941). Habit of plant (103); longitudinal section of thallus showing cell types (104); cross section of thallus (105); cross section showing plurilocular sporangia (106).

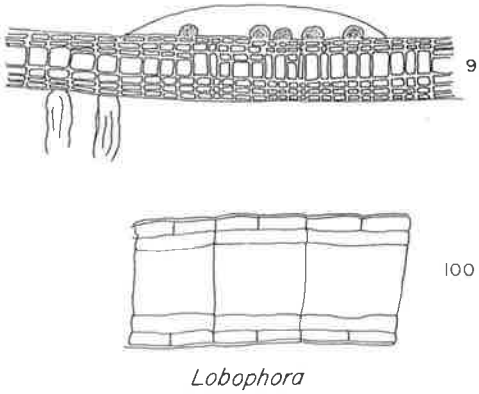
Plants normally reach heights of 20-40 cm, depending upon the species, and most commonly occur on rocks in shallow water. One species is found in sheltered locations; the others grow in more exposed habitats.

MAGNIFICATION FACTORS:

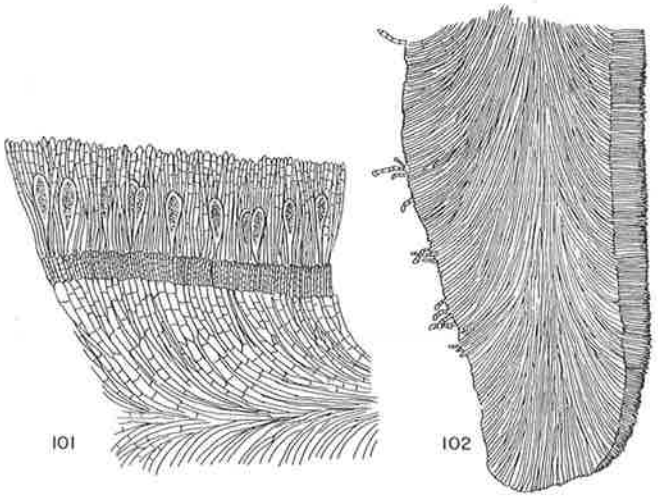
Fig. 93: 0.5×; Fig. 94: 10×; Fig. 95: 300×; Fig. 96: 100×; Fig. 97: 50×; Fig. 98: 50×; Fig. 99: 40×; Fig. 100: 70×; Fig. 101: 45×; Fig. 102: 30×; Fig. 103: 0.4×; Fig. 104: 140×; Fig. 105: 125×; Fig. 106: 110×.



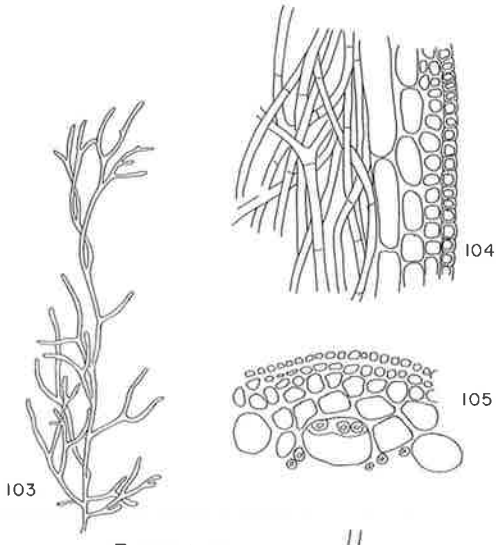
Padina



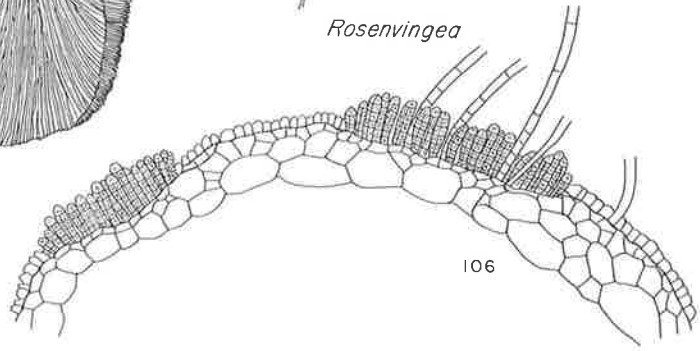
Lobophora



Ralfsia



Rosenvingea



FIGS. 107-108. SARGASSUM FILIPENDULA C. AGARDH VAR. MONTAGNEI (BAILEY) GRUNOW. (Harvey 1852, as S. montagnei). Habit of plant (107); branch showing leaf, vesicles (air bladders), and receptacles (108).
Most species of Sargassum occur on rocks in the sublittoral zone of rocky coasts and can attain heights of over 100 cm. Two species occur in an unattached state and are responsible for the naming of the Sargasso Sea. These two are always sterile, lack holdfasts, and are usually covered with bryozoans.

FIG. 109. SCYTOSIPHON LOMENTARIA (LYNGBYE) C. AGARDH (After Oltmanns 1922). Habit
Plants normally do not exceed 50 cm in length and occur on sublittoral rocks in areas protected from strong wave action.

FIG. 110. SPATOGLOSSUM SCHROEDERI (MERTENS) KÜTZING (Original). Habit.
Plants of Spatoglossum often appear irridescent when growing; they attain heights of 10-30 cm and usually occur on rocks in areas of slight to moderate wave action.

FIG. 111. SPHACELARIA SP. SHOWING APEX AND GROWTH PATTERN. (After Oltmanns 1922).

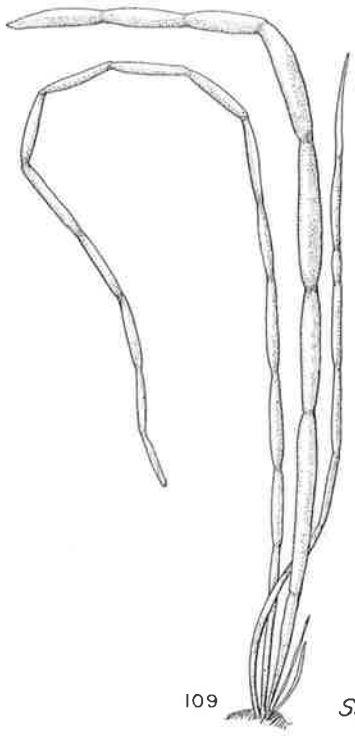
FIG. 112. SPHACELARIA TRIBULOIDES MENEGHINI (After Oltmanns 1922). Showing propagule.

FIG. 113. SPHACELARIA FUCIGERA KÜTZING (After Oltmanns 1922). Branch bearing a number of propagulae.
Sphacelaria plants vary from 5 mm to 3 cm in height and appear as coarse tufts of filaments in the aufwuchs and lithos of exposed coasts. The polysiphonous-like appearance of the branches makes them readily recognizable.

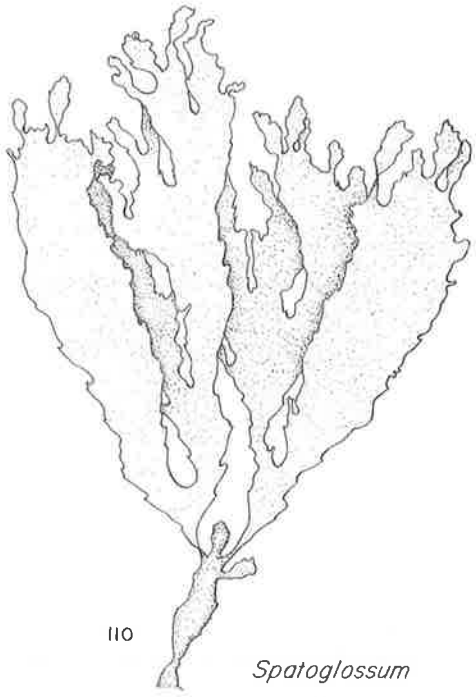
MAGNIFICATION FACTORS:

Fig. 107: 0.2×; Fig. 108: 1.0×; Fig. 109: 0.3×; Fig. 110: 0.3×; Fig. 111: 135×; Fig. 112: 120×; Fig. 113: 100×.

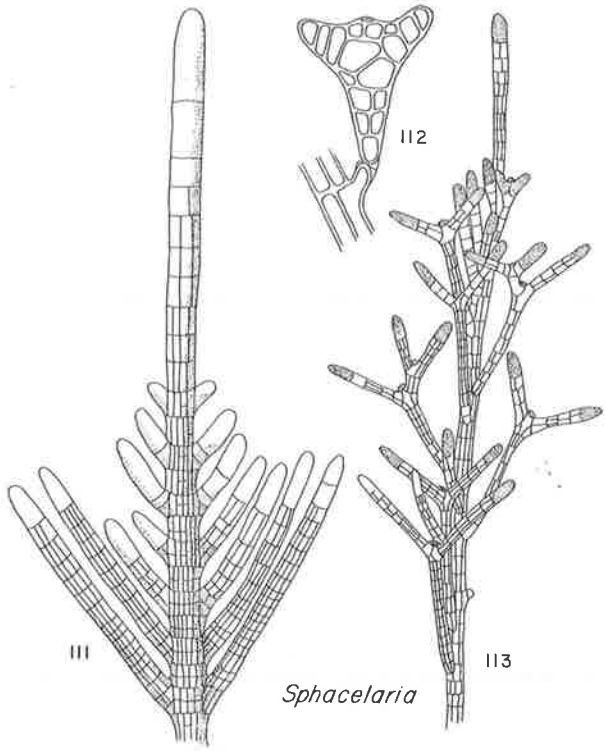
Sargassum



Scytosiphon



Spatoglossum



Sphacelaria

FIG. 114. SPOROCHNUS BOLLEANUS MONTAGNE

(Original). Habit.

Sporochnus plants often reach heights of over 80 cm and occur on rocks along open coasts. One species is known only from deep water, but the other can occur close to the low tide mark in shallow water. It is among the most elegant of brown algae.

FIG. 115. STILOPHORA RHIZOIDES (EHRHART) J. AGARDH

(Original). Habit of plant.

Stilophora plants can grow to 30 cm tall and often appear stiff and brittle. They occur most commonly in the lithos of sheltered localities.

FIG. 116. STYPOPODIUM ZONALE (LAMOUROUX) PAPENFUSS

(Original). Habit of plant.

Stypopodium plants commonly are irridescent when growing and attain lengths of 40 cm. They usually occur in shallow water on exposed coasts and can be present in abundance.

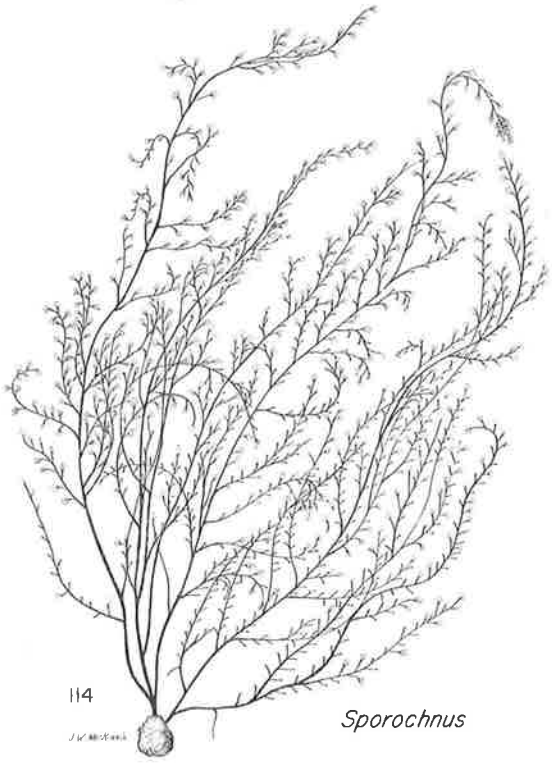
FIG. 117. TURBINARIA TURBINATA (LINNEAUS) KUNTZE

(After Boergesen 1914). Portion of thallus showing turbinate leaves.

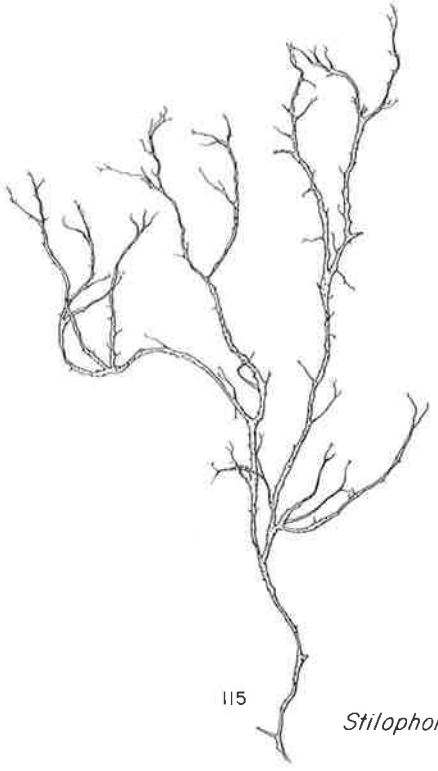
Turbinaria can grow to 40 cm or more and is found on rocky coasts both in the sublittoral and intertidal zones, often in tide pools.

MAGNIFICATION FACTORS:

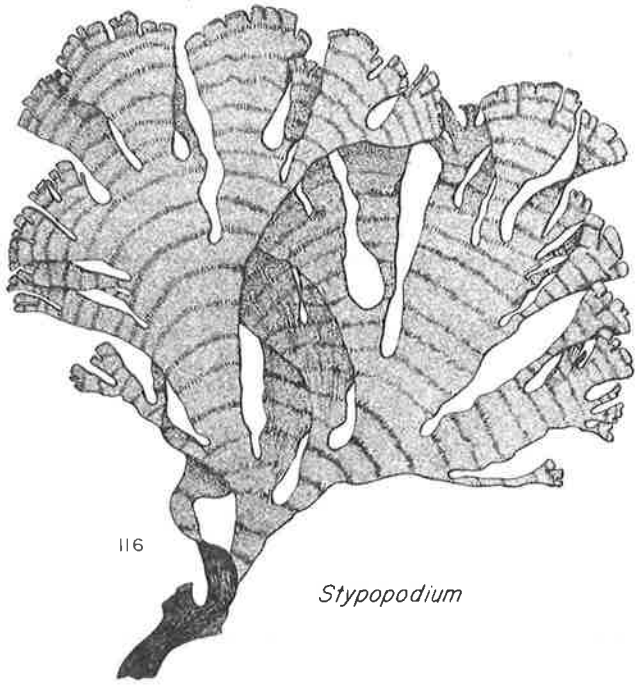
Fig. 114: 0.1×; Fig. 115: 0.4×; Fig. 116: 0.2×; Fig. 117: 1.1×.



114 *Sporochnus*



115 *Stilophora*



116 *Stypopodium*

117 *Turbinaria*

FIGS. 118-120. ACANTHOPHORA SPICIFERA (VAHL) BOERGESEN

(After Boergesen 1915-1920 [119, 120] and Harvey 1853 [118, as A. thierii]). Habit of portion of plant (118); cross section of branch (119); axis showing spinose-warty ultimate branchlets (120).

Plants grow to 25 cm tall and are common in shallow water of rocky coasts both in exposed and sheltered localities.

FIGS. 121-124. ANTITHAMNION ANTILLANUM BOERGESEN

(After Boergesen 1930). Drawings of a species from the Virgin Islands to be expected in Florida. Portions of erect axes bearing mature (121, 124) and immature (123) tetrasporangia; spermatangia (122).

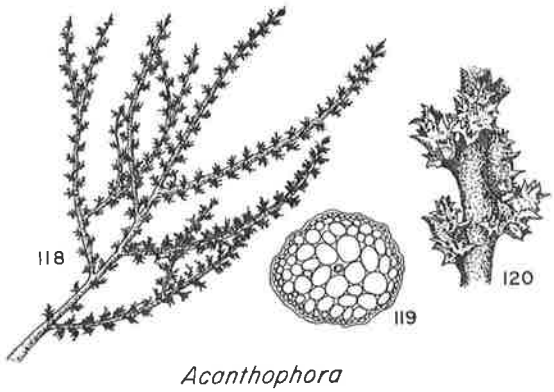
Plants commonly reach 5-12 cm in length and occur both in the lithos and aufwuchs of both sheltered and exposed coasts.

FIGS. 125-127. ASPARAGOPSIS TAXIFORMIS (DELILE) COLLINS AND HERVEY. (Original [125] and after Boergesen 1915-1920 [126-127]). Habit and sections of branches of sexual plants.

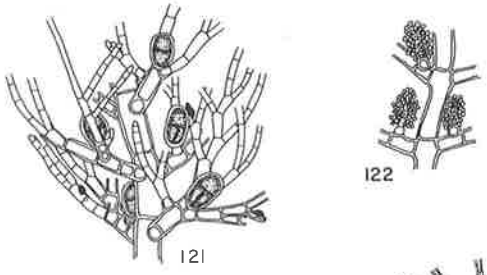
To date, only tetrasporophyte plants of this taxon have been reported for Florida, and these have been placed under the name Falkenbergia (See Chihara 1960 for details on the life cycle). See also Figs. 209-215.

MAGNIFICATION FACTORS:

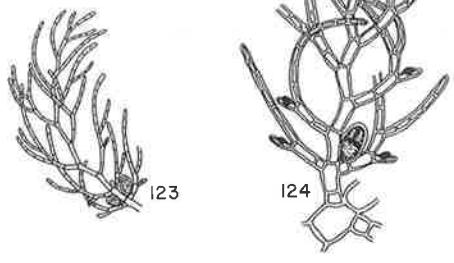
Fig. 118: 0.9×; Fig. 119: 20×; Fig. 120: 4×; Fig. 121: 75×; Fig. 122: 120×; Fig. 123: 25×; Fig. 124: 65×; Fig. 125: 0.7×; Fig. 126: 23×; Fig. 127: 30×.



Aconthophora



Antithamnion



Asparagopsis

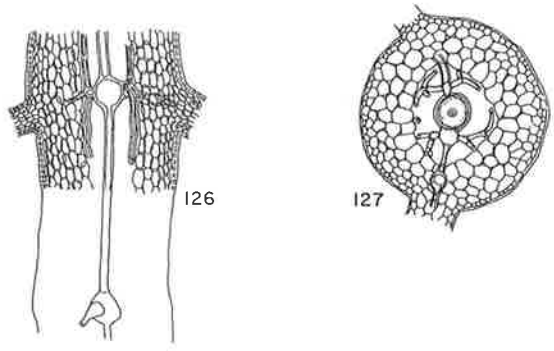


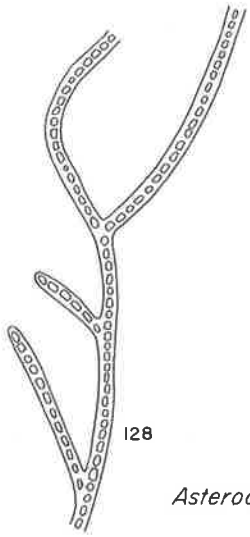
FIG. 128 ASTEROCYTIS RAMOSA (THWAITES) GOBI (After Boergesen 1915-1920).
Plants rarely exceed 15 mm in length and occur in the aufwuchs communities of shallow water.

FIGS. 129-131. THREE TAXA OF THE AUDOUINELLA COMPLEX (ACROCHAETIACEAE). (After Boergesen 1915-1920). Fig. 129: Audouinella microscopica (Naegeli in Kutzing) Woelkerling; Fig. 130: Acrochaetium globosum Boergesen; Fig. 131: Audouinella liagorae (Boergesen) Woelkerling.
Acrochaetioid algae are common in aufwuchs samples but are often missed because of their small size. Certain species only grow to 20 µm tall; others reach 5 mm. Endophytic forms are completely immersed in host tissue and thus become hidden. These algae occur in all sublittoral environments and occasionally are found in the lower intertidal zone.

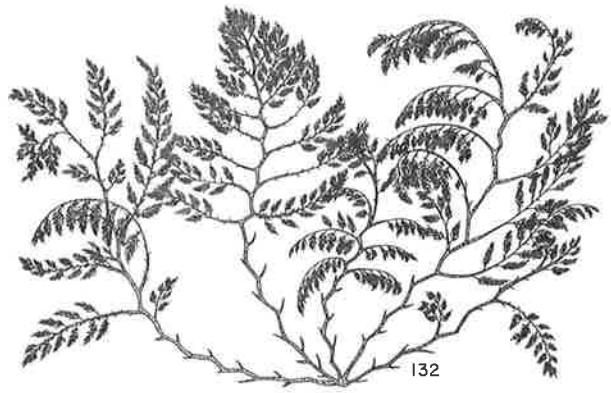
FIGS. 132-134. BOSTRYCHIA. (Figs. 132, 134: B. montagnei Harvey) (After Harvey 1853) showing habit (132) and branch with tetrasporangia (134). Fig. 133: B. tenella (Vahl) J. Agardh (after Boergesen 1915-1920) showing cross section of branch.
Most species of Bostrychia reach heights of 2-7.5 cm. They are especially common in the intertidal zone on mangrove roots, but also occur commonly on intertidal rocks under both sheltered and exposed conditions.

MAGNIFICATION FACTORS:

Fig. 128: 80×; Fig. 129: 500×; Fig. 130: 50×; Fig. 131: 120×; Fig. 132: 0.75×; Fig. 133: 60×; Fig. 134: 12×.

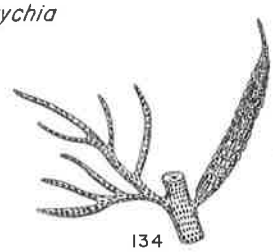


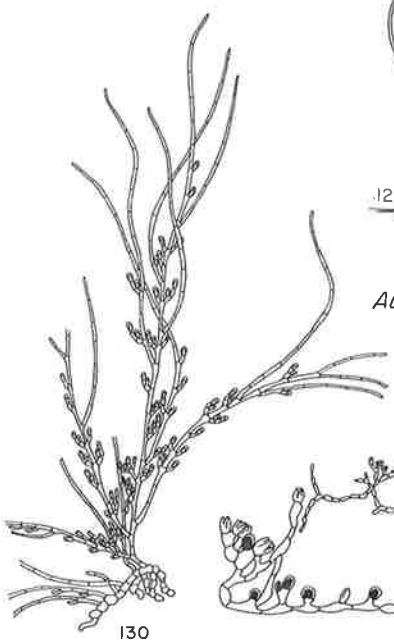
Asterocytis



Bostrychia

Audouinella





FIGS. 135-137. BOTRYOCLADIA PYRIFORMIS (BOERGESEN) KYLIN

(After Boergesen 1915-1920, as Chrysymenia pyriformis). Habit (135, 136) and cross section of branch (137).

Botryocladia plants occur on rocky shores from the low intertidal down and can reach lengths of 25 cm.

FIGS. 138-142. BRYOTHAMNION. B. triquetrum (Gmelin) Howe

(After Harvey 1853, Figs. 138-140, 142), as Alsidium triquetrum). Figs. 138-139: Habit and individual branch; Fig. 140: Tetrasporangial branchlets; Fig. 142: cross section. B. seaforthii (Turner Fig. 141 (after Boergesen 1915-1920). Cross section of branch.

Plants attain lengths of 25 cm and occur on rock in the upper sublittoral zone of open coasts.

FIGS. 143-145. CALLITHAMNION BYSSOIDES ARNOTT IN HOOKER

(After Boergesen 1915-1920). Habit of tetrasporangial plant (143); cell with chromoplast (144); branch with spermatangia (145).

Plants grow to 10 cm tall and occur in the aufwuchs and lithos.

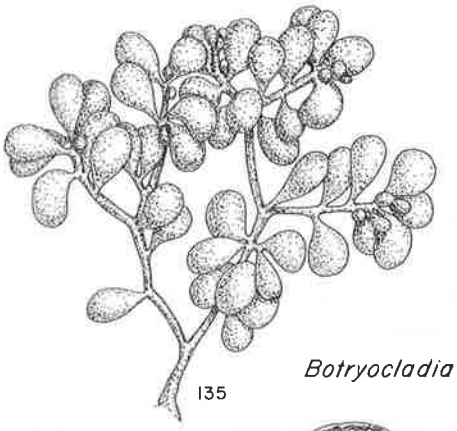
FIGS. 146-148. CALOGLOSSA LEPRIEURII (MONTAGNE) J. AGARDH

(After Harvey 1853, as Delesseria leprieurii) showing habit (146); a branch system (147); and a branch tip (148).

Caloglossa plants commonly grow in sheltered intertidal communities on rocks or on mangroves and often form clumps 4-5 cm across.

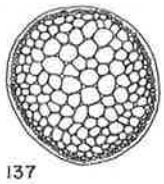
MAGNIFICATION FACTORS:

Fig. 135: 0.9×; Fig. 136: 0.6×; Fig. 137: 25×; Fig. 138: 0.6×; Fig. 139: 1.3×; Fig. 140: 40×; Fig. 141: 12×; Fig. 142: 15×; Fig. 143: 40×; Fig. 144: 265×; Fig. 145: 65*; Fig. 146: 1×; Fig. 147: 2×; Fig. 148: 16×.



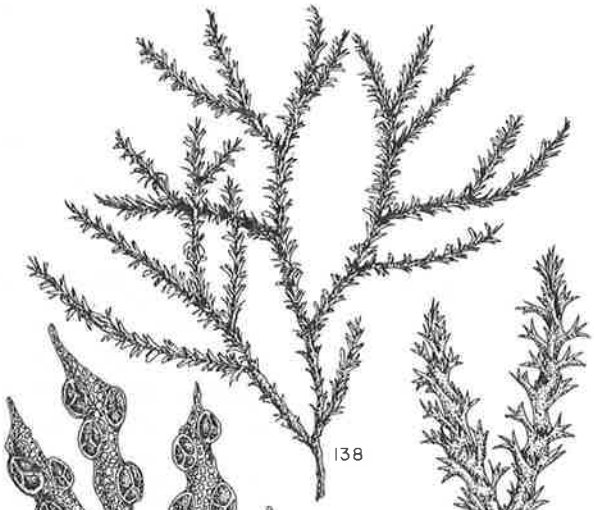
135

Botryocladia



137

136

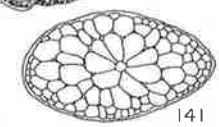


138

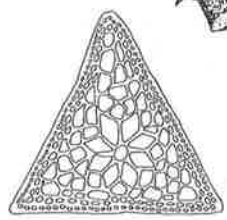
139

Bryothamnion

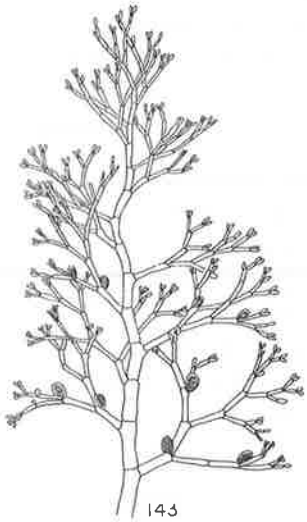
140



141



142

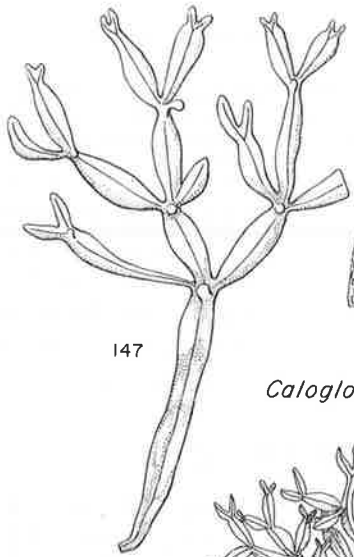


143

144

Callithamnion

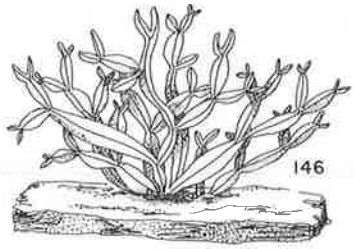
145



147

148

Caloglossa



146

FIGS. 149-152. CATENELLA REPENS (LIGHTFOOT) BATTERS

(After Harvey 1853, as Catenella pinnata). Habit (149); branch showing constrictions (150); cross section (151) and longitudinal section (152) of a branch.

Catenella plants rarely exceed 3 cm in height and are most common in the intertidal zone on mangroves in lagoons.

FIGS. 153-157. CENTROCERAS CALAVULATUM (C. AGARDH) MONTAGNE

(Original [155] and after Harvey 1853 [153, 154, 156, 157]). Habit (153); successive enlargements of branches (154-156) and a node showing 2 celled spines (157).

Plants reach lengths of 10-20 cm and commonly occur in sheltered localities either attached or in loose lying masses. Specimens are exceedingly variable.

FIGS. 158-161. CERAMIUM BYSSOIDEUM HARVEY

(Original [158] and after Collins and Hervey 1917 [159-161], as C. transversale). Vegetative filaments (158-160) and tetrasporangia (161).

Species of Ceramium vary from under 1 cm to over 15 cm long and occur in the aufwuchs and lithos of almost all communities. They are especially common in shallow water and the banding of cells about the nodes often can be seen with the unaided eye. Certain species are almost completely corticated.

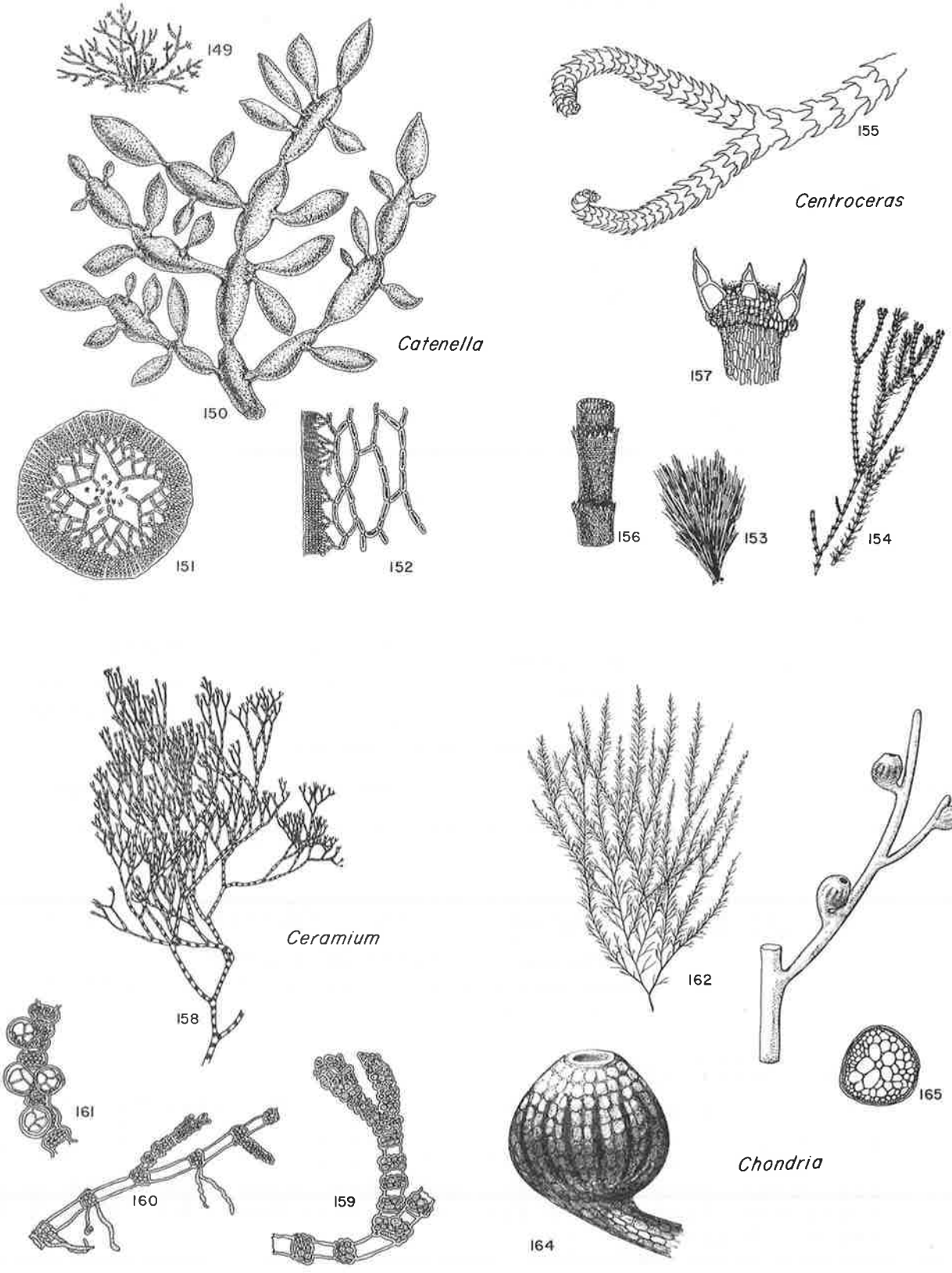
FIGS. 162-165. CHONDRIA LITTORALIS HARVEY

(After Harvey 1853 [162-164] and Boergesen 1915-1920 [165]). Habit (162); branch bearing cystocarps (163) and a single cystocarp (164); branch cross section (165) showing central axis and 5 pericentral cells.

Plants of Chondria usually grow to 10-30 cm tall and usually occur in the lithos of somewhat sheltered localities. They are common in shallow water.

MAGNIFICATION FACTORS:

Fig. 149: 0.5×; Fig. 150: 2.5×; Fig. 151: 15×; Fig. 152: 15×; Fig. 153: 6.5×; Fig. 154: 10×; Fig. 155: 60×; Fig. 156: 60×; Fig. 157: 100×; Fig. 158: 2×; Fig. 159: 50×; Fig. 160: 50×; Fig. 161: 100×; Fig. 162: 0.25×; Fig. 163: 8×; Fig. 164: 40×; Fig. 165: 25×.


149
150
Catenella
151
152
155
Centroceras
157
156
153
154
158
Ceramium
161
160
159
162
165
164
Chondria

FIGS. 166-168. CHRYSYMENIA HALYMENIOIDES HARVEY

(After Harvey 1853). Habit (166); cross section showing cystocarps (167); cross section of tetrasporangial plant (168).
Plants grow to 10-30 cm and occur in the lithos of deeper waters. Specimens occasionally wash ashore.

FIGS. 169-177. COTTONIELLA

(After Boergesen 1915-1920). A series of drawings of C. arcuata from the Virgin Islands showing salient features of the genus needed for identification.
Plants generally attain lengths of 4-16 cm and occur in the aufwuchs of shallow and deeper waters.

FIGS. 178-180. COELOTHRIX IRREGULARIS (HARVEY) BOERGESEN

(After Boergesen 1915-1920). Branch of plant (178); cross section (179) and longitudinal section (180) both showing gland cells.
Plants usually grow to 3 cm and occur in the intertidal and sublittoral lithos in shaded areas.

FIGS. 181-183. CORALLINA CUBENSIS (MONTAGNE) KÜTZING

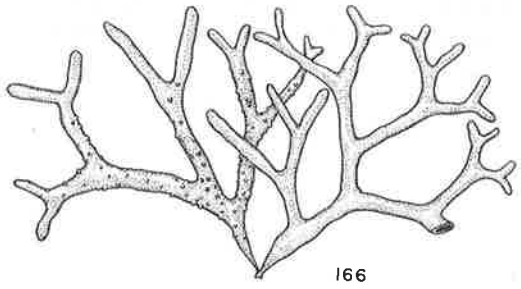
(After Boergesen 1915-1920). Segment of plant showing branching (181); conceptacle (182); and longitudinal section through a node (183).
Corallina occurs in the lithos and aufwuchs in tide pools and in sublittoral situations; plants usually do not exceed 3 cm in height.

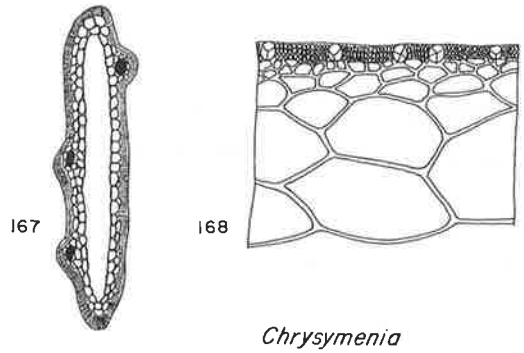
FIGS. 184-187. CORYNOMORPHA CLAVATA (HARVEY) J. AGARDH

(Original). Habit of plants.
Corynomorpha occurs in lithos from the lower intertidal downwards and usually is less than 5 cm tall.

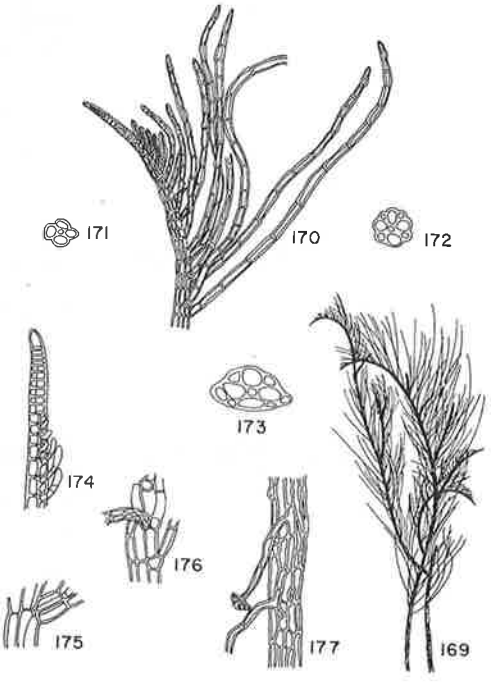
MAGNIFICATION FACTORS:

Fig. 166: 0.3×; Fig. 167: 5×; Fig. 168: 40×; Fig. 169: 18×; Fig. 170: 90×; Fig. 171: 100×; Fig. 172: 100×; Fig. 173: 100×; Fig. 174: 180×; Fig. 175: 135×; Fig. 176: 135×; Fig. 177: 30×; Fig. 178: 1.3×; Fig. 179: 140×; Fig. 180: 100×; Fig. 181: 6.5×; Fig. 182: 35×; Fig. 183: 80×; Figs. 184-7: 1.0×;

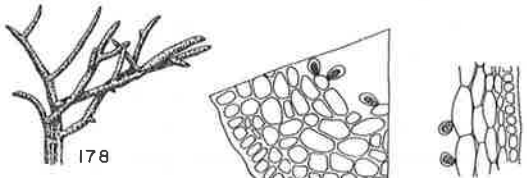




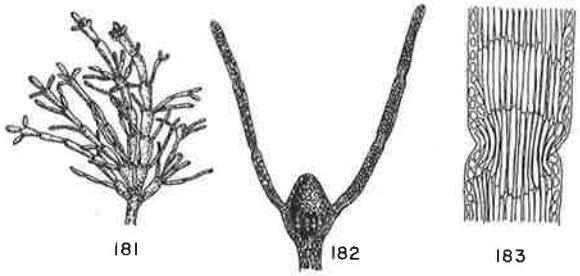
Chrysymenia



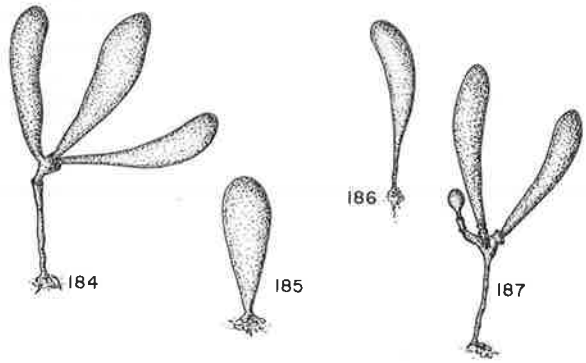
Cottoniella



Coelothrix



Corallina



Corynomorpha

FIGS. 188-192. CRYPTARACHNE AGARDHII (HARVEY) KYLIN

(After Boergesen 1915-1920 [191-192] and Harvey 1853 [188-190], both as Chrysymenia agardhii). Habit (188); longitudinal and cross sections (189-190); gland cells (191-192).
Plants grow to 20 cm and apparently are confined to the lithos of deeper waters.

FIG. 193. CRYPTONEMIA CRENULATA J. AGARDH

(Original). Habit of plant.
Plants reach 15 cm long and occur in sublittoral lithos, mostly from deeper waters.

FIGS. 194-196. CROUANIA ATTENUATA (BONNEMAISON) J. AGARDH

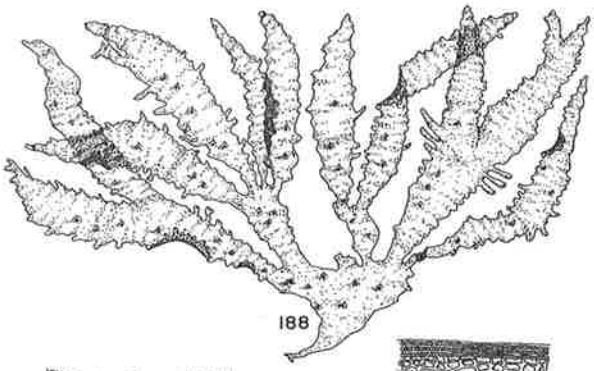
(After Boergesen 1915-1920 [195-196] and Harvey 1853 [194]). Branch (194); main axis with lateral branches.
Crouania occurs both in the aufwuchs and lithos in both shallow and deeper water; plants grow to 5 cm.

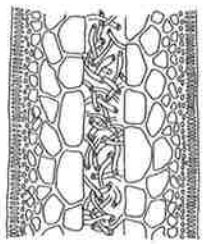
FIG. 197. DASYA BAILLOUVIANA (GMELIN) MONTAGNE

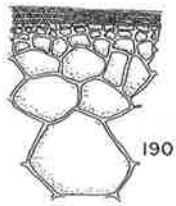
(Original). This taxon includes as a synonym the name D. pedicellata.
Species of Dasya vary from less than 2 cm to over 75 cm tall and occur in both the lithos and aufwuchs in shallow water. Many species have a feathery appearance due to the occurrence of numerous monosiphonous branchlets.

MAGNIFICATION FACTORS:

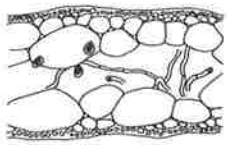
Fig. 188: 0.25×; Fig. 189: 50×; Fig. 190: 50×; Fig. 191: 30×; Fig. 192: 145×; Fig. 193: 0.4×; Fig. 194: 0.8×; Fig. 195: 120×; Fig. 196: 45×; Fig. 197: 0.2×.

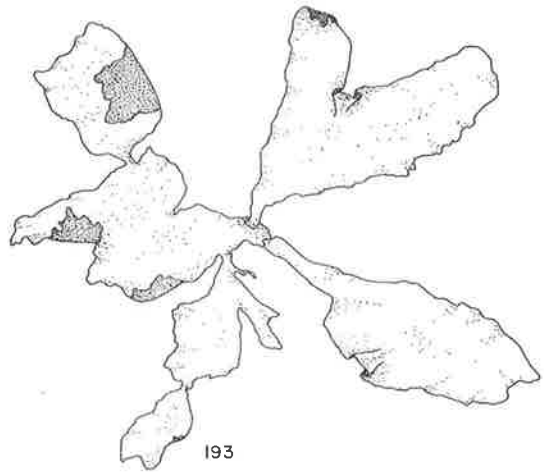




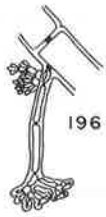


Cryptarachne





Cryptonemia



Crouania

Dasya

FIGS. 198-202. DICTYURUS OCCIDENTALIS J. AGARDH

(After Boergesen 1915-1920). Cross sections of entire thallus (198) and main stem (199); portions of erect shoots in face view (200, 202); and face view of polysiphonous main axis (201).

Plants grow to 4-12 cm tall and generally occur in shallow water lithos communities. The meshwork appearance is distinctive of the genus.

FIGS. 203-205. DIGENIA SIMPLEX (WULFEN) C. AGARDH

(Original [203] and after Harvey 1853 [204, 205]). Habit (203); branch system (204); very young branchlets still showing polysiphonous nature (205).

Digenia grows to 3-25 cm and is a common plant of rocky intertidal zones in exposed localities. It often has a wiry aspect and is heavily epiphytized.

FIGS. 206-208. EUCHEUMA ISIFORME (C. AGARDH) J. AGARDH

(After Harvey 1853). Habit (206), branch with spherical cystocarps (207); cross (208a) and longitudinal (208b) sections of stem.

Species of Eucheuma reach maximum heights of 5-75 cm and occur in shallow waters and deeper waters on rocks and other debris. Plants occur in both sheltered and exposed situations.

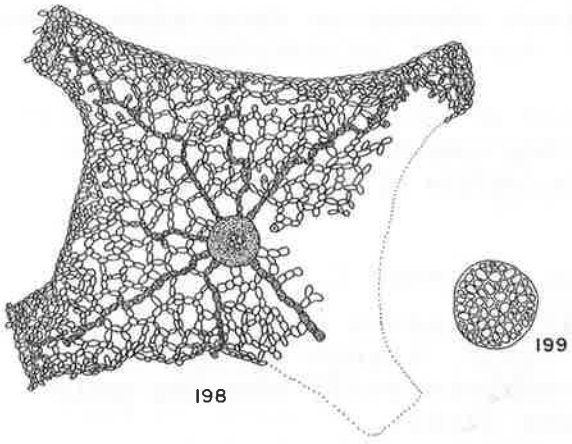
FIGS. 209-215. FALKENBERGIA HILLEBRANDII (BORNET) FALKENBERG

(After Boergesen 1915-1920). Habit of portion of a plant (209); cross section (210); haptera (214); and branches showing cell arrangement (211, 212, 213, 215).

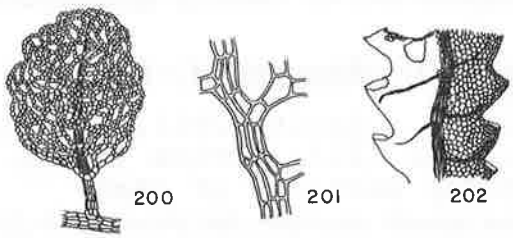
Plants rarely exceed 2 cm in height and occur in the shallow water aufwuchs. This is the tetrasporophyte stage; sexual stages have been referred to Asparagopsis (Figs. 125-127) in the past.

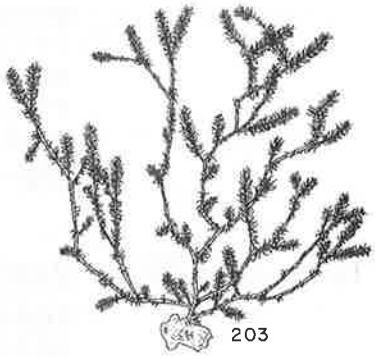
MAGNIFICATION FACTORS:

Fig. 198: 9×; Fig. 199: 25×; Fig. 200: 7×; Fig. 201: 40×; Fig. 202: 3×; Fig. 203: 0.2×; Fig. 204: 0.3×; Fig. 205: 10×; Fig. 206: 0.4×; Fig. 207: 0.6×; Fig. 208: 6×; Fig. 209: 17×; Fig. 210: 165×; Fig. 211: 135×; Fig. 212: 135×; Fig. 213: 135×; Fig. 214: 130×; Fig. 215: 135×.

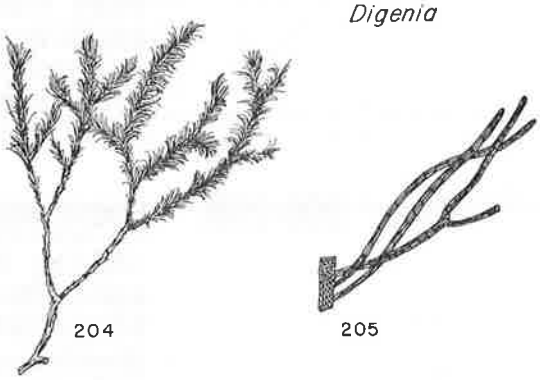


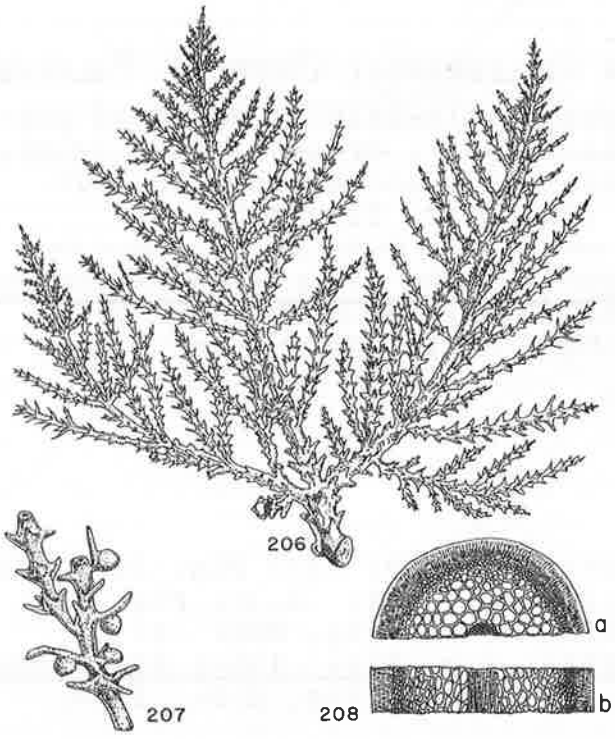
Dictyurus



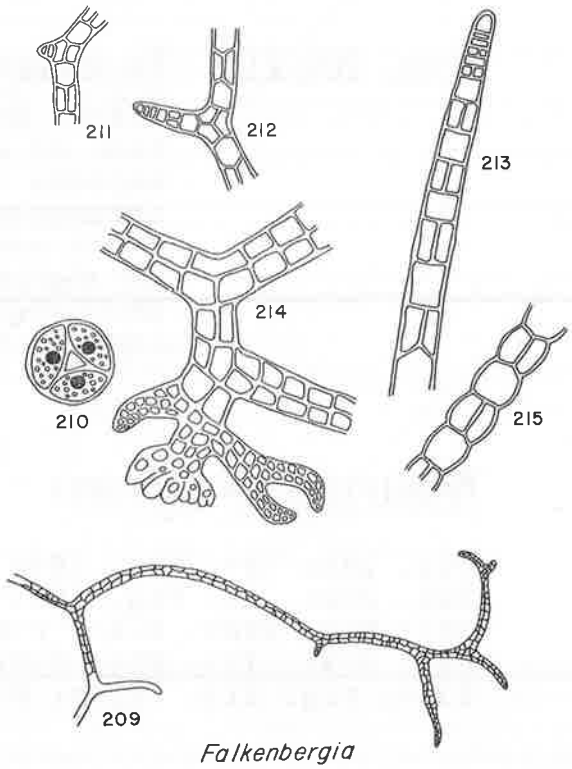


Digenia





Eucheuma



Falkenbergia

FIGS. 216-218. GALAXAURA SQUALIDA KJELLMAN

(After Boergesen 1915-1920). Habit of portion of plant (216); cross section of branch (217); cross section showing assimilators (hairs) (218).

Galaxaura plants range from 5-15 cm tall, may be flattened or cylindrical, may be hairy or smooth, and are always calcified. They occur in the lithos from the low tide mark down on both sheltered and exposed coasts.

FIGS. 219-222. GELIDIELLA ACEROSA (FORSSKAL) FELDMANN & HAMEL. (After Boergesen 1915-1920, as Gelidiopsis rigida). Cross section (219); longitudinal section showing medulla (221); branch tip (220); apices of 2 branches (222).

Plants of Gelidiella grow up to 14 cm tall and occur most commonly in the intertidal zone on rocks and other solid objects.

FIGS. 223-226. GONIOTRICHUM ALSIDII (ZANARDINI) HOWE

(After Boergesen 1915-1920, as G. elegans). Portions of erect system (223, 224); branch tip (225), base of plant (226).

Plants reach 6 mm in length and occur as aufwuchs, primarily in more sheltered situations.

FIGS. 227-230. GRACILARIA CYLINDRICA BOERGESEN

(After Boergesen 1915-1920). Habit (227); cross section (229); partial cross section showing tetraspores (228); surface view showing developing tetraspores (230).

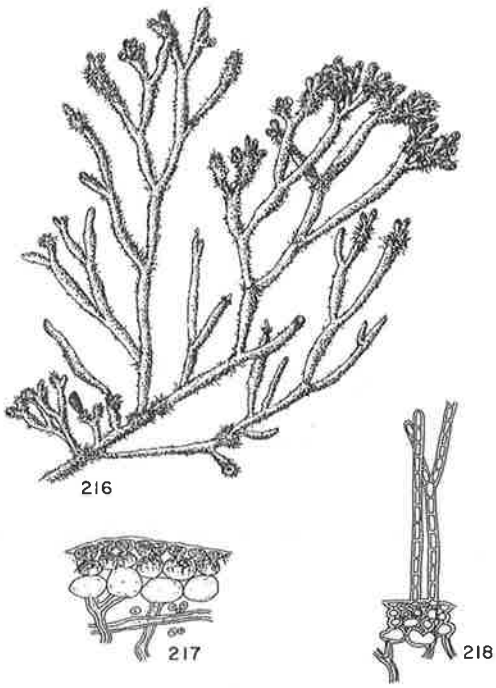
Gracilaria includes many species which vary greatly in size and appearance. They occur primarily in the sublittoral lithos.

FIGS. 231-233. GRATELOUPIA. Habit (231) of G. gibbesii Harvey. (After Harvey 1853). Partial cross section (232) of G. cuneifolia J. Agardh showing tetraspores and star shaped cells (233) of medulla (after Boergesen 1915-1920).

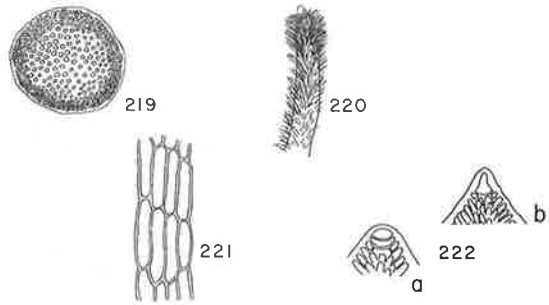
Gratelopia plants range from 10-80 cm tall and occur mostly in sublittoral lithos in sheltered areas.

MAGNIFICATION FACTORS:

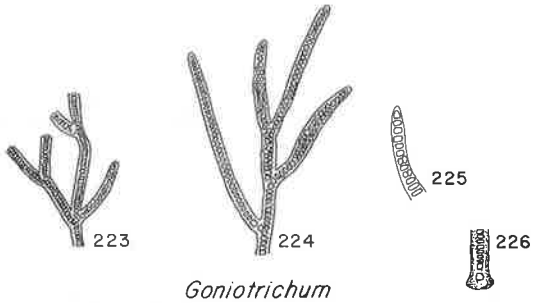
Fig. 216: 1.0×; Fig. 217: 94×; Fig. 218: 60×; Fig. 219: 28×; Fig. 220; 19×; Fig. 221: 80×; Fig. 222: 215×; Fig. 223: 86×; Fig. 224; 86×; Fig. 225: 86×; Fig. 226: 86×; Fig. 227: 0.6×, Fig. 228: 4.5×; Fig. 229: 50×; Fig. 230: 120×; Fig. 231: 0.2×; Fig. 232: 160×; Fig. 233: 100×.



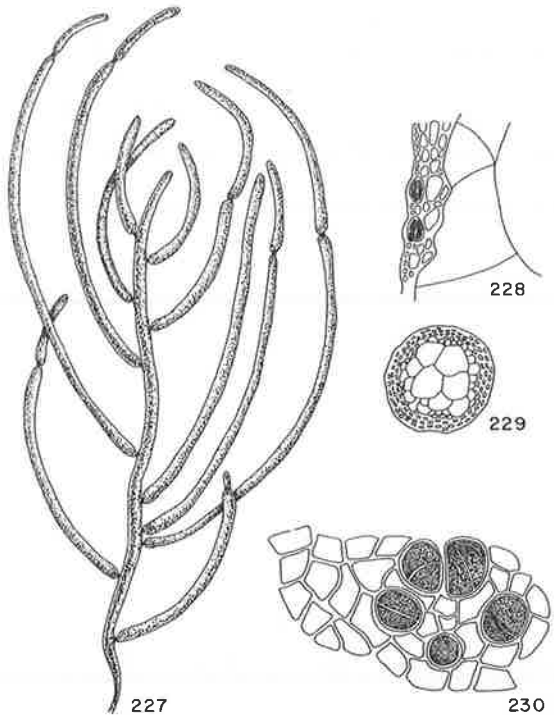
Galaxaura



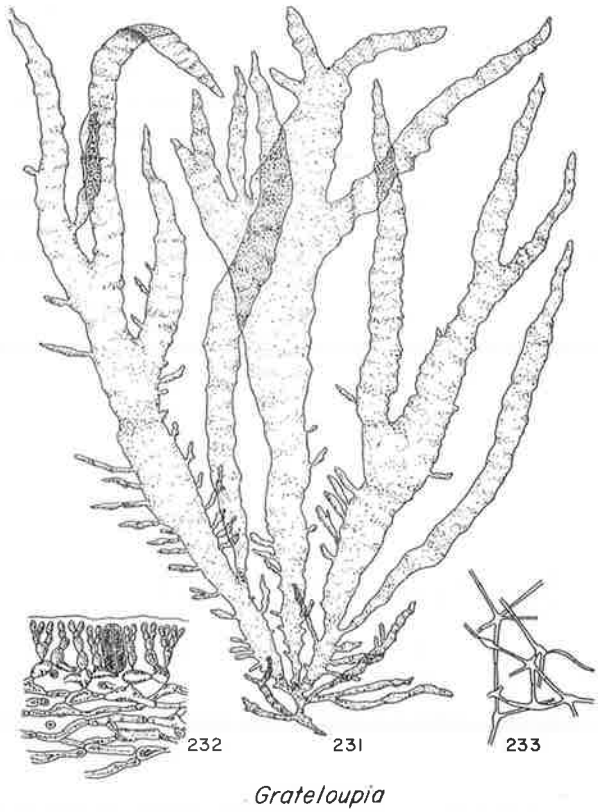
Gelidiella



Goniotrichum



Gracilaria



Grateloupia

FIGS. 234-236. GRIFFITHSIA GLOBULIFERA HARVEY

(After Harvey 1853 as G. corallina). Habit (234); branches near apex (235); cystocarp near branch apex (236).

Plants normally grow to 2-7 cm and occur in the sublittoral lithos and aufwuchs of open coasts.

FIG. 237. GRINNELLIA AMERICANA (C. AGARDH) HARVEY

(After Harvey 1853). Habit of plant (237).

Grinnellia plants often grow to over 50 cm in length and normally develop in the upper sublittoral as a component of the lithos.

FIGS. 238-240. HALYMENIA BERMUDENSIS COLLINS AND HOWE

(Original [239], and after Collins and Hervey [238, 240]). Habit of young plant (238) and older plant (239); cross section of thallus (240) showing medulla and cortex.

Blades of Halymenia range from 5-70 cm in length and are known from the aufwuchs and lithos of both sheltered and exposed localities.

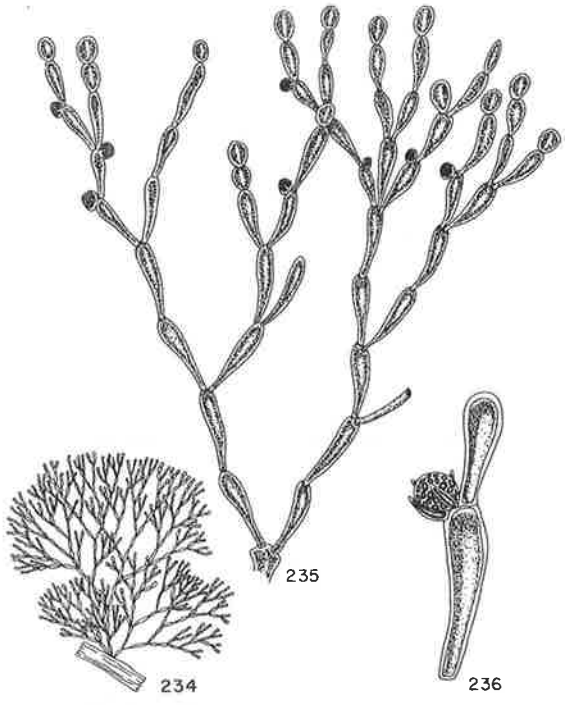
FIGS. 241-244. HERPOSIPHONIA TENELLA (C. AGARDH) AMBRONN

(After Boergesen 1915-1920). Habit (241); cross section (243); tetrasporangia (242); spermatangia on erect branches (244). Note the hair-like trichoblasts at the tips of the branches (241).

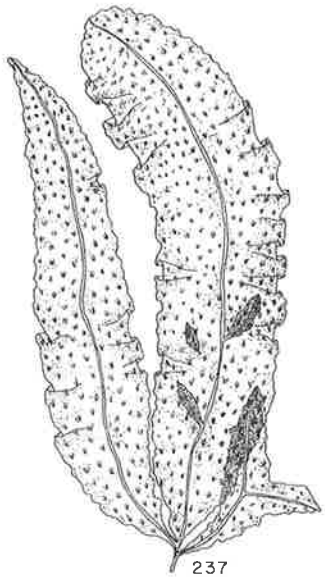
Species of Herposiphonia grow on a variety of objects in both the lithos and aufwuchs and often form extensive patches from the stolon-like runners. Erect filaments rarely exceed 5 mm in height.

MAGNIFICATION FACTORS:

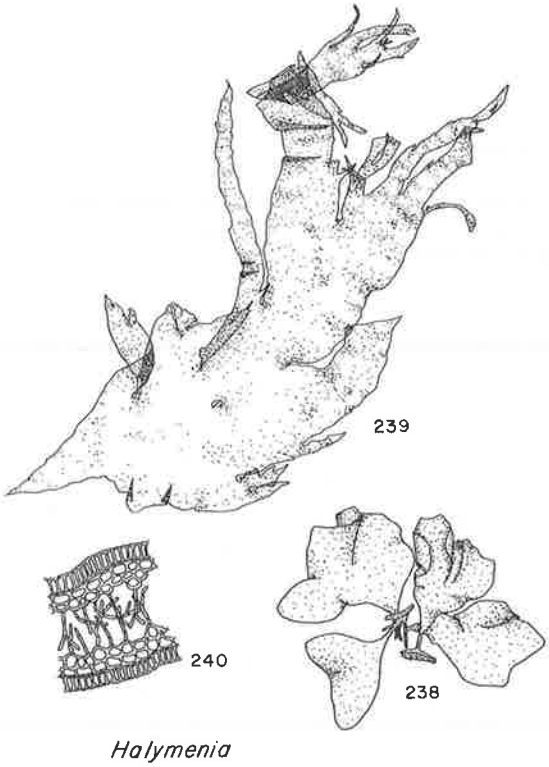
Fig. 234: 0.4×; Fig. 235: 3×; Fig. 236: 8×; Fig. 237: 0.2×; Fig. 238: 0.2×; Fig. 239: 0.2×; Fig. 240: 120×; Fig. 241: 20×; Fig. 242: 50×; Fig. 243: 60×; Fig. 244: 35×.



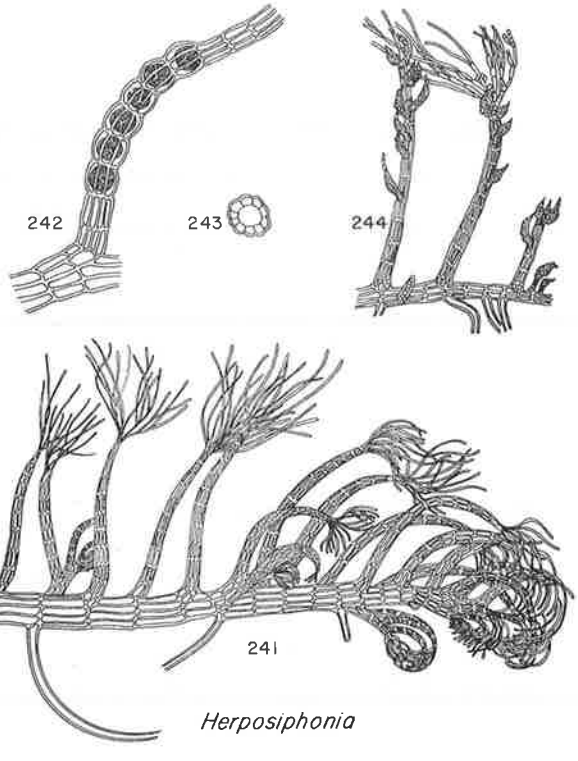
Griffithsia



Grinnellia



Halymenia



Herposiphonia

FIGS. 245-251. HETEROSIPHONIA GIBBESII (HARVEY) FALKENBERG

(After Harvey 1853, as Dasya gibbesii). Habit (245); monosiphonous branch tip (246); branch bearing tetrasporangial stichidia (247); one stichidium (248) and one tetrasporangium (249); longitudinal (250) and cross (251) sections of thallus branch.

Plants of Heterosiphonia range from 1-25 cm tall and grow both in the lithos and aufwuchs in shallow water in regions of slight to moderate wave action.

FIGS. 252-253. HYPNEA CORNUTA (LAMOUROUX) J. AGARDH

(After Boergesen 1915-1920). Habit of part of plant (252); cross section (253) of a branch.

Hypnea species vary from 2-50 cm or more in height and most commonly occur in the lithos of exposed localities. Plants also occur in sheltered areas and form tangled masses. In one species the tips of certain branches form distinctive enlarged hooks.

FIGS. 254-256. HYPOGLOSSUM INVOLVENS (HARVEY) J. AGARDH

(After Harvey 1853, as Delesseria involvens). Habit of plant (254); tetrasporangial branch (255), tetrasporangia in surface view (256).

Hypoglossum plants grow to 1-10 cm tall and are known chiefly from specimens cast ashore from deeper waters.

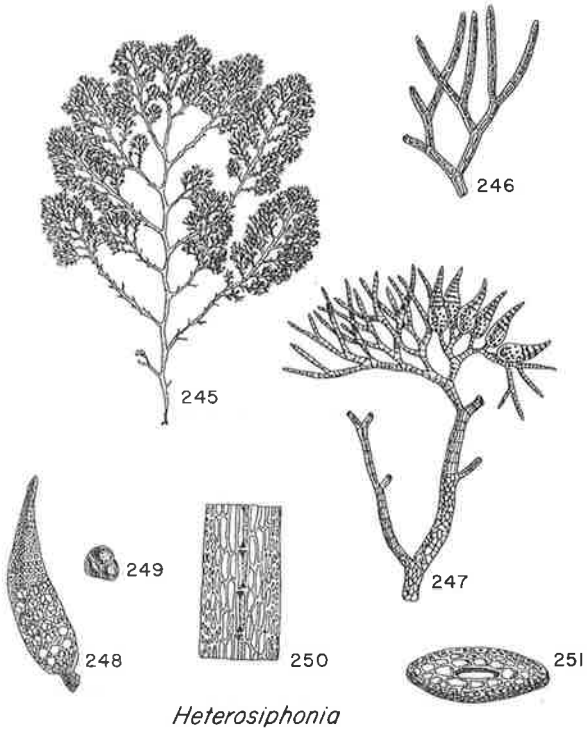
FIGS. 257-259. JANIA ADHAERENS LAMOUROUX

(After Boergesen 1915-1920). Portions of plants showing branching (257, 258); branch bearing conceptacles (259).

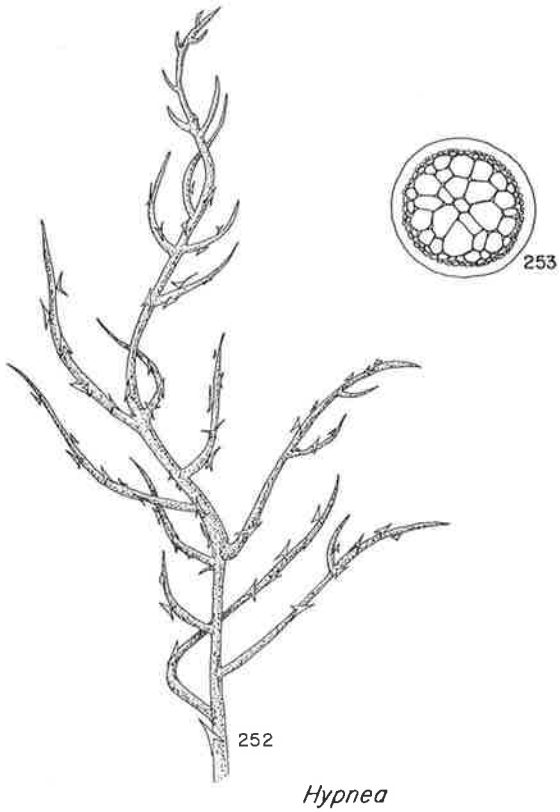
Certain species rarely exceed 8 mm in height; others grow to 1-6 cm regularly. Plants are most common in the aufwuchs in sheltered localities, but they can also occur in the lithos in shallow water.

MAGNIFICATION FACTORS:

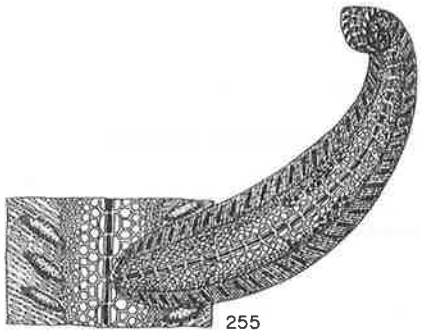
Fig. 245: 0.25×; Fig. 246: 30×; Fig. 247: 20×; Fig. 248: 60×; Fig. 249: 200×; Fig. 250: 12×; Fig. 251: 20×; Fig. 252: 3×; Fig. 253: 50×; Fig. 254: 1×; Fig. 255: 17×; Fig. 256: 65×; Fig. 257: 2×; Fig. 258: 10×; Fig. 259: 10×.

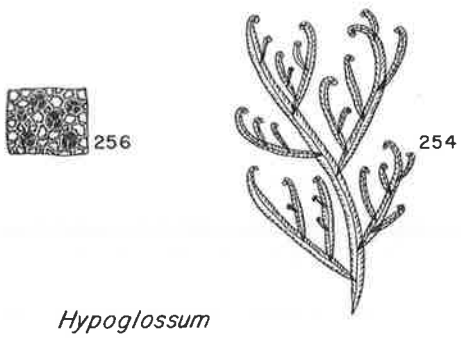


Heterosiphonia

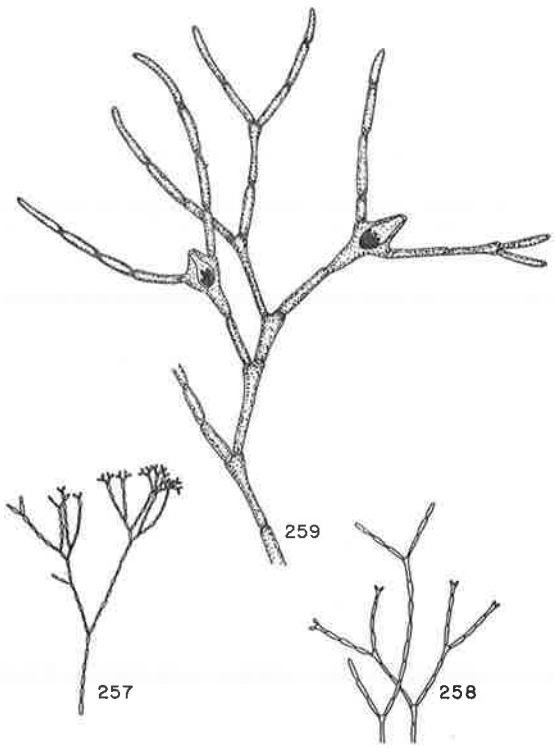


Hypnea





Hypoglossum



Jania

FIGS. 260-262. KALLYMENIA

Habit (260) of K. reniformis (Turner) J. Agardh from England (after Harvey 1846-1851). Cross section (261) and medulla (262) of K. perforata J. Agardh (after Boergesen 1915-1920).

Plants range from 2 cm to over 20 cm tall and can occur in deep waters on near the low tide mark on deeply shaded rocks and in crevices.

FIGS. 263-264. LAURENCIA INTRICATA LAMOUROUX

(After Boergesen 1915-1920, as L. implicata). Portion of a plant (263); cross section (264).

Species of Laurencia range from 1-25 cm tall. Plants are common and often abundant in the intertidal zone, but are also frequently encountered in sublittoral collections. Specimens occur both in the lithos and in the aufwuchs and most species have short ultimate branchlets with conspicuous apical depressions.

FIGS. 265-269. LIAGORA VALIDA HARVEY

(After Harvey 1853). Habit (265); axis segment (266); longitudinal section showing cortex and medulla (267); cortical filaments (268-269).

Plants range from 2-35 cm or more tall and occur both in the lithos and aufwuchs in areas of little or moderate wave action. The degree of calcification varies from species to species.

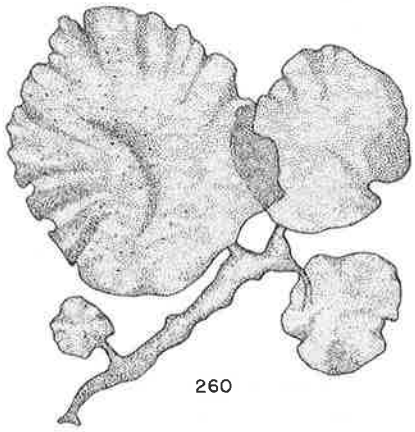
FIGS. 270-274. LOMENTARIA BAILEYANA (HARVEY) FARLOW

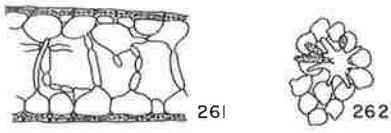
(After Harvey 1853, as Chylocladia baileyana). Habit (270, 271); tetrasporangial branch (272); cross sections of thallus (273, 274).

Lomentaria plants range from 0.5-20 cm tall and are known both in the aufwuchs and lithos of shallow waters.

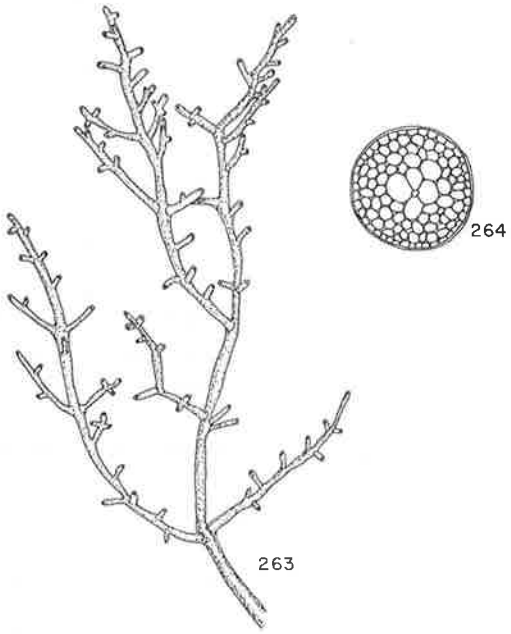
MAGNIFICATION FACTORS:

Fig. 260:0.8×; Fig. 261: 63×; Fig. 262: 50×; Fig. 263: 1.5×; Fig. 264: 23×; Fig. 265: 0.9×; Fig. 266: 15×, Fig. 267: 30×; Fig. 268: 200×; Fig. 269: 100×; Fig. 270: 0.4×; Fig. 271: 1×; Fig. 272: 1.2×; Fig. 273: 18×; Fig. 274: 60×.

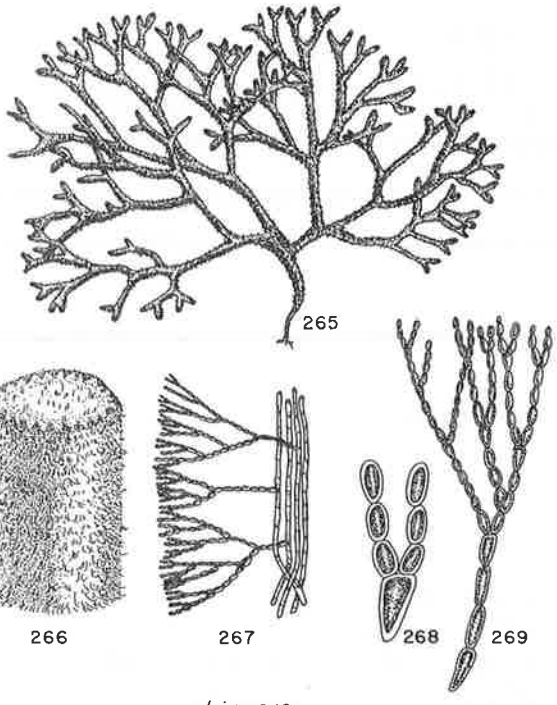




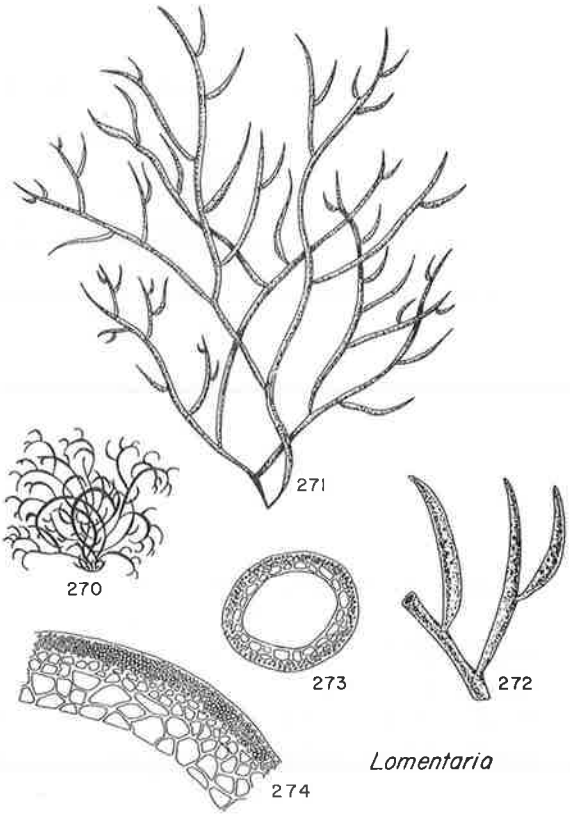
Kallymenia



Laurencia



Liagora



Lomentaria

FIGS. 275-279. LOPHOCLADIA TRICHOCLADOS (MERTENS IN C. AGARDH) SCHMITZ. (After Boergesen 1915-1920). Branch with trichoblasts (275); male (276), female (277), and tetrasporangial (278) branches; basal part of plant showing haptera (279). *Plants reach 7-10 cm in height and are usually cast ashore from deeper water.*

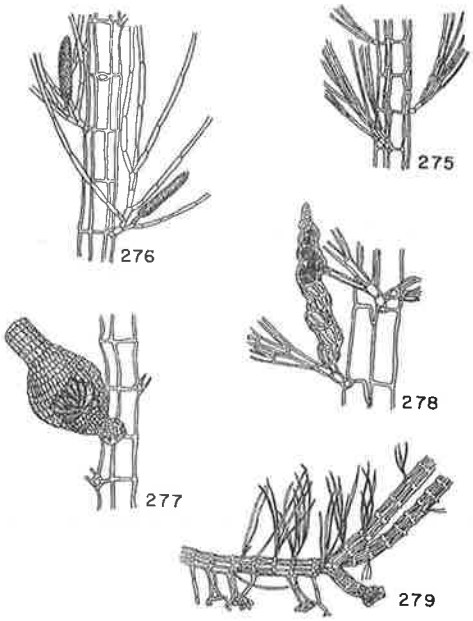
FIGS. 280-283. LOPHOSIPHONIA. L. saccorhiza Collins and Hervey from Bermuda showing saccate rhizoids (280). After Collins and Hervey 1917). L. cristata Falkenberg. (After Boergesen 1915-1920). Habit (281); branch tip (282); cross section (283). *Specimens can become several mm tall and occur in both the aufwuchs and lithos, usually in shallow water.*

FIGS. 284-285. MARTENSIA PAVONIA (J. AGARDH) J. AGARDH (After Boergesen 1915-1920). Habit of portion of thallus (284); segment of plant bearing tetrasporangia (285).

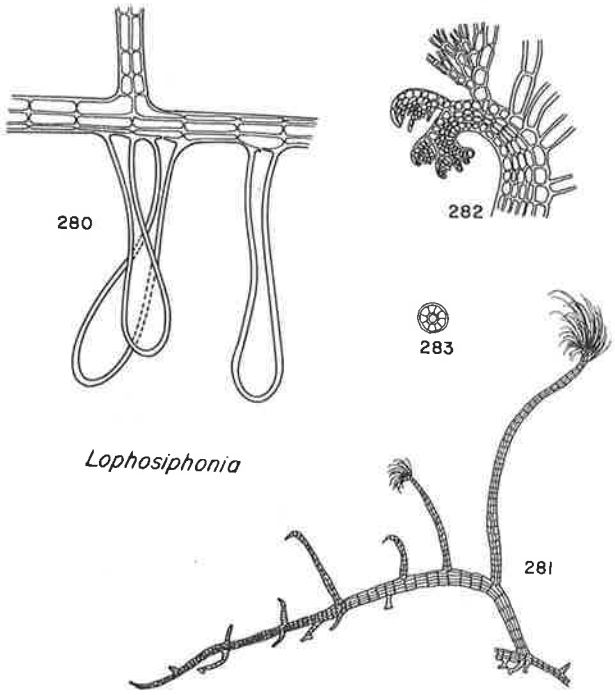
FIGS. 286-288. MERISTOTHECA FLORIDANA KYLIN (Original [286] and after Kylin [287-288]). Habit (286); cross section of cystocarp (287); longitudinal section showing tetrasporangia (288). *Plants attain heights of up to 35 cm and are known primarily from specimens washed ashore from deeper waters.*

MAGNIFICATION FACTORS:

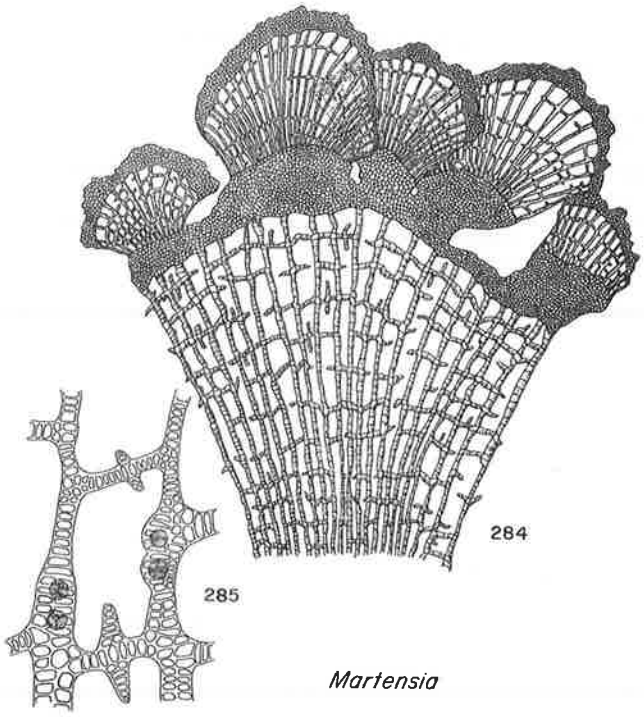
Fig. 275: 19×; Fig. 276: 30×; Fig. 277: 25×; Fig. 278; 30×; Fig. 279: 30×; Fig. 280: 85×; Fig. 281: 15×; Fig. 282: 65×; Fig. 283: 60×; Fig. 284: 8×; Fig. 285: 40×; Fig. 286:



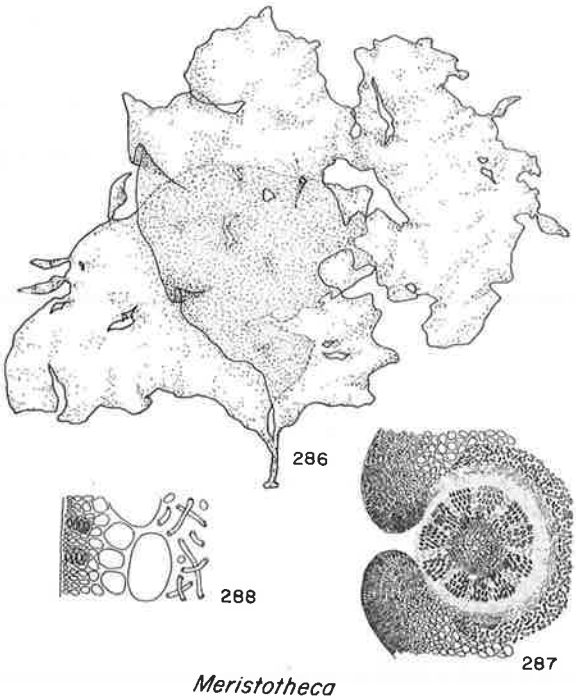
Lophocladia



Lophosiphonia



Martensia



Meristotheca

FIGS. 289-293. MURRAYELLA PERICLADOS (C. AGARDH) SCHMITZ
(After Boergesen 1915-1920 and Harvey 1853, as Bostrychia tuomeyi). Habit of parts of plants (289, 290); polysiphonous segment (292); creeping portion showing descending rhizoids (293); tetrasporangia (291).
Murrayella plants reach heights of 2-5 cm and are most common in mangrove thickets and on rock in sheltered waters.

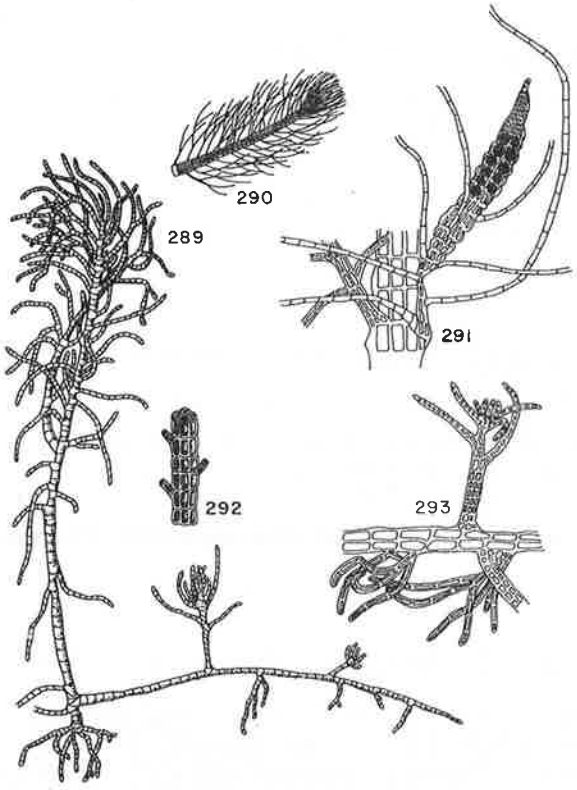
FIGS. 294-298. NEOAGARDHIELLA RAMOSISSIMA (HARVEY) WYNNE AND TAYLOR. (Original and after Harvey 1853 as Chrysymenia ramosissima). Habit (294-296); cross section (297); longitudinal section (298).
Plants grow to 30 cm and occur primarily in deeper water lithos.

FIG. 299. NITOPHYLLUM PUNCTATUM (STACKHOUSE) GREVILLE
(Original). Habit of plant.
Plants rarely exceed 20 cm in height and usually grow only 3-8 cm tall.

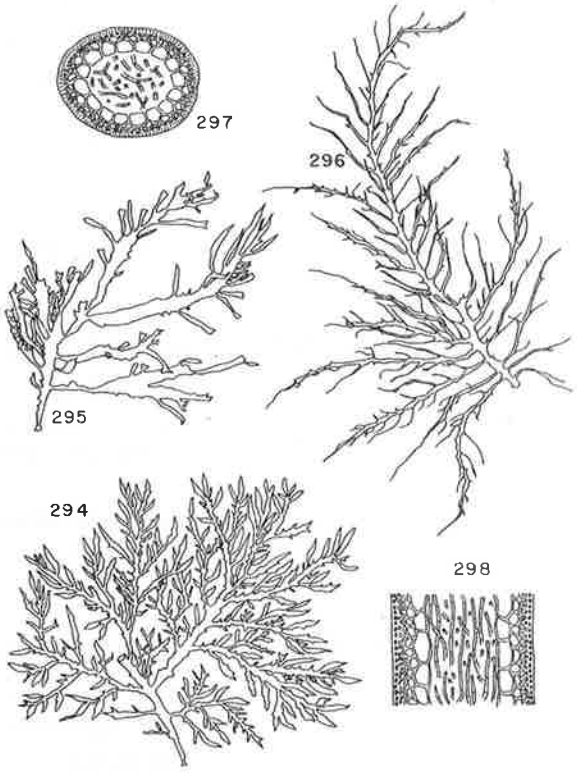
FIGS. 300-302. POLYSIPHONIA HAVANENSIS MONTAGNE
(After Boergesen 1915-1920). Parts of plants with trichoblasts (300); branch tip with trichoblasts and scar cells (301); basal part of axis with a hapteron and an adventitious branch (302).
Plants of Polysiphonia occur in almost all habitats as lithos and aufwuchs. Plants range from 5 mm to 40 cm tall. Species concepts are poorly defined and critical studies of Florida members of this group are badly needed.

MAGNIFICATION FACTORS:

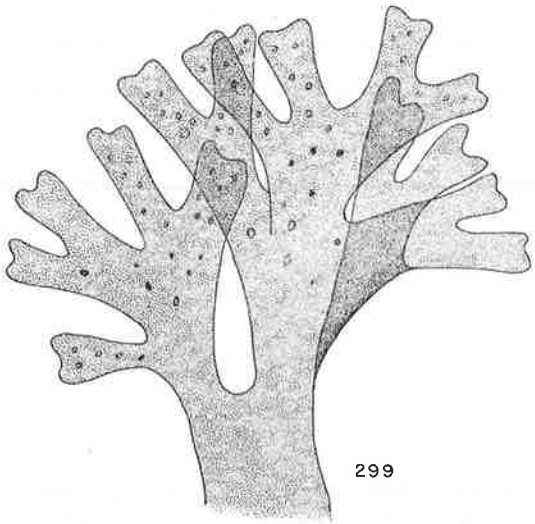
Fig. 289: 6×; Fig. 290: 6×; Fig. 291: 30×; Fig. 292: 25×; Fig. 293: 26×; Fig. 294: 0.2×; Fig. 295: 0.2×; Fig. 296: 0.2×; Fig. 297: 7×; Fig. 298: 7×; Fig. 299: 1.5 ×; Fig. 300: 8×; Fig. 301: 195×; Fig. 302: 20×.



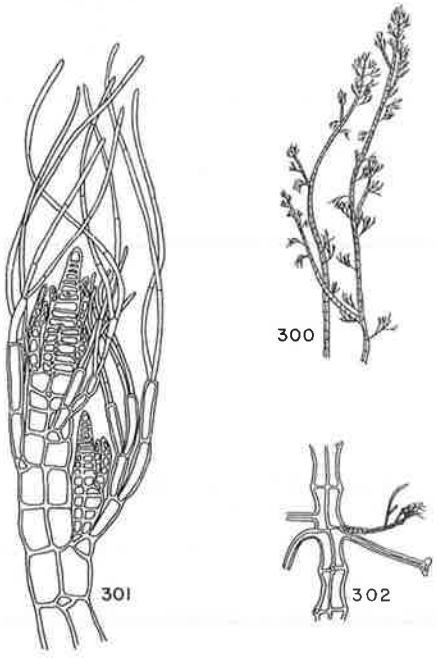
Murrayella



Neoagardhiella



Nitophyllum



Polysiphonia

FIG. 303. PORPHYRA UMBILICALIS (LINNEAUS) J. AGARDH (Original). Habit of plant.
Plants range from 10-80 cm in length and occur almost exclusively on intertidal rocks.

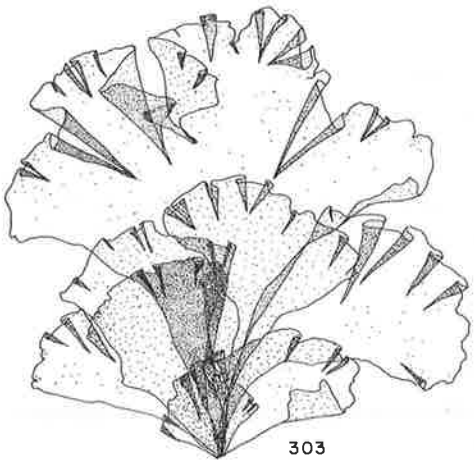
FIGS. 304-305. SEIROSPORA OCCIDENTALIS BOERGESEN (After Boergesen 1915-1920). Portion of female plant (304); part of plant with seirospores (305).
Seiospora grows to 2.5 cm tall and occurs in the lithos under very shaded conditions, especially on walls and in crevices.

FIGS. 306-307. SCINAIA COMPLANATA (COLLINS) COTTON (Original and after Boergesen 1915-1920). Habit (306) and branch tip showing position of central axis (307).
Scinaia plants attain heights of 5-8 cm and usually occur in deeper waters on rocks and old shells and coral fragments.

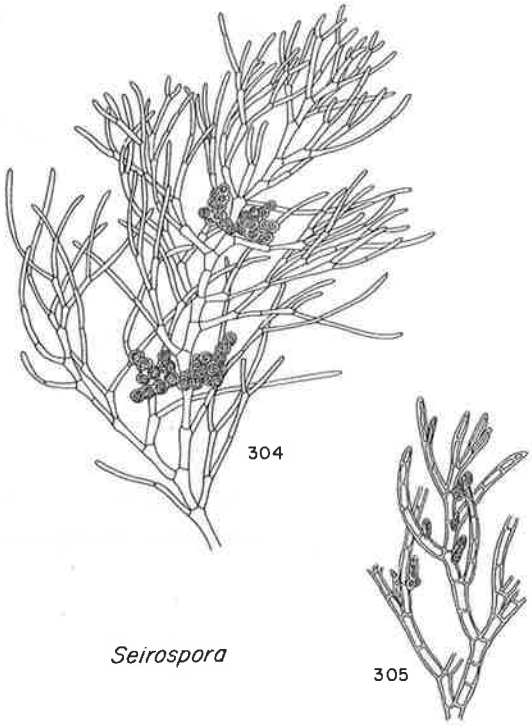
FIGS. 308-311. SOLERIA TENERA (J. AGARDH) WYNNE AND TAYLOR (After Harvey 1853, as Soleria chordalis and Boergesen 1915-1920, as Agardhiella tenera). Habit (308); longitudinal section (309); cross section (310); tetrasporangia (311).
Plants of Soleria commonly occur on sublittoral rocks in both sheltered and exposed situations.

MAGNIFICATION FACTORS:

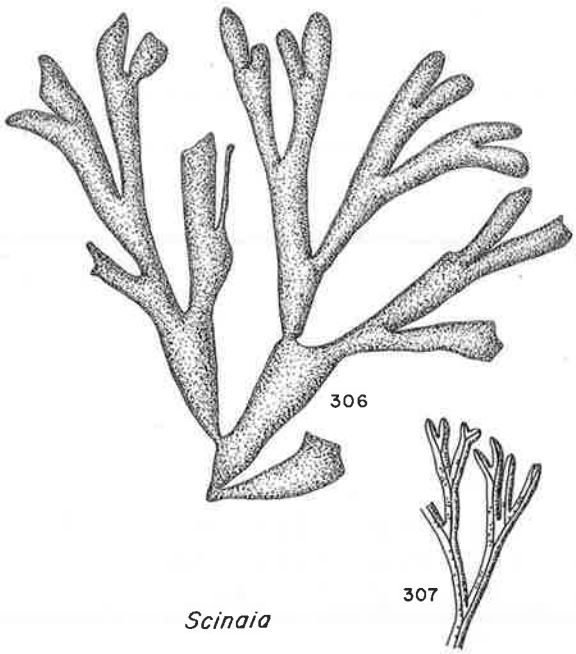
Fig. 303: 0.3×; Fig. 304: 35×; Fig. 305: 60×; Fig. 306: 4×; Fig. 307: 1×; Fig. 308: 0.3×; Fig. 309: 20×; Fig. 310: 30×; Fig. 311: 175×.



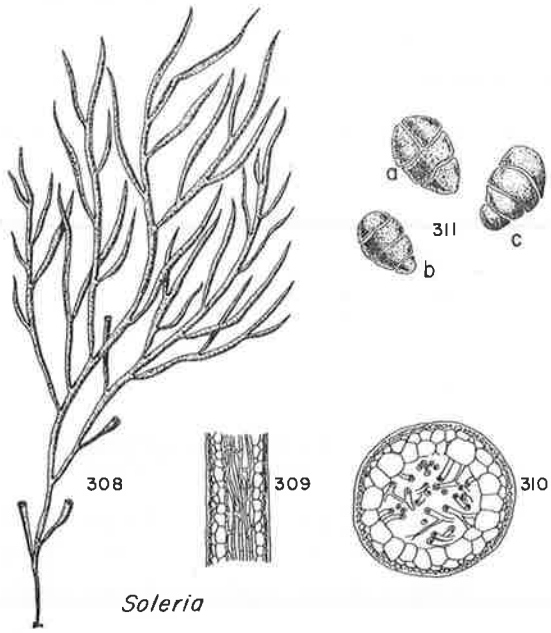
Porphyra



Seirospora



Scinaia



Soleria

FIGS. 312-315. SPERMOTHAMNION INVESTIENS (CROUAN) VICKERS
(After Boergesen 1915-1920). Plants from neighboring Virgin Is. showing habit (312-313) and tetrasporangia (314-315).
Plants of Spermothamnion grow from 2 mm - 5 cm tall and usually occur as aufwuchs in shallow waters.

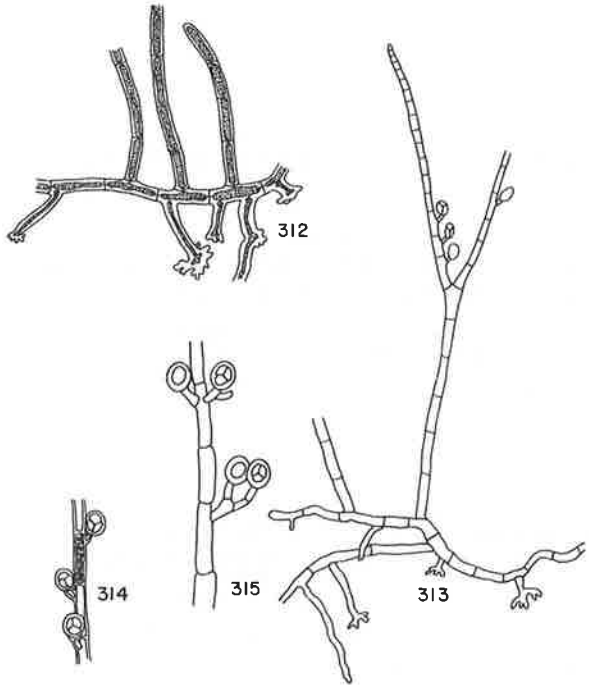
FIGS. 316-318. SPYRIDIA FILAMENTOSA (WULFEN) HARVEY
(After Boergesen 1915-1920). Habit of parts of plants (316-317); ultimate branchlets showing ring-like cortication (318).
Plants range from 5-30 cm tall. Various species prefer warm quiet waters or more exposed sites and they can occur in the lithos or aufwuchs or in small floating masses.

FIGS. 319-320. TAENIOMA NANUM (KÜTZING) PAPENFUSS
(After Boergesen 1915-1920, as T. perpusillum). Part of plant (319); branch tip with hairs (320).
Plants normally are 2-3 mm tall and grow in the lithos near low tide mark in exposed localities.

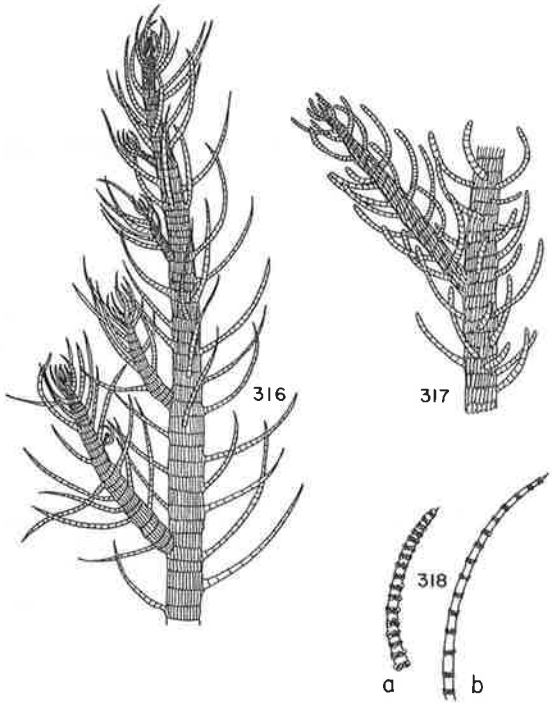
FIG. 321. VIDALIA OBTUSILOBA (MERTENS) J. AGARDH
(Original). Habit.
Plants reach heights of 10-25 cm and usually occur in deeper waters in the lithos.

MAGNIFICATION FACTORS:

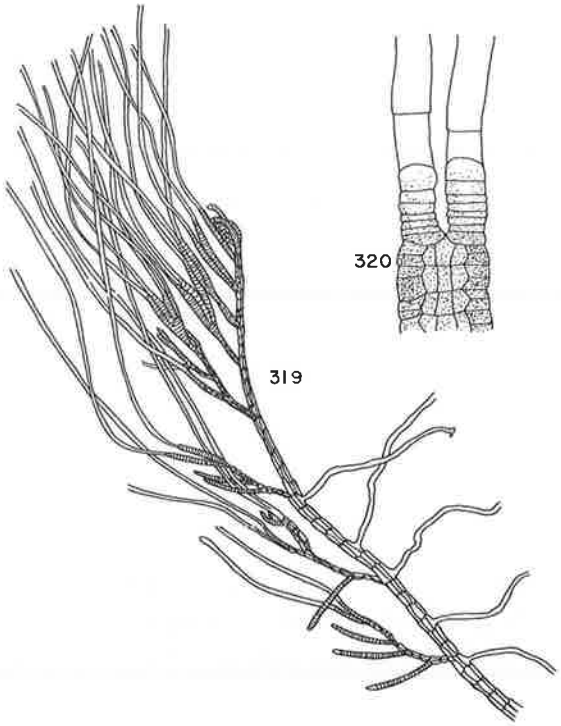
Fig. 312: 85×; Fig. 313: 32×; Fig. 314: 26×; Fig. 315: 80×; Fig. 316: 13×; Fig. 317: 13×; Fig. 318: 70×; Fig. 319: 20×; Fig. 320: 180×; Fig. 321: 0.4×.



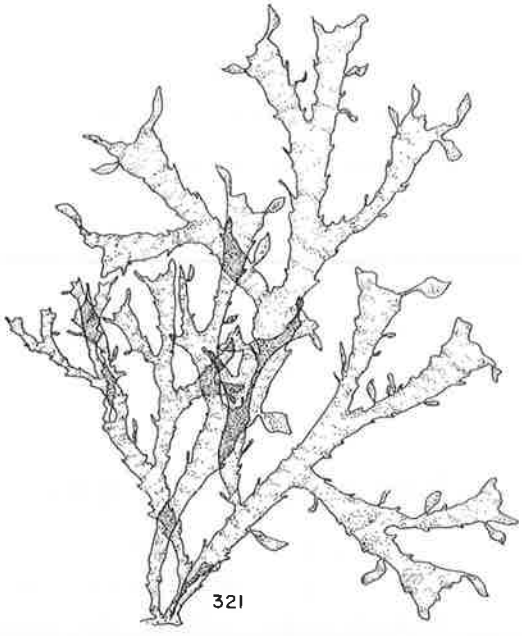
Spermothamnion



Spyridia



Taenioma



Vidalia

FIGS. 322-325. WRANGELIA PENICILLATA C. AGARDH

(After Harvey 1853). Branches of plant (322-324); cross section (325) of branch.
Species of Wrangelia range from 1.0-18 cm tall and they occur on rocks and in the aufwuchs both in shallow and deeper water.

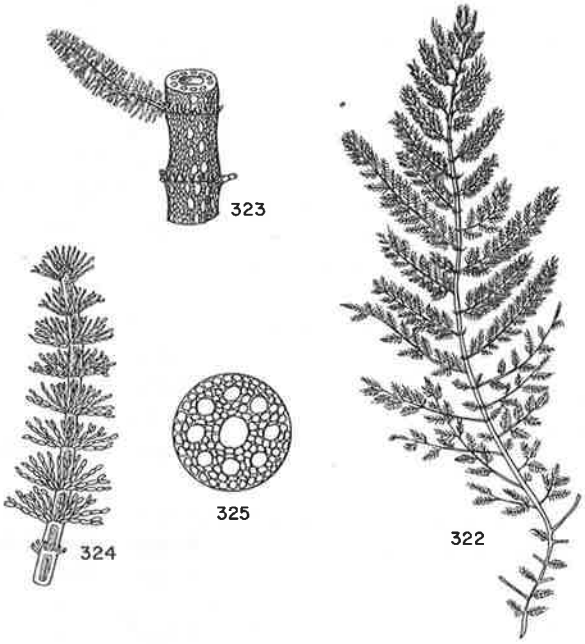
FIGS. 326-328. WRIGHTIELLA TUMANOWICZI (GATTY) SCHMITZ

(After Boergesen 1915-1920). Part of main axis showing trichoblast and stichidium (326); portion of partially corticated main axis with spine-like branchlets and trichoblasts (327); cross section at spot where branch emerges (328).
Plants grow to 75 cm or more tall and usually occur in deeper waters in the lithos.

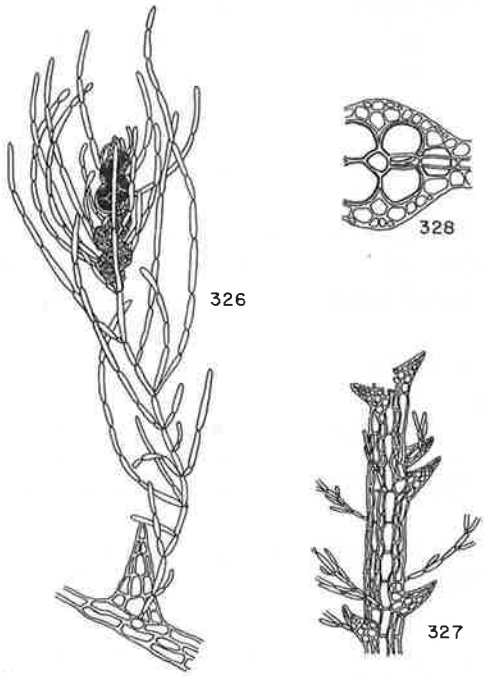
FIGS. 329-332. WURDEMANNIA MINIATA (DRAPARNAUD) FELDMANN AND HAMEL. (After Boergesen 1915-1920, as W. setacea). Part of plant (329); branch tip (330); cross section (331); longitudinal section (332).
Wurdemannia plants usually form extensive turf-like expanses on intertidal rocks in exposed localities, but also occur in more sheltered situations. Erect branches rarely exceed 3 cm in height.

MAGNIFICATION FACTORS:

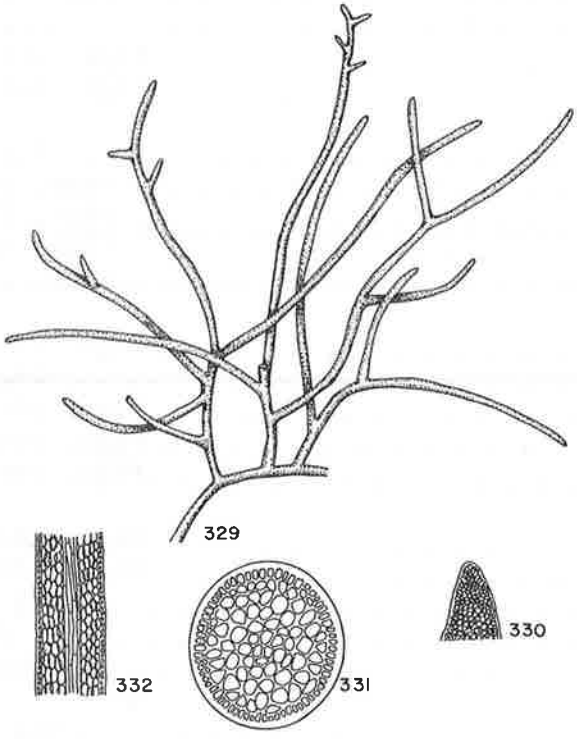
Fig. 322: 1×; Fig. 323: 14×; Fig. 324: 4×; Fig. 325: 30×; Fig. 326: 40×; Fig. 327: 23×; Fig. 328: 40×, Fig. 329: 2.5×; Fig. 330: 30×; Fig. 331: 100×; Fig. 332: 60×.



Wrangelia



Wrightiella



Wurdemannia

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Hydrobiologia vol. 48, 3, pag. 209-232, 1976

WISCONSIN DESMIDS. I. AUFWUCHS AND PLANKTON COMMUNITIES OF SELECTED ACID BOGS, ALKALINE BOGS, AND CLOSED BOGS

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Keywords: Aufwuchs. Plankton communities. Desmidiaceae. Alkaline bogs.

Abstract

Data are presented for 28 acid bogs, five alkaline bogs, and 12 closed bogs in Wisconsin with respect to the summer composition of the aufwuchs and plankton ccommunities, the relative importance of desmids in these communities, and the structure of aufwuchs communities associated with different macrophyte hosts. Generic diversity of desmids is highest in acid bogs and lowest in alkaline bogs and generally is greater in the aufwuchs community than in the plankton community at a given site. Whenever it was present, the greatest diversity occurred in association with the macrophyte host *Utricularia*. Among lakes of a given type, relationships between the occurrence of desmid genera and parameters of the chemical environment were not apparent for either the aufwuchs or plankton communities. Similarly, no clear-cut distinctions occur in the desmid communities of the three lake types in terms of population densities and percentage contribution to the total population, but acid bogs tend to have a somewhat more prominent flora quantitatively. Statistically significant differences in desmid population densities from one host to another within a given lake did occur in lakes of all three types, and this suggests that the nature of the substrate can definitely influence community size and composition. Data for other algal groups are similarly treated, and brief comparisons of the mat and open water communities of alkaline bogs are included.

Dr. W. Junk b.v. Publishers - The Hague, The Netherlands

Introduction

The principal source of information on Wisconsin desmids (Desmidiales, Chlorophyta) has been the floristic account of Smith (1924) which incorporates the results of phytoplankton surveys of 228 lakes, located mostly in the northern part of the state. Other records of occurrence are included in the papers of Ahlstrom (1936), Birge & Juday (1911), Hasler & Jones (1949), Juday, Blair & Wilda (1943), Marsh (1903), Prescott (1970), Prescott, Croasdale & Vinyard (1972), Sloey & Blum (1972), Smith (1918), Tressler & Domogalla (1931), and Wohlschlag & Hasler (1951). Some additional data are contained in several unpublished theses (Kelly 1909, Reid 1918) cited in the bibliography of Greene & Curtis (1955) and in other unpublished theses (McLay, 1923; Ryser, 1915; Silsby, 1963) on file in the University of Wisconsin-Madison Botany Department.

In spite of these reports, virtually no information is available with reference to Wisconsin waters on 1) the nature and role of benthic desmid communities, 2) the relative importance of planktonic and benthic desmids in various types of aquatic habitats, 3) the relationships of environmental factors (particularly water chemistry) to the composition of desmid communities and to the distribution of individual taxa, and 4) the extent of morphological variation occurring in populations of individual taxa under both natural and experimental conditions. Moreover, preliminary observations strongly indicate that major gaps occur in our floristic knowledge of Wisconsin desmids. Extensive systematic studies are needed on both Wisconsin taxa and the Desmidiales in general to help clarify species concepts, to develop a better basis for understanding desmid ecology, and to provide

meaningful data for evaluating the potential of desmid communities to serve as environmental indicators. This series of investigations aims to contribute data on Wisconsin taxa which hopefully will aid in clarifying some of the problems associated with desmid ecology, morphology, and systematics.

The present paper considers briefly the terminology associated with freshwater habitats and summarizes quantitative data from 28 acid bog lakes, 5 alkaline bog lakes, and 12 closed bogs with respect to the summer composition of the aufwuchs and plankton communities, the relative importance of desmids in these communities, and the structure of aufwuchs communities associated with different macrophyte hosts.

Terminology and literature review

As noted by Hutchinson (1967), Sladeckova (1962), and others, the nomenclature of aquatic environments is both diverse and open to differing interpretations; consequently a precise statement on terms used in these studies appears desirable. Following Krieger (1933), desmid communities can be categorized as planktonic or benthic. The plankton includes all forms not associated with a solid substrate (i.e., suspended in water). Two elements comprise the plankton: A) the euplankton or all forms which appear to lead a planktonic existence throughout their lives; and B) the tychoplankton or forms which have become detached from a substrate and secondarily have assumed a planktonic existence.

The benthos, in contrast, refers to forms associated with a definite substrate and includes three components: A) the 'aufwuchs' or forms associated with a biological substrate (i.e., other plants or animals); B) the 'lithos' or forms associated with a solid substrate of a non-biological nature (e.g., rocks, metal objects); and C) the 'pelos' or forms associated with particulate substrates (e.g., sand, mud,

Table 1. Study sites: geographic and biological data.

A. Acid Bogs

County	Lake	Location T	R	S	Reference	Area (ha)	Aufwuchs Hosts	% shore in bog mat
Ashland	Trout Lk.	42N	1W	7	Sather and Threinen 1966	11.7	Sphagnum	100%
Barron	Lake 7-9d	36N	10W	7	Sather and Threinen 1964	1.4	Sphagnum, Utricularia	100%
Bayfield	Lake 17-5	45N	7W	17	Johannes, et al 1970	1.7	Sphagnum	100%
Bayfield	Lake 7-2	46N	7W	7	Johannes, et al 1970	0.1	Sphagnum	100%
Bayfield	Lake 6-10d	47N	7W	6	Johannes, et al 1970	0.5	Utricularia	100%
Bayfield	Lake 33-14	47N	8W	33	Johannes, et al 1970	2.3	Utricularia	100%
Bayfield	Lake 1-16c	47N	8W	1	Johannes, et al 1970	0.2	Utricularia	100%
Burnett	Lake 9-2	40N	14W	9	Blackman, et al 1966	0.8	Utricularia	100%
Burnett	Lake 10-6	40N	14W	10	Blackman, et al 1966	4.5	Utricularia	100%
Burnett	Lake 16-2	40N	16W	16	Blackman, et al 1966	0.8	Utricularia	100%
Burnett	Lake 17-4	40N	16W	17	Blackman, et al 1966	2.1	Sphagnum, Utricularia	100%

silt). Some authors (e.g., Round, 1965) refer to the latter as epilithic and epipelic communities, respectively.

The general nature and characteristics of bogs and bog lakes have been discussed in detail by Ruttner (1963) and Welch (1952) among others. During the course of field investigations of Wisconsin desmid communities, it has become evident that the bog environments of this region could be divided conveniently into three general types: acid bog lakes, alkaline bog lakes, and closed bogs. All three are characterized by the presence of a bog mat (see Curtis, 1959, p. 235, 278 ff.), usually containing an abundance of *Sphagnum*. Closed bogs are readily distinguished from acid bog lakes and alkaline bog lakes by the absence of an open area of water. Acid bog lakes differ from alkaline bog lakes among other ways in having open water pH readings of 7.0 or less rather than over 7.0.

A considerable body of information has emerged from investigations of desmids (Desmidiales, Chlorophyta) in acid bog lakes, and much of this data has been incorporated into the review papers of Fritsch (1953), Heimans (1969), Hutchinson (1967), Krieger (1933), Prescott (1946), and others. Valuable ecological data based on field observations also have been contributed by a number of workers (e.g., Duthie, 1965; Flensburg & Sparling, 1973;

Table 1. (continued).

County	Lake	Location T	R	S	Reference	Area (ha)	Aufwuchs Hosts	% shore in bog mat
Burnett	Lake 33-14	41N	14W	33	Blackman, et al 1966	1.9	Sphagnum	100%
Chippewa	Larrabee	32N	9W	24	Sather and Threinen, 1963	20.4	Utricularia	100%
Chippewa	Leo Joerg	32N	8W	8	Sather and Threinen, 1963	4.8	Brasenia Sphagnum, Utricularia	100% (?)
Chippewa	Lake 2-8	32N	9W	2	Sather and Threinen, 1963	4.4	Utricularia	100%
Iron	Lake 26-9	43N	3E	26	Andrews and Threinen, 1969	1.9	Sphagnum, moss	100%
Iron	Lake 13-2d	44N	4E	13	Andrews and Threinen, 1969	2.5	Potamogeton, Sphagnum, Utricularia	100%
Oneida	Lake 11-5	39N	6E	11	Andrews and Threinen, 1966	0.1	Sphagnum	100%
Polk	Evelyn	35N	16W	1	Sather and Threinen, 1961	1.0	Utricularia	100% (?)
Price	Unnamed	34N	2E	7	---	?	Sphagnum	100%
Rusk	Round	33N	7W	8	Sather et al, 1971	42.3	Utricularia	80%
Rusk	Saxton	34N	7W	28	Sather et al, 1971	2.0	Sphagnum	100%
Rusk	School	33N	8W	28	Sather et al, 1971	2.8	Utricularia	100%
Vilas	Spruce	41N	7E	12	Block et al, 1963	6.1	Sphagnum	100%
Vilas	Unnamed	42N	5E	8	---	?	Sphagnum	100%
Washburn	Unnamed (1)	38N	10W	24	---	?	Potamogeton	100%
Washburn	Unnamed (2)	38N	10W	26	---	?	Utricularia	100%
Washburn	Unnamed (3)	42N	13W	25	---	?	Sphagnum	100%

Table 1. (continued).

B. Alkaline Bogs

Lake	County	Location T	R	S	Reference	Area (ha)	Aufwuchs hosts
Bog	Rusk	33N	8W	3	Sather et al 1971	17.5	Potamogeton
Bullhead	Sawyer	42N	9W	36	Sather & Threinin 1968	3.6	Chara, Najas, Potamogeton, Utricularia
Cedar	Chippewa	32N	8W	9	Sather & Threinin 1963	2.5	Ceratophyllum
Hegmeister	Sawyer	37N	4W	11	Sather & Threinin 1968	29.9	Myriophyllum, Potamogeton (3 spp.), Sphagnum, Utricularia
Mystery	Vilas	41N	7E	1	Black et al 1963	9.4	Carex, Sphagnum

C. Closed Bogs

Locality number	County	T	R	S	1/4 - 1/4 S	Aufwuchs Hosts
1	Ashland	42N	2W	4	NW 1/4 of NW 1/4	Sphagnum A and B
2	Ashland	43N	4W	30	SE 1/4 of SW 1/4	Utricularia
3	Iron	43N	3E	26	NW 1/4 of SW 1/4	Sphagnum
4	Oneida	39N	7E	20	SE 1/4 of SW 1/4	Sphagnum
5	Price	39N	3E	5	SW 1/4 of SW 1/4	Sphagnum
6	Price	40N	3E	14		Sphagnum
7	Sawyer	38N	3W	21	NE 1/4 of NW 1/4	Sphagnum
8	Sawyer	39N	3W	15	NE 1/4 of NE 1/4	Sphagnum, Potamogeton
9	Sawyer	39N	4W	14	NW 1/4 of NW 1/4	Sphagnum
10	Vilas	41N	8E	10	SW 1/4 of NW 1/4	Sphagnum
11	Vilas	41N	8E	27	NW 1/4 of SE 1/4	Sphagnum, Carex
12	Vilas	42N	7E	29	SW 1/4 of SW 1/4	Sphagnum

Foerster, 1972; Foerster & Schlichting, 1965; Franken, 1933; Hirano, 1960; Lande, 1973; Laporte, 1931; van Oye, 1935; Pearsall, 1932; Rawson, 1956. However, nearly all of these papers deal with qualitative aspects of desmid biology, and very little quantitative data have emerged to date.

Our knowledge of alkaline bog lakes appears limited and comes mainly from information reported by Gates (1942), Goe *et al.* (1925), Jewell & Brown (1929), Skadowsky (1922), and Welch (1936, 1952). Except for a species list and total phytoplankton counts in Mud Lake, Michigan (Welch 1936), data on the algal communities of alkaline bog lakes appear to be lacking.

According to Welch (1952, Table 48, p. 390) alkaline bog

lakes differ from acid bog lakes chemically in having open water pH values normally above 7.0 and in having markedly higher alkalinity and conductivity levels. These differences, however, are based on data from a very limited number of lakes, and further studies are needed to obtain confirming observations. Since all three alkaline bog lakes cited by Welch (1952) have outlet drainage streams (see Gates, 1942), the presence of such a stream has been used in part to define an alkaline bog (Prescott, 1962; see also references in Table 1). Such a definition, however, appears to be arbitrary and must be modified because alkaline bog lakes of both the seepage and drainage types occur in Wisconsin.

The literature on closed bogs and peatlands appears to be extensive (e.g., see the bibliographies in Gorham, 1957; Heinselman, 1963, 1970) and includes a number of investigations of varying quality of Wisconsin environments (e.g., Andrews, 1915; Clausen, 1957; Curtis, 1959; Grittenger, 1970; Habeck, 1958; Hansen, 1933; Huels, 1915; Pammel, 1902; Rhodes, 1933). A feature common to nearly all closed bog and peatland studies, however, is the virtual absence of quantitative data on the algal communities present. Franken (1933) provided data on the desmids occurring in the mats surrounding several European lakes but did not consider any closed bogs. Laporte (1931) reported some information on desmids associated with *Sphagnum* mats, but he did not include any quantitative data. As far as can be determined, information on the algal communities of closed bogs in Wisconsin is lacking totally.

Materials and methods

The 28 acid bogs, 5 alkaline bogs, and 12 closed bogs involved in this study (Table 1) have been selected at random; all were characterized by the presence of a bog mat which, with one exception, contained a predominance of *Sphagnum*. A summary of water chemistry date (range and mean values) for each type of locality appears in Table 2.

Chemical data on carbon dioxide and oxygen have been obtained with the aid of a HACH Chemical Company (Ames, Iowa) Water Analysis Field Kit, model

Table 2. Summary of water chemistry conditions in the various lake types. All values expressed as mg./l. except for conductivity (μmhos/cm) and pH (units).

	Acid Bogs		Lake Samples: Alkaline Bogs		Mat Samples: Alkaline Bogs		Closed Bogs	
Parameter	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Conductivity	14-61(180?)	27	37-103	79	41-78	59	30-429	104.5
pH	5.6-7.0	6.2	7.1-9.1	8.08	4.4-7.3	5.7	4.0-5.9	4.55
CO_2	0-21	8.2	0-10	3.8	40-54(?)			
O_2	2-15	9.2	9-17	12	4	4		
PO_4-P	.011-.058	.0335	<.005-.104	.0516	.017-.095	.0685	.015-.967	.31
Total P	.02-.12	.064	.02-.13	.082	.03-.16	.2575	.04-2.12	.85
NO_2-N	<.002-.014	.0059	.003-.021	.01125	.002-.036	.0195	.01-.62	.0915
NO_3-N	<.04-.27	.0875	<.04-.27	.068	.04-1.94	.5975	.16-3.44	1.029
NH_3-N	<.03-.27	.0625	<.03-.70		.04-.94	.2975	<.03-2.26	.4425
Org. N	.24-1.85	.90	.34-1.36	.776	.72-3.53	1.995	.95012.63	3.96
Total N	.33-1.95	1.06	.39-2.25	1.006	.80-6.43	2.91	1.19-13.30	5.52
Total Alkalinity	0-21	2.6	14-50	38.4	0.38	20.25	0-17	1.58

Table 2. (continued).

	Acid Bogs		Lake Samples Alkaline Bogs		Mat Samples Alkaline Bogs		Closed Bogs	
Parameter	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Ca^{++}	9.9	3.10	7.5-20.8	14.84	<2.0-12.0	8.7	2.3-12.3	5.72
Mg^{++}	<2.0-2.5		<2.0-7.6	5.1	<2.0-7.9		<2.0-5.2	
K^{+}	<.5-2.2		<.5-1.9	1.0	<.5-2.1		<.5-6.6	
Na^{+}	<1.0-11.5		<1.0-4.8	2.4	<1.0-4.7		<1.0-83.1	14.8
Cl^{-}	2-39	6.8	4-28	10.4	5-8	6	2-140	27.7
$SO_4^{=}$	1-12	5.9	3-8	6.2	3-35(92?)	17.7	7.49(139?)	21

DR-EL, and calcium levels have been determined using the EDTA titrimetric method (APHA 1971). Information on the remaining chemical parameters has been obtained from water samples sent to the Delafield Laboratory of the Wisconsin Department of Natural Resources. Specific methods and references used by the DNR are listed in Table 3; the spectrophotometric testing and read outs were facilitated by a Beckman Automatic DB-G Spectrophotometer System with Teletype.

All aufwuchs samples were collected from depths of 1 m. or less in inshore areas. Portions of macrophyte host plants were placed in 250 ml. jars, immediately preserved with FAA (10:7:2:1::95% ethanol:distilled water:formalin: acetic acid), and returned to the lab for subsequent analysis. Surface plankton samples were gathered by passing 20 l. of water through a No. 25 silk mesh plankton net; the resulting concentrates were preserved by the addition of enough formalin to tyield a 1:10::formalin:concentrate mixture in each sample.

Population density data have been obtained by means of Sedgwick-Rafter cell counts (see Woelkerling *et al.*, 1975 for details) using a counting regime of 2 tallies in each of 12 different Sedgwick-Rafter cells. Aufwuchs removal has been effected by agitation and acid hydrolysis (see Gough & Woelkerling, 1975 for details); results for plankton have been expressed as numbers per ml. of lake

Table 3. Methods of Water Chemistry Analysis Utilized by the Wisconsin Department of Natural Resources.

Parameter		Method	Reported As
pH		Glass electrode pH meter	units
Specific conductance		Platinum electrode conductivity meter	micro-mhos/cm at 25°C
Alkalinity (Tot)		Potentiometric or Indic. method Brom Cresol green - methyl red mixed	mg/l as $CaCO_3$
Nitrite-nitrogen	(1)	Diasotization method	mg/l NO_3-N
Nitrate-nitrogen	(2)	Modified brucine method	mg/l NO_2-N
Ammonia-nitrogen	(1)	Distillation with nesslerization	mg/l NH_3-N
Organic-nitrogen	(4)	Sulfuric acid digestion, distillation, nesslerization	mg/l Org.-N
Dissolved phosphorus (PO_4)	(1)	Stannous chloride-molybdate procedure	mg/l PO_4-P
Total phosphorus	(3)	Stannous chloride-molybdate procedure after perchloric/nitric acid digestion	mg/l P (Tot)
Sulfate	(1)	Turbidimetric procedure	mg/l SO_4
Chloride	(2)	Mercuric nitrate method	mg/l Cl

References:

(1) Standard Methods for the Examination of Water and Wastewater, American Public Health Association, 12th edition (1965).

(2) FWPCA Methods for Chemical Analyses of Water and Wastes, U.S. Department of the Interior, November 1969.

(3) Katz & Proctor, ANAL CHEM 19. (1947).

(4) Techniques of Water Resources Investigations of the USGS, Chap. A1 - Methods for collecting and analysis of H_2O samples, U.S. Department of the Interior, 1970.

water while results for aufwuchs have been expressed as numbers per mg. dry weight of host tissue. The nonparametric procedures (see Woelkerling *et al.*, 1975 for discussion on the advantages of using nonparametric tests) described by Wilcoxon & Wilcox (1964) have been employed in testing for statistical significance. Critical rank differences which exceed table values at the 5% probability level are considered significant.

For each sample, quantitative data have been obtained on the Desmidiales, Chlorococcales, other Chlorophyceae, Bacillariophyceae, Cyanophyceae, Euglenophyceae, Dinophyceae, and Chrysophyceae; other groups did not occur. These taxa have been chosen because of their use in phytoplankton quotients (Brook, 1965; Nygaard, 1949; Thunmark, 1945) and/or other proposed environmental indicator systems. Species composition and most other qualitative aspects will be considered at a later date.

Results and discussion

Generic diversity

Twenty-two genera of desmids occurred in the acid bog aufwuchs samples analyzed during this study (Table 4), and one genus – *Spinoclosterium* – apparently has not been reported previously from Wisconsin. This number is markedly higher than those for alkaline bogs and closed bogs where only 10 desmid genera and 12 desmid genera occurred in the respective aufwuchs samples. The data suggest that greater generic diversity is apt to occur in acid bog environments (see Table 2) where the open water pH range is usually 5.0-7.0 than in alkaline bogs where the pH range is 7.0-9.0 or in closed bogs where the pH is generally (10 of 12 cases) below 5.0. A number of hypotheses (e.g., Hutchinson, 1967; Moss, 1973; Pearsall, 1932; Ruttner, 1963, p. 222; Tassigny, 1971; West & West 1909) have been offered to account for desmid distribution based on water chemistry differences, however, and the matter is discussed in greater detail elsewhere (Woelkerling & Gough, 1975).

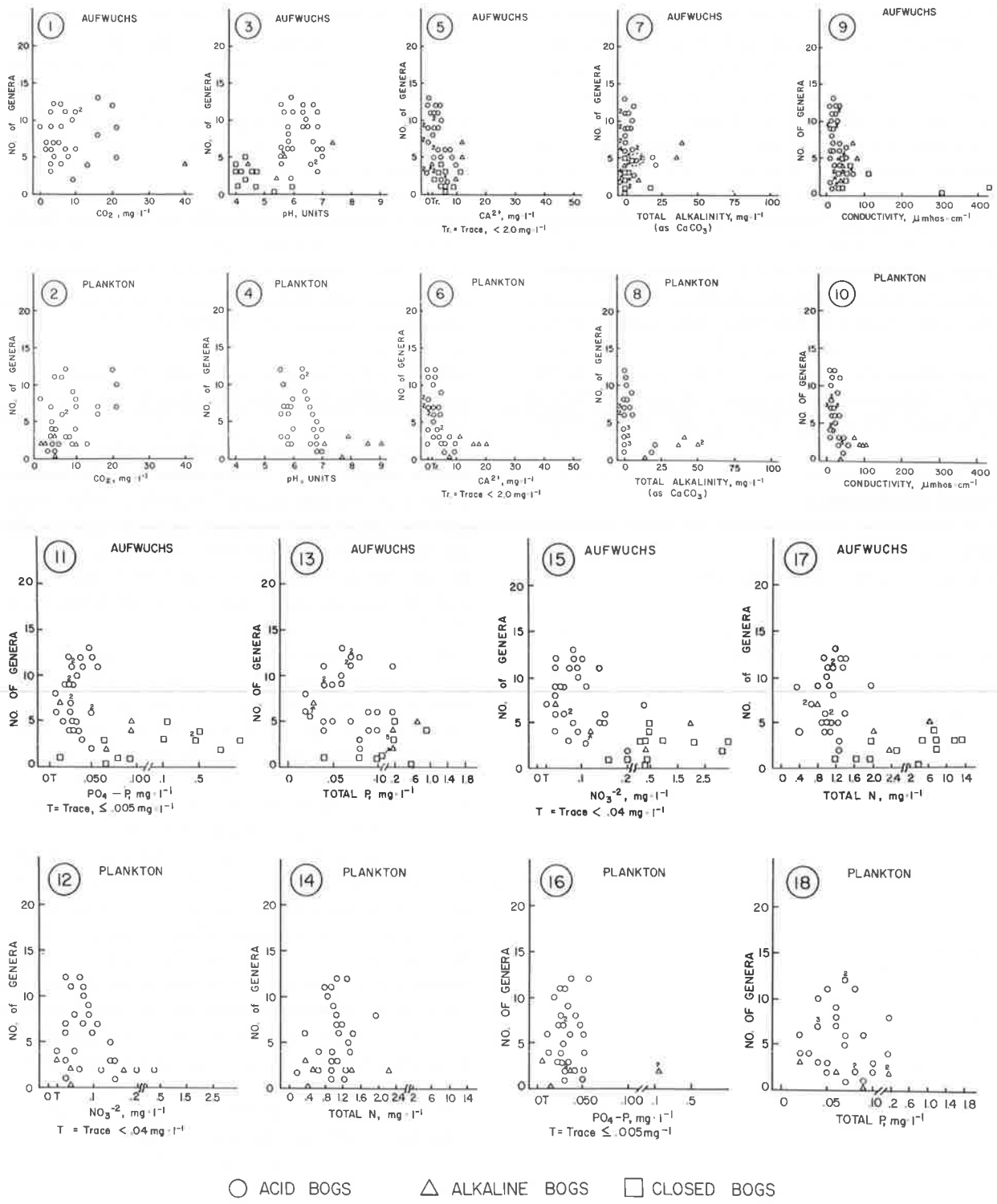
Table 4. The presence (+) or absence (–) of genera in the aufwuchs and plankton communities of various lake types.

	Acid Bogs		Alkaline Bogs		Closed Bogs
	Aufwuchs	Plankton	Aufwuchs	Plankton	Aufwuchs
Arthrodesmus	+	+	+	+	+
Bambusina	+	+	–	+	+
Closterium	+	+	+	–	+
Cosmarium	+	+	+	+	+
Cylindrocystis	+	–	+	–	+
Desmidium	+	+	+	–	+
Docidium	+	–	–	–	–
Euastrum	+	+	+	–	+
Gonatozygon	+	–	–	–	–
Hyalotheca	+	+	–	–	+
Micrasterias	+	+	+	–	–
Netrium	+	+	+	–	+
Penium	+	+	–	–	+
Phymatodocis	–	+	–	–	–
Pleurotaenium	+	+	–	–	–
Spinoclosterium	+	–	–	–	–
Spirotaenia	+	+	–	–	–
Sphaerozosma	+	+	–	–	–
Spondylosium	+	+	–	–	–
Staurastrum	+	+	+	+	+
Tetmemorus	+	+	–	–	+
Triploceras	+	+	–	–	–
Xanthidium	+	+	+	–	–

Within acid bog lakes, the number of aufwuchs genera present varied from 2-13. In alkaline bogs the number varied from 2-7, and in closed bogs the number varied from 1-5. These variations among lakes of a given type did not appear to be correlated with any particular factors in the chemical environment, as evidenced by plots (Figs. 1-18, odd numbers only) of generic numbers against levels of various chemical parameters.

In four of the five acid bog lakes where more than one macrophyte was collected, the greatest generic diversity occurred in association with *Utricularia;* in the fifth lake *Utricularia* was not collected and the greatest diversity occurred in association with *Sphagnum. Utricularia* harbored between 3 and 13 different genera at the various localities while *Sphagnum* harbored between 2 and 12 genera. Too few samples of other hosts were analyzed to provide meaningful range data. Among the three alkaline bog lakes where more than one host was analyzed, the greatest generic diversity also occurred in association with *Utricularia* in the two cases where it was present. In Mystery Lake, the third locality, the two hosts *(Carex, Sphagnum)* each harbored three genera. *Utricularia* was not detected in the closed bogs sampled, but in the two cases where one of the hosts present was not *Sphagnum,* the greatest generic diversity of desmids occurred on the non-*Sphagnum* host.

Eighteen genera of desmids occurred in the acid bog euplankton (Table 4), and one genus – *Phymatodocis* – appears to represent a new record for Wisconsin. *Staurastrum* plants were found in 86% of the samples analyzed, and four additional genera (*Arthrodesmus,* 61%; *Bambusina,* 68%; *Cosmarium,* 60%; *Desmidium,* 50%) were



Figs. 1-18. Relationship between the number of desmid genera present in the aufwuchs and the plankton and various chemical parameters at the study sites.

Table 5. Summary of Aufwuchs Population Density Data. Data Expressed as Number of Organisms per Mg. Dry Weight of Host Tissue.

A. Acid Bogs

County & Lake	Host	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Euglenophyceae	Dinophyceae	Total Population
Ashland Co.									
Trout Lk.	Sphagnum	9.16×10^{2}	2.60×10^{2}	3.50×10^{3}	6.91×10^{3}	5.00×10^{3}	---	1.60×10^{2}	1.67×10^{4}
Barron Co.									
Lk. 7-9d	Sphagnum	1.73×10^{2}	3.33×10^{1}	1.21×10^{3}	1.98×10^{3}	1.53×10^{3}	---	3.33×10^{1}	4.96×10^{3}
	Utricularia	4.24×10^{3}	1.96×10^{3}	2.62×10^{4}	1.80×10^{4}	1.44×10^{4}	---	4.24×10^{3}	6.71×10^{4}
Bayfield Co.									
Lk. 17-5	Sphagnum	4.45×10^{2}	5.79×10^{3}	1.34×10^{3}	1.72×10^{3}	6.61×10^{3}	---	---	1.59×10^{4}
Lk. 7-2	Sphagnum	2.15×10^{3}	1.29×10^{2}	5.25×10^{3}	2.69×10^{3}	6.05×10^{3}	---	--	1.63×10^{4}
Lk. 33-14	Utricularia	3.49×10^{3}	6.14×10^{2}	5.81×10^{3}	4.65×10^{3}	5.89×10^{3}	1.01×10^{3}	2.63×10^{3}	2.42×10^{4}
Lk. 1-16c	Utricularia	2.18×10^{3}	8.54×10^{3}	1.79×10^{3}	3.75×10^{4}	2.36×10^{4}	6.20×10^{2}	---	7.42×10^{4}
Lk. 6-10d	Utricularia	2.06×10^{3}	2.44×10^{3}	6.04×10^{2}	5.25×10^{3}	4.27×10^{3}	7.32×10^{1}	---	1.47×10^{4}
Burnett Co.									
Lk. 9-2	Utricularia	9.81×10^{3}	1.52×10^{4}	4.23×10^{3}	2.58×10^{4}	1.21×10^{4}	---	1.15×10^{3}	6.83×10^{4}
Lk. 10-6	Utricularia	1.45×10^{4}	1.41×10^{4}	3.37×10^{3}	1.45×10^{4}	2.88×10^{4}	---	8.42×10^{2}	7.61×10^{4}
Lk. 16-2	Utricularia	5.87×10^{3}	7.87×10^{3}	5.87×10^{3}	1.48×10^{4}	1.93×10^{4}	---	1.37×10^{2}	5.38×10^{4}
Lk. 17-4	Sphagnum	8.23×10^{2}	2.40×10^{3}	2.61×10^{3}	1.23×10^{3}	1.10×10^{4}	---	---	1.81×10^{4}
	Utricularia	1.63×10^{4}	1.12×10^{4}	4.32×10^{3}	1.93×10^{4}	2.96×10^{4}	---	1.80×10^{2}	8.09×10^{4}
Lk. 33-14	Sphagnum	8.62×10^{2}	3.27×10^{3}	2.41×10^{3}	7.13×10^{3}	5.90×10^{3}	5.15×10^{1}	---	1.96×10^{4}
Chippewa Co.									
Larrabee Lk.	Utricularia	2.21×10^{3}	7.37×10^{2}	8.84×10^{3}	3.05×10^{4}	1.11×10^{4}	---	4.60×10^{2}	5.38×10^{4}
Leo Joerg Lk.	Brassinia	8.15×10^{2}	2.79×10^{1}	1.77×10^{3}	8.15×10^{3}	1.92×10^{3}	---	2.79×10^{1}	1.27×10^{4}
	Sphagnum	3.21×10^{2}	4.40×10^{1}	2.98×10^{3}	2.94×10^{3}	3.03×10^{3}	---	---	9.32×10^{3}
	Utricularia	4.01×10^{3}	1.00×10^{3}	1.17×10^{4}	1.56×10^{4}	8.36×10^{3}	---	6.69×10^{2}	4.13×10^{4}

Table 5. (continued).

County & Lake	Host	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Euglenophyceae	Dinophyceae	Total Population
Lk. 2-8	Utricularia	$2.97x10^3$	$9.41x10^2$	$4.26x10^3$	$5.68x10^3$	$2.70x10^3$	---	$2.03x10^2$	$1.68x10^4$
Iron Co.									
Lk. 26-9	Sphagnum	$1.50x10^3$	---	$3.10x10^3$	$5.58x10^2$	$1.53x10^3$	---	---	$6.69x10^3$
	"Moss"	$6.66x10^3$	$9.29x10^2$	$8.06x10^3$	$1.11x10^4$	$4.49x10^3$	---	---	$3.12x10^4$
Lk. 13-2d	Potamogeton	$7.92x10^2$	$5.43x10^1$	$2.89x10^3$	$3.17x10^3$	$5.15x10^3$	---	---	$1.21x10^4$
	Sphagnum	$2.10x10^2$	---	$2.40x10^3$	$3.18x10^3$	$1.26x10^3$	---	---	$7.05x10^3$
	Utricularia	$1.10x10^4$	$9.53x10^2$	$1.13x10^4$	$2.01x10^4$	$3.03x10^4$	---	---	$7.36x10^4$
Oneida Co.									
Lk. 11-5	Sphagnum	$8.87x10^3$	$3.01x10^2$	$9.02x10^3$	$5.71x10^3$	$2.72x10^4$	---	$4.69x10^2$	$5.16x10^4$
Polk Co.									
Evelyn Lk.	Utricularia	$1.33x10^3$	$1.28x10^2$	$6.13x10^3$	$1.33x10^4$	$3.73x10^3$	---	$3.33x10^3$	$2.80x10^4$
Price Co.									
Unnamed	Sphagnum	$2.74x10^2$	---	$4.98x10^3$	$2.52x10^3$	$2.90x10^3$	---	---	$1.07x10^4$
Rusk Co.									
Round Lk.	Utricularia	$8.31x10^3$	$2.74x10^3$	$5.09x10^3$	$1.51x10^4$	$4.84x10^3$	---	$3.87x10^2$	$3.65x10^4$
Saxton Lk.	Sphagnum	$1.69x10^2$	$3.25x10^1$	$2.33x10^3$	$2.67x10^3$	$1.59x10^3$	---	---	$6.79x10^3$
School Lk.	Utricularia	$6.58x10^3$	$9.56x10^2$	$3.90x10^3$	$7.96x10^3$	$4.59x10^3$	$8.31x10^1$	$7.79x10^2$	$2.48x10^4$
Vilas Co.									
Spruce Lk.	Sphagnum	$9.30x10^2$	$9.92x10^1$	$5.06x10^3$	$1.12x10^4$	$5.47x10^3$	---	---	$2.28x10^4$
Unnamed	Sphagnum	$2.20x10^3$	$2.01x10^2$	$7.64x10^3$	$7.64x10^3$	$4.19x10^3$	---	$1.46x10^3$	$2.33x10^4$
Washburn Co.									
Unnamed (1)	Potamogeton	$5.08x10^2$	---	$5.59x10^3$	$9.02x10^3$	$2.80x10^3$	---	$1.22x10^2$	$1.82x10^4$
Unnamed (2)	Utricularia	$1.90x10^3$	$7.11x10^2$	$5.57x10^3$	$8.46x10^3$	$6.93x10^3$	---	$5.53x10^2$	$2.43x10^4$
Unnamed (3)	Sphagnum	$2.80x10^3$	$4.07x10^1$	$2.71x10^3$	$8.95x10^2$	$3.77x10^3$	---	---	$1.02x10^4$

encountered in at least half of the study lakes. Plants of *Penium, Phymatodocis* and *Tetmemorous* occurred only once. With the exception of *Phymatodocis,* all genera recorded in the euplankton also were represented in the aufwuchs, and with five exceptions [Bayfield Co.–Lake 17-5; Chippewa Co.–Leo Joerg Lake; Iron

Table 5. (continued).

B. Alkaline Bogs

Note: Hosts designated with an asterisk (*) are from the lake; the remainder are from the mat.

Lake	Host	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Euglenophyceae	Dinophyceae	Total Population
Bog	Potamogeton*	2.50×10^2	2.08×10^2	1.91×10^3	7.90×10^3	2.54×10^3	--	--	1.28×10^4
Bullhead	Chara*	4.65×10^2	3.19×10^1	1.10×10^3	3.49×10^3	1.59×10^3	--	9.96×10^2	7.67×10^3
	Najas*	4.28×10^1	8.23×10^0	1.37×10^2	4.28×10^2	3.34×10^2	--	1.63×10^2	1.11×10^3
	Potamogeton*	2.09×10^2	--	3.28×10^2	1.40×10^3	1.73×10^3	--	7.76×10^2	4.44×10^3
	Utricularia*	1.97×10^3	1.46×10^2	2.12×10^3	4.78×10^3	3.88×10^3	--	6.67×10^3	1.96×10^4
	Utricularia	1.32×10^3	2.65×10^2	4.24×10^3	1.27×10^4	5.30×10^3	--	3.97×10^2	2.42×10^4
Cedar	Ceratophyllum*	8.33×10^2	1.39×10^3	8.33×10^3	3.75×10^4	4.44×10^3	--	--	5.25×10^4
Hegmeister	Myriophyllum*	6.26×10^1	--	8.81×10^2	2.35×10^3	1.92×10^3	--	--	5.21×10^3
	Potamogeton A*	--	--	5.94×10^2	1.87×10^3	6.22×10^2	--	--	3.09×10^3
	Potamogeton B*	3.83×10^1	--	1.48×10^3	3.61×10^3	1.12×10^3	--	3.83×10^1	6.29×10^3
	Potamogeton C*	--	--	1.35×10^3	1.09×14^4	1.96×10^3	--	--	1.42×10^4
Hegmeister	Sphagnum A	3.46×10^1	--	1.44×10^3	2.84×10^3	1.22×10^3	--	--	5.53×10^3
	Sphagnum B	2.05×10^1	--	1.07×10^3	9.38×10^2	7.24×10^2	--	--	2.75×10^3
	Utricularia	1.53×10^3	--	9.32×10^3	1.28×10^4	4.89×10^3	--	1.47×10^2	2.87×10^4
Mystery	Carex (?)*	6.96×10^2	2.74×10^2	2.02×10^3	9.66×10^3	2.28×10^3	--	--	1.49×10^4
	Sphagnum	7.29×10^2	1.56×10^2	2.59×10^3	3.56×10^3	3.65×10^3	--	--	1.07×10^4

Co.–Lake 13-2d; Price Co.–Unnamed; Washburn Co.–Unnamed (1)] the number of genera present in the euplankton did not exceed the number of genera present in the aufwuchs. At any given locality, from 1-12 desmid genera were recorded in the euplankton, but the degree of generic diversity did not appear to be linked with any particular factors in the chemicul environment (Fig. 1-18, even numbers only).

Only four genera of desmids occurred in the alkaline bog euplankton (Table 4) with *Staurastrum* present in four of the five lakes. *Bambusina,* recorded in the euplankton of Hegmeister Lake, did not occur in any of the aufwuchs samples analyzed. The absence of desmids in the plankton of Mystery Lake may have been due to the development of a bloom of *Anacystis* (Cyanophyta) at the time of collection. The absence of open water in closed bogs precludes euplankton sampling. The data again suggest that acid bogs provide a more suitable environment for a diverse desmid flora.

Desmid population densities

Population densities of desmids in the aufwuchs of acid bogs ranged from 1.69×10^2 organisms/mg. host dry weight on *Sphagnum* in Saxton Lake [Rusk Co.] to 1.63×10^4 organisms/mg. host dry weight on *Utricularia* in Lake 17-4 [Burnett Co.] (Table 5). In only five of the

Table 5. (continued).

C. Closed Bogs

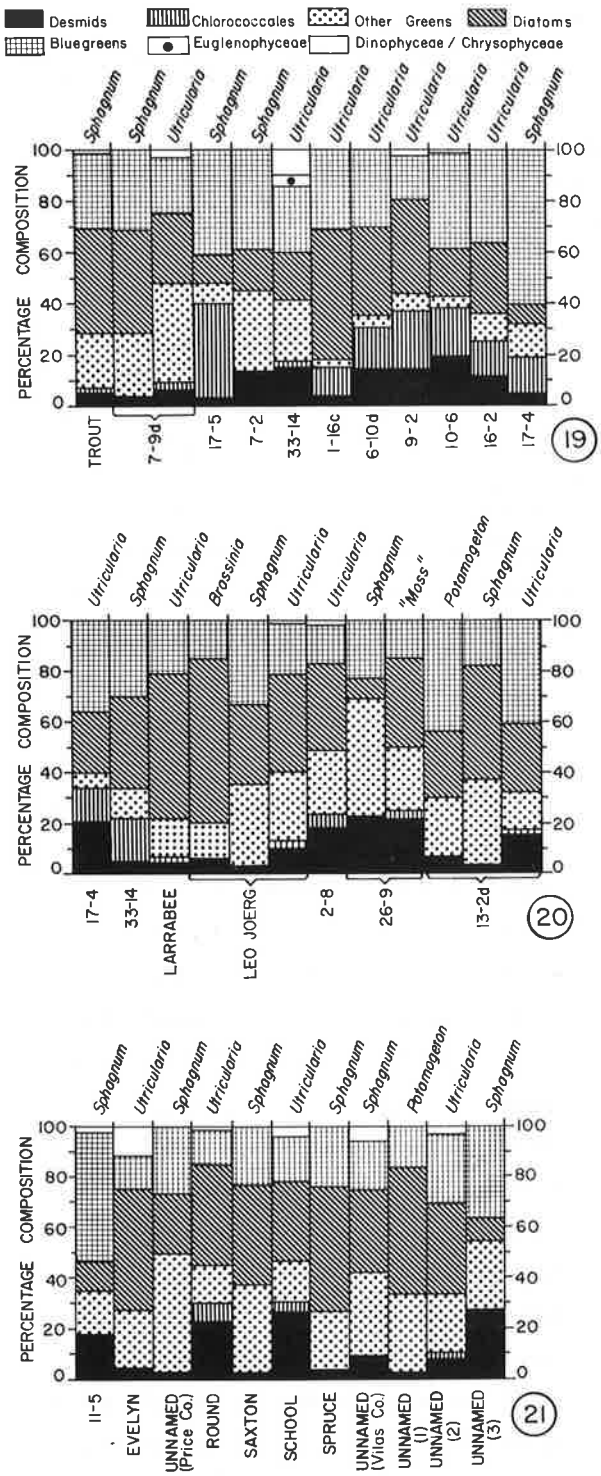
Locality number	Host	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Euglenophyceae	Dinophyceae	Total
1	Sphagnum A	6.06×10^1	---	7.29×10^3	6.06×10^3	5.80×10^3	---	---	1.92×10^4
	Sphagnum B	6.29×10^2	---	1.15×10^4	7.44×10^3	2.83×10^3	---	---	2.24×10^4
2	Utricularia	2.94×10^2	1.47×10^2	6.13×10^3	1.44×10^4	1.42×10^4	---	4.78×10^2	3.56×10^4
3	Sphagnum	5.52×10^2	---	2.55×10^3	9.35×10^2	2.68×10^3	---	---	6.72×10^3
4	Sphagnum	---	---	2.89×10^2	1.27×10^3	9.66×10^3	9.83×10^2	---	1.22×10^4
5	Sphagnum	1.12×10^3	---	6.98×10^2	3.26×10^3	1.20×10^3	---	---	6.28×10^3
6	Sphagnum	2.40×10^2	---	2.22×10^3	7.44×10^3	1.56×10^3	---	---	1.15×10^4
7	Sphagnum	9.40×10^2	---	1.76×10^3	9.46×10^3	2.35×10^3	---	---	1.45×10^4
8	Sphagnum	1.12×10^3	5.56×10^1	5.65×10^3	5.65×10^3	2.00×10^3	---	---	1.45×10^4
	Potamogeton	1.44×10^2	6.79×10^1	1.88×10^3	3.26×10^3	1.80×10^3	---	1.44×10^2	7.26×10^3
9	Sphagnum	1.93×10^2	---	1.91×10^3	5.50×10^3	3.27×10^3	---	---	1.09×10^4
10	Sphagnum	1.85×10^2	2.24×10^1	1.00×10^3	7.00×10^2	1.54×10^3	---	2.24×10^1	3.47×10^3
11	Sphagnum	8.15×10^1	---	2.80×10^3	6.37×10^2	1.32×10^3	---	---	4.84×10^3
	Carex	2.22×10^2	---	1.41×10^3	6.29×10^2	2.52×10^3	---	---	4.78×10^3
12	Sphagnum	1.75×10^1	---	4.91×10^2	5.09×10^2	1.24×10^3	---	---	2.26×10^3

fifteen *Sphagnum* samples analyzed did the population density of desmids exceed 10^3 organisms/mg. host dry weight whereas on *Utricularia,* population densities of desmids surpassed 10^3 organisms/mg. host dry weight in all cases, and in three of sixteen samples, population densities in excess of 10^4 organisms/mg. host dry weight were recorded. Not only was the generic diversity of desmids greater on *Utricularia* than on *Sphagnum* in the four lakes where samples of both macrophytes were analyzed, but population densities of desmids associated with *Utricularia* eclipsed those associated with *Sphagnum* by at least 3.69×10^3 organisms/mg. host dry weight in each case.

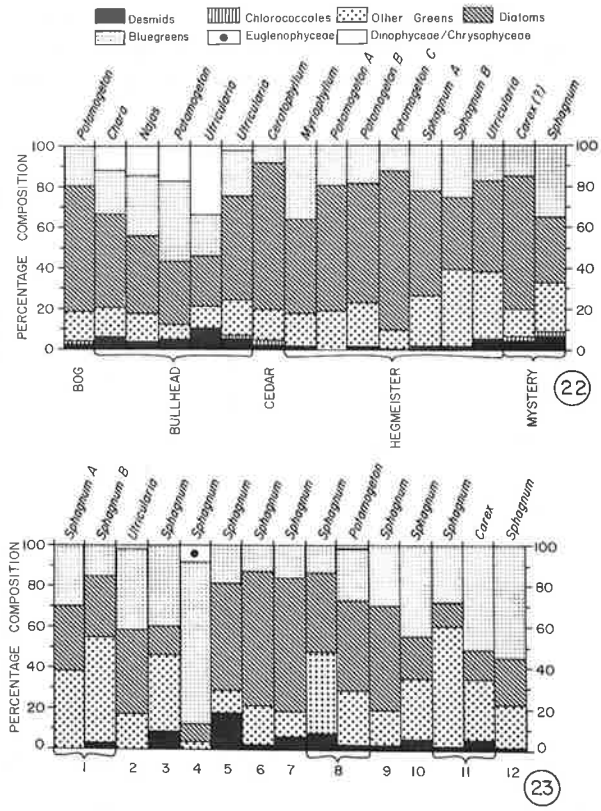
In 6 of the 35 acid bog aufwuchs samples analyzed, the population densities of desmids accounted for over 20% of the total population, but in no case did the percentage figure exceed 27.5 (Figs. 19-21). In 13 of the 35 samples, desmids accounted for less than 5% of the total aufwuchs population; at an additional 7 localities the desmid content ranged from 5-10%; and in the remaining 9 samples, desmid densities amounted to 10.1-20% of the total population.

Population densities of desmids in the alkaline bog aufwuchs ranged from 0 organisms/mg. host dry weight on two species of *Potamogeton* in Hegmeister Lake to 1.97×10^3 on the open water sample of *Utricularia* from Bullhead Lake (Table 5). Densities greater than 1×10^3 organisms/mg. host dry weight occurred only on the three *Utricularia* samples; densities less than 6.3×10^1 occurred in 7 of the 16 samples analyzed. In 5 of the 16 samples, desmids accounted for over 5% of the total population, but in no case did the percentage total exceed 10.1 (Fig. 22). Three of the five densest samples were taken from the bog mat while the other two came from open water. In 8 of the 16 cases, desmids accounted for 2.0% or less of the total population, and with two exceptions, all 8 were associated with hosts taken from the open water.

Population densities of desmids in the aufwuchs of



Figs. 19-21. Percentage composition of aufwuchs communities associated with various macrophyte hosts in acid bog lakes (Percentages < 1.0 not indicated).



Figs. 22-23. Percentage composition of aufwuchs communities associated with various macrophyte hosts. Fig. 22 – Alkaline bogs. Fig. 23 – Closed bogs (Percentages < 1.0 not indicated).

closed bogs ranged from 0 organisms/mg. host dry weight on *Sphagnum* at locality 4 to 1.12 x 10^3 on *Sphagnum* at locality 5 and locality 8 (Table 5). Densities exceeding 1 x 10^3 occurred only at locality 5 and locality 8, while densities less than 1 x 10^3 appeared in 4 of the 15 samples. At 5 study sites, desmids accounted for more than 5% of the total aufwuchs population (Fig. 23), but in only one case (locality 5) did the percentage total exceed 10.0. On 8 of the 15 hosts, the percentage of desmids in the total population was 2.1 or less.

Taken as a whole, the data suggest that no *clear-cut* differentiation can be made between the three lake types either on the basis of actual numbers of desmids present or in terms of the percentage contributions of desmids to the total algal population. It appears, however, that acid bogs are apt to have a quantitatively more prominent desmid flora than alkaline bogs which, in turn, are apt to have a more prominent desmid flora than closed bogs, but no hard and fast generalizations can be made. Thus,

population densities of desmids in the aufwuchs of both closed bogs and alkaline bogs never exceeded 2.0 x 10^3 organisms/mg. host dry weight whereas higher desmid densities occurred in 19 of the 35 aufwuchs samples from acid bogs. Densities less than 1.0 x 10^2 organisms/mg. host dry weight appeared in 4 of 15 closed bog samples and

Table 6. Summary of plankton population density data. Figures expressed as # organisms per ml.

A. Acid Bogs

County	Lake	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Euglenophyceae	Dinophyceae/ Chrysophyceae*	Total
Ashland	Trout	$8.16x10^{-2}$	$8.16x10^{-2}$	$6.73x10^{-1}$	$1.29x10^{1}$	$9.38x10^{-1}$	---	$9.38x10^{-1}$	$1.56x10^{1}$
Barron	Lk. 7-9d	$5.95x10^{1}$	$8.17x10^{-1}$	$1.24x10^{1}$	$5.92x10^{0}$	$1.32x10^{1}$	---	$3.88x10^{0}$	$9.58x10^{1}$
Bayfield	Lk. 17-5	$1.18x10^{0}$	$2.98x10^{0}$	$2.98x10^{0}$	$8.16x10^{-2}$	$5.02x10^{0}$	---	$1.69x10^{0}$	$1.40x10^{1}$
	Lk. 7-2	$1.97x10^{0}$	$1.72x10^{-1}$	$1.00x10^{1}$	$1.43x10^{1}$	$1.25x10^{1}$	---	$3.56x10^{0}$	$4.27x10^{1}$
	Lk. 33-14	$1.42x10^{1}$	$1.68x10^{0}$	$6.58x10^{0}$	$5.10x10^{0}$	$1.58x10^{1}$	---	$3.42x10^{0}$	$4.68x10^{1}$
	Lk. 1-16c	$1.10x10^{0}$	$2.31x10^{0}$	$8.57x10^{-1}$	$8.16x10^{-2}$	$5.53x10^{0}$	---	$8.16x10^{-2}$	$9.96x10^{0}$
	Lk. 6-10d	$7.65x10^{0}$	$1.48x10^{0}$	$5.76x10^{0}$	$2.35x10^{0}$	$1.51x10^{1}$	---	$1.28x10^{0}$	$3.32x10^{1}$
Burnett Co.	Lk. 9-2	$4.41x10^{1}$	$1.20x10^{1}$	$2.13x10^{1}$	$1.26x10^{2}$	$1.12x10^{2}$	---	$5.23x10^{0}$	$3.25x10^{2}$
	Lk. 10-6	$1.74x10^{1}$	$4.66x10^{0}$	$1.13x10^{1}$	$2.05x10^{1}$	$4.69x10^{1}$	$4.90x10^{-1}$	$6.62x10^{0}$	$1.08x10^{2}$
	Lk. 16-2	$1.19x10^{1}$	$4.29x10^{0}$	$1.32x10^{1}$	$1.79x10^{1}$	$3.21x10^{1}$	$4.08x10^{-1}$	$5.11x10^{0}$	$8.51x10^{1}$
	Lk. 17-4	$1.60x10^{1}$	$1.98x10^{0}$	$6.28x10^{0}$	$1.07x10^{1}$	$4.16x10^{1}$	---	$4.65x10^{-1}$	$7.71x10^{1}$
	Lk. 33-14	$1.98x10^{0}$	$9.30x10^{-1}$	$1.02x10^{1}$	$2.33x10^{1}$	$3.20x10^{-1}$	$4.65x10^{-1}$	$8.66x10^{1}$	$1.56x10^{2}$
Chippewa Co.	Larrabee Lk.	$5.10x10^{-1}$	$2.65x10^{-1}$	$1.80x10^{0}$	$1.63x10^{-1}$	$2.55x10^{0}$	---	$2.90x10^{0}$	$8.16x10^{0}$
	Leo Joerg Lk.	$2.11x10^{1}$	$2.75x10^{0}$	$2.06x10^{1}$	$1.32x10^{1}$	$1.32x10^{1}$	---	$1.49x10^{1}$	$8.44x10^{1}$
	Lk. 2-8	$5.10x10^{0}$	$8.06x10^{0}$	$4.49x10^{0}$	$2.78x10^{1}$	$2.17x10^{1}$	---	$1.94x10^{0}$	$6.91x10^{1}$
Iron Co.	Lk. 26-9	$1.07x10^{0}$	$4.08x10^{-1}$	$2.13x10^{1}$	$1.28x10^{0}$	$1.11x10^{1}$	---	$7.65x10^{0}$	$4.29x10^{1}$
	Lk. 13-2d	$1.36x10^{1}$	$1.07x10^{0}$	$2.08x10^{1}$	$1.21x10^{1}$	$2.51x10^{1}$	---	$1.68x10^{0}$	$7.44x10^{1}$
Oneida Co.	Lk. 11-5	$1.63x10^{-1}$	$8.16x10^{-2}$	$8.57x10^{-1}$	$4.28x10^{-1}$	$3.73x10^{0}$	---	$1.14x10^{1}$	...$67x10^{1}$
Polk Co.	Evelyn Lk.	$4.08x10^{-1}$	$4.08x10^{-1}$	$2.14x10^{0}$	$1.74x10^{0}$	$8.17x10^{-1}$	---	$2.65x10^{2}$	$2.71x10^{2}$
Price Co.	Unnamed	$5.10x10^{0}$	$2.04x10^{-1}$	$6.29x10^{1}$	$2.96x10^{0}$	$1.94x10^{0}$	---	$1.48x10^{0}$	$7.46x10^{1}$
Rusk Co.	Round	$2.74x10^{2}$	$6.94x10^{0}$	$3.27x10^{0}$	$1.18x10^{1}$	$3.06x10^{1}$	---	$6.12x10^{1}$	$3.86x10^{2}$
	Saxton	$1.46x10^{1}$	$3.26x10^{-1}$	$1.06x10^{0}$	$1.06x10^{0}$	$1.71x10^{0}$	$3.26x10^{-1}$	$4.88x10^{1}$	$6.77x10^{1}$
	School	$1.04x10^{1}$	---	$8.57x10^{-1}$	$1.02x10^{0}$	$2.37x10^{2}$	---	$1.36x10^{1}$	$2.63x10^{2}$
Vilas Co.	Spruce Lk.	$2.39x10^{0}$	---	$8.93x10^{-1}$	$2.44x10^{1}$	$2.82x10^{0}$	$3.44x10^{1}$	$5.10x10^{1}$	$1.16x10^{2}$
	Unnamed	$5.10x10^{1}$	$1.29x10^{0}$	$1.88x10^{0}$	$8.57x10^{-1}$	$3.22x10^{0}$	---	$6.04x10^{0}$	$1.38x10^{1}$

Table 6. (continued).

County	Lake	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Euglenophyceae	Dinophyceae/ Chrysophyceae*	Total
Washburn Co.	Unnamed (1)	$3.14x10^{0}$	$5.10x10^{-1}$	$3.22x10^{0}$	$1.10x10^{0}$	$3.92x10^{0}$	$8.16x10^{-2}$	$5.10x10^{-1}$	$1.25x10^{1}$
	Unnamed (2)	$2.69x10^{1}$	$4.70x10^{0}$	$1.36x10^{1}$	$1.87x10^{1}$	$3.28x10^{1}$	$9.39x10^{0}$	$2.55x10^{0}$	$1.09x10^{2}$
	Unnamed (3)	$1.96x10^{0}$	$1.63x10^{-1}$	$5.69x10^{0}$	$6.73x10^{-1}$	$3.41x10^{0}$	---	---	$1.19x10^{1}$

* Data for Vilas Co. lakes is for Chrysophyceae; Dinophyceae were not seen. In all other cases, the reverse situation exists.

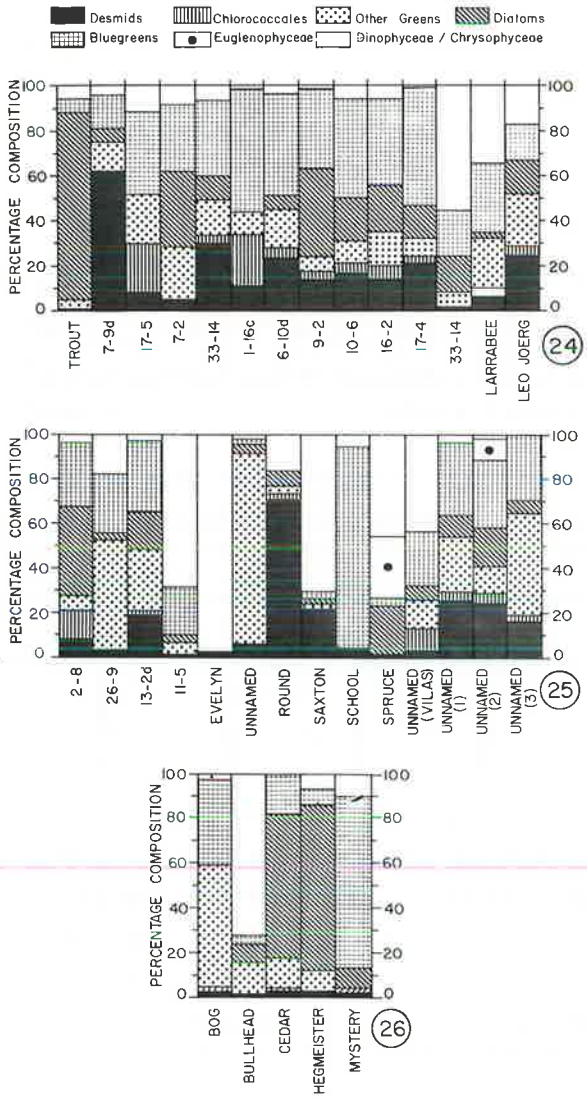
B. Alkaline Bogs

Lake	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Euglenophyceae	Dinophyceae	Total Population
Bog	4.76×10^{0}	3.40×10^{0}	1.12×10^{2}	--	8.10×10^{1}	3.40×10^{0}	1.36×10^{0}	2.05×10^{2}
Bullhead	1.02×10^{0}	--	9.18×10^{0}	5.47×10^{0}	2.38×10^{0}	--	4.80×10^{1}	6.60×10^{1}
Cedar	2.1×10^{0}	1.6×10^{0}	1.48×10^{1}	6.68×10^{1}	1.89×10^{1}	5.00×10^{-1}	--	1.05×10^{2}
Hegmeister	1.02×10^{0}	--	4.08×10^{0}	3.25×10^{1}	2.72×10^{0}	--	3.22×10^{0}	4.35×10^{1}
Mystery	5.10×10^{-1}	--	5.10×10^{-1}	2.73×10^{0}	2.18×10^{1}	--	3.23×10^{0}	2.87×10^{1}

7 of 16 alkaline bog samples, but never occurred in acid bog samples. In both closed bogs and alkaline bog lakes, desmids contributed less than 5% to the total aufwuchs population in about ⅔ of the samples, and in approximately ½ of the samples, the percentage contribution was under 2.1. This contrasts sharply with acid bogs where nearly ⅔ of the macrophyte hosts analyzed contained over 5% desmids and none of the hosts harbored less than 2.5% desmids.

Population densities of desmids in the acid bog plankton ranged from 8.16×10^{-2} to 2.74×10^{2} organisms/ml. (Table 6); they exceeded 1.00×10^{2} organisms/ml. in 12 of the 28 study lakes. In Lake 7-9d (Barron Co.) and Round Lake (Rusk Co.), desmids accounted for over 60.0% of the total euplankton population (Figs. 24-25). In the remaining 26 lakes, desmids accounted for 30.3% or less of the total plankton population, and in 9 cases the percentage of desmids in the total plankton population exceeded the percentage of desmids in the total aufwuchs population on at least one of the hosts present.

Population densities of desmids in the alkaline bog plankton ranged from 5.10×10^{-1} organisms/ml. in Mystery Lake to 4.76×10^{0} organisms/ml. in Bog Lake (Table 6), and in no case did these densities account for more than 2.3% of the total population (Fig. 26). In Bog Lake and in Cedar Lake, the percentage of desmids in the total euplankton population exceeded the percentage of desmids in the total aufwuchs population on the hosts



Figs. 24-26. Percentage composition of plankton communities at the study sites. Figs. 24-25 – Acid bogs. Fig. 26 – Alkaline bogs. (Percentages < 1.0 not indicated).

analyzed, and with the exception of *Utricularia,* the same situation prevailed in Hegmeister Lake. In Bullhead Lake and Mystery Lake, however, the percentage of desmids in the total euplankton population was less than the percentage of desmids in the total aufwuchs population in all instances.

The desmids appear to form a less conspicuous element of alkaline bog lake euplankton as compared with acid bog lake euplankton. Although the population density ranges of euplankton desmids in acid bogs and

Table 7. Presence (+) or Absence (–) of Significant Differences (95% Level) in the Population Densities of the Various Groups of Algae Associated With Different Hosts at a Given Acid Bog Locality.

County & Lake	Hosts Compared	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Dinophyceae	Total Population
Barron Co.								
Lk. 7-9d	Sphagnum vs Utricularia	+	+	+	–	–	+	+
Burnett Co.								
Lk. 17-4	Sphagnum vs Utricularia	+	+	+	+	–	–	+
Chippewa Co.								
Leo Joerg Lk.	Brasenia vs Sphagnum	+	–	–	+	–	–	+
	Brasenia vs Utricularia	–	–	–	+	–	+	+
	Sphagnum vs Utricularia	+	–	–	+	–	–	+
Iron Co.								
Lk. 26-9	Sphagnum vs "Moss"	–	+	+	+	+	–	–
Lk. 13-2d	Potamogeton vs Sphagnum	–	+	+	+	+	–	–
	Potamogeton vs Utricularia	+	–	–	+	–	–	+
	Sphagnum vs Utricularia	+	+	–	–	+	–	+

alkaline bogs appear to overlap, desmids never accounted for more than 2.3% of the total euplankton population in alkaline bogs. In acid bogs, however, desmids accounted for over 2.3% of the total euplankton population in 23 of 28 cases and contributed over 10% to the total euplankton population in 15 lakes. Thus it would appear that acid bogs are apt to have a more prominent euplankton desmid flora than alkaline bogs, but no clear-cut distinctions can be made because of the overlap in range values.

Host to host variation within lakes

Within a given locality, statistically significant variation in desmid population densities from one host to another was far more common in acid bogs (Table 7) than in alkaline bogs (Table 8) or closed bogs (Table 9). In acid bogs, a comparison of all possible pairs of hosts from the same locality revealed that statistically significant differences in desmid population densities occurred in 67% of the cases. Plants of *Utricularia* contained significantly greater densities than did plants of *Sphagnum* in all cases where the two macrophytes occurred together; indeed *Utricularia* harbored from 12.5 to 52.4 times as many desmids as did *Sphagnum* in any given locality! In Leo Joerg Lake (Chippewa Co.), both *Brasenia* and *Utricularia* harbored significantly more desmids than did *Sphagnum.*

Table 8. Presence (l) or absence (–) of significant differences in the population densities of the various groups of algae associated with different hosts at a given alkaline bog locality.

Lake	Hosts Compared	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Dinophyceae	Total Population
Bullhead	Chara vs Najas	-	-	-	+	-	-	+
	Chara vs Potamogeton	+	-	+	+	-	-	+
	Chara vs Utricularia (lake)	-	-	-	+	-	+	-
	Chara vs Utricularia (mat)	-	-	-	-	-	+	-
	Najas vs Potamogeton	-	-	-	-	-	-	-
	Najas vs Utricularia (lake)	-	-	-	-	-	+	+
	Najas vs Utricularia (mat)	-	-	+	+	-	-	-
	Potamogeton vs Utricularia (lake)	-	-	+	-	-	+	+
	Potamogeton vs Utricularia (mat)	-	-	+	+	-	-	-
	Utricularia (lake) vs Utricularia (mat)	-	-	-	-	-	+	-
Hegmeister	Myriophyllum vs Potamogeton A	-	-	-	-	+	-	+
	Myriophyllum vs Potamogeton B	-	-	-	-	+	-	-
	Myriophyllum vs Potamogeton C	-	-	-	+	-	-	-
	Myriophyllum vs Sphagnum A	-	-	-	-	-	-	-
	Myriophyllum vs Sphagnum B	-	-	-	-	-	-	-
	Myriophyllum vs Utricularia	-	-	+	-	-	-	-
	Potamogeton A vs Potamogeton B	-	-	-	-	-	-	+
	Potamogeton A vs Potamogeton C	-	-	-	+	-	-	+
	Potamogeton A vs Sphagnum A	-	-	-	-	-	-	+
	Potamogeton A vs Sphagnum B	-	-	+	-	-	-	-
	Potamogeton A vs Utricularia	-	-	+	-	-	-	+
	Potamogeton B vs Potamogeton C	-	-	-	-	-	-	+
	Potamogeton B vs Sphagnum A	-	-	-	-	-	-	-

Table 8. (continued).

Lake	Hosts Compared	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Dinophyceae	Total Population
	Potamogeton B vs Sphagnum B	-	-	-	+	-	-	-
	Potamogeton B vs Utricularia	-	-	-	-	-	-	-
	Potamogeton C vs Sphagnum A	-	-	-	+	-	-	+
	Potamogeton C vs Sphagnum B	-	-	+	+	-	-	+
	Potamogeton C vs Utricularia	-	-	+	+	-	-	-
	Sphagnum A vs Sphagnum B	-	-	-	+	-	-	-
	Sphagnum A vs Utricularia	-	-	-	-	-	-	-
	Sphagnum B vs Utricularia	-	-	-	+	-	-	+
Mystery	Carex (?) vs Sphagnum	-	-	-	+	+	-	+

This contrasts sharply with the situation in alkaline bogs where population densities of desmids varied significantly from one host to another in only 1 of 32 cases. At the three closed bogs where two macrophyte species were analyzed, significant differences in the desmid population densities occurred only once between two different hosts. The apparently far greater uniformity of desmid distributions from one host to another in alkaline bogs and closed bogs did not appear to be correlated with any parameters of the chemical environment.

Table 9. Presence (+) or absence (-) of significant differences in the population densities of the various groups of algae associated with different hosts at a given closed bog locality.

Locality	Hosts Compared	Desmidiales	Chlorococcales	Other Chlorophyceae	Bacillariophyceae	Cyanophyceae	Dinophyceae	Total Population
1.	Sphagnum A vs Sphagnum B	-	-	-	+	+	-	+
8.	Sphagnum vs Potamogeton	+	-	+	-	+	-	+
11.	Sphagnum vs Carex	-	-	+	-	+	-	+

Among the various hosts analyzed from alkaline bog lakes, plants of *Utricularia* harbored the greatest population densities, a situation paralleling that in acid bogs. In 7 of 11 cases, however, the total population densities associated with *Utricularia* were not significantly greater than those associated with other hosts in a given alkaline bog. In acid bogs, in contrast, significant differences occurred in 5 of 6 cases. *Utricularia* plants did not occur in the closed bogs visited.

The significant differences found in community composition and population density of the aufwuchs community from one host to another growing side by side in the same locality support the findings of Foerster & Schlichting (1965) and the observations of Young (1945) that substrate does influence community composition

and population density. Furthermore, Foerster & Schlichting (1965) provide data which indicate that artificial substrates (widely recommended for studies of algal aufwuchs; see APHA, 1971 and Sladeckova, 1962 for methods) are similarly selective and harbor communities which are qualitatively and quantitatively different from those associated with macrophyte hosts. In view, therefore, of the potentially misleading results which can arise from the use of artificial substrates, greater consideration should be given to measuring aufwuchs communities directly by means of host analysis, and reduced emphasis should be placed upon results obtained from indirect measurement with artificial substrates.

Lake to lake variation for given hosts

Significant differences in desmid population densities also occurred on a given host from one lake to another. A comparison of all possible pairs of acid bog lakes from which *Utricularia* samples were analyzed revealed statistically significant differences to occur in 24% of the cases (Table 10). A similar comparison involving *Sphagnum* showed statistically significant differences to occur in 21% of the cases (Table 11). Among the most distinctive acid bog lakes (i.e., those showing the greatest number of pairwise significant differences) were Lake 17-4 (Burnett Co.) which harbored the highest desmid population densities of all *Utricularia* samples and Lake 11-5 (Oneida Co.)

Table 10. Presence (+) or Absence (–) of Significant Differences in the Population Densities of Desmids Associated with Utricularia at Different Acid Bog Localities.

Lake	Barron Co. Lk. 7-9d	Bayfield Co. Lk. 33-14	Bayfield Co. Lk. 1-16c	Bayfield Co. Lk. 6-10d	Burnett Co. Lk. 9-2	Burnett Co. Lk. 10-6	Burnett Co. Lk. 16-2	Burnett Co. Lk. 17-4	Chippewa Co. Larrabee Lk.	Chippewa Co. Leo Joerg Lk.	Chippewa Co. Lk. 2-8	Iron Co. Lk. 13-2d	Polk Co. Evelyn Lk.	Rusk Co. Round Lk.	Rusk Co. School Lk.	Washburn Co. Unnamed (2)
Lk. 7-9d		-	-	-	-	+	-	+	-	-	-	+	-	+	+	+
Lk. 33-14			-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lk. 1-16c				-	+	+	-	+	-	-	-	+	-	+	+	+
Lk. 6-10d					-	-	-	+	-	-	-	-	-	-	+	-
Lk. 9-2						-	-	-	-	-	-	-	+	-	-	-
Lk. 10-6							-	-	+	-	-	-	+	-	-	-
Lk. 16-2								-	-	-	-	-	-	-	-	-
Lk. 17-4									+	+	-	-	+	-	-	-
Larrabee Lk.										-	-	+	-	+	+	+
Leo Joerg											-	-	-	-	-	-
Lk. 2-8												-	-	-	-	-
Lk. 13-2d													+	-	-	-
Evelyn														+	+	+
Round															-	-
School																-
Unnamed (2)																

Table 11. Presence (+) or absence (–) of significant differences in the population densities of desmids associated with Sphagnum at different acid bog localities.

Lake	Ashland Co. Trout Lk.	Barron Co. Lk. 7-9d	Bayfield Co. Lk. 17-5	Bayfield Co. Lk. 7-2	Bayfield Co. Lk. 17-4	Bayfield Co. Lk. 33-14	Chippewa Co. Leo Joerg Lk.	Iron Co. Lk. 26-9	Iron Co. Lk. 13-2d	Oneida Co. Lk. 11-5	Price Co. Unnamed	Rusk Co. Saxton Lk.	Vilas Co. Spruce Lk.	Vilas Co. Unnamed	Washburn Co. Unnamed (3)
Trout Lk.		–	–	–	–	–	–	–	–	+	–	–	–	–	–
Lk. 7-9d			–	+	–	–	–	+	–	+	–	–	–	–	+
Lk. 17-5				–	–	–	–	+	–	+	–	–	–	–	–
Lk. 7-2					–	–	–	–	–	–	+	+	–	–	–
Lk. 17-4						–	–	–	–	+	–	–	–	–	–
Lk. 33-14							–	–	–	+	–	–	–	–	–
Leo Joerg Lk.								+	–	+	–	–	–	–	–
Lk. 26-9									+	–	+	+	+	–	–
Lk. 13-2d										+	–	–	–	–	–
Lk. 11-5											+	+	+	–	–
Unnamed												–	–	–	+
Saxton Lk.													–	–	–
Spruce Lk.														–	–
Unnamed															–
Unnamed (3)															

which harbored 3.2 times more desmids per mg dry weight of *Sphagnum* than any other *Sphagnum* sample analyzed. Unfortunately, these biological differences did not appear to be correlated with any trends in the chemical parameters.

Comparisons of desmid densities on a given host from one alkaline bog to the next were not made because a particular host never occurred in more than two of the five lakes. A comparison of all possible pairs of closed bogs from which *Sphagnum* samples were analyzed revealed statistically significant differences in desmid population densities to occur in 18% of the cases (Table 12). In all instances, the differences involved locality 5 or locality 8, the two localities having the greatest desmid population density figures. Unfortunately, these relatively high densities did not appear to be correlated with any differences in the water chemistry parameters measured.

Data on other algal groups

In addition to the Desmidiales, the aufwuchs communities of the three lake types contained members of the Chlorococcales, other Chlorophyceae, Chrysophyceae, Bacillariophyceae, Cyanophyceae, Euglenophyceae, and/or Dinophyceae. Population density data for these groups are summarized in Table 5 and the percentage contribution of the groups to the total population is summarized in Figs. 18-23.

Of the various groups encountered, the Bacillariophyceae and Cyanophyceae were most conspicuous both in terms of population densities and percentage contribu-

Table 12. Presence (+) or absence (–) of significant differences in the population densities of Desmids associated with *Sphagnum* at different closed bog localities.

Locality → ↓	1 (A)	3	4	5	6	7	8	9	10	11	12
1 (A)		–	–	–	–	–	–	–	–	–	–
3			–	–	–	–	–	–	–	–	–
4				+	–	–	+	–	–	–	–
5					+	–	–	+	–	+	+
6						–	+	–	–	–	–
7							–	–	–	–	–
8								+	–	+	+
9									–	–	–
10										–	–
11											–
12											

tion to the total population. Diatoms constituted at least 25% of the total population on 25 of 35 acid bog hosts examined, on all 16 alkaline bog hosts sampled, and on 9 of 15 closed bog hosts sampled. Blue-green algae registered similar percentages on 18 of 35 acid bog hosts, 5 of 16 alkaline bog hosts, and 9 of 15 closed bog hosts. The remaining groups were of lesser importance with the Euglenophyceae, Chrysophyceae, and Dinophyceae occurring only sporadically.

Within given lakes, each host clearly showed the potential for harboring a unique algal community. At the five acid bog localities where two or more macrophytes were analyzed, considerable variation occurred in aufwuchs population densities and community composition from one host to another (Table 6). Within a given lake, significant differences occurred between all possible host pairs in at least two of the six groups comprising the algal aufwuchs communities, and significant differences occurred in the total population in 7 of 9 instances.

At the three alkaline bog localities where two or more hosts were analyzed, significant variation appeared in aufwuchs population densities and community composition from one host to another (Table 7). Within a given lake, significant differences in population densities occurred between all possible host pairs in at least one of the six groups comprising the aufwuchs in 26 of 32 instances. Significant differences most often occurred in the densities of diatoms present, and significant differences in total population densities appeared in 14 of the 32 samples analyzed.

At the three closed bog localities where two hosts were analyzed, considerable variation occurred in aufwuchs population densities and community composition from one host to another (Table 8). Within a given locality, significant differences occurred not only between total population densities but also between at least two of the six component aufwuchs groups in each case. Thus the data for these groups parallel that for the desmids, and the use of artificial substrates for gathering information apparently must be viewed with caution.

The plankton communities of acid bogs and alkaline bogs contained members of the same algal groups mentioned for the aufwuchs; population density data appear in Table 6 and percentage composition data are summarized in Figs. 24-26.

Members of the Cyanophyceae appeared to be the most conspicuous plankton group of acid bogs, occurring at all study sites and accounting for over 25% of the total plankton population in 17 of 28 instances. At three of the 17 localities, blue-greens dominated with over 50% of the total population. The Dinophyceae contributed over 50% to the total population in 4 lakes, but in only one additional lake did the percentage rating exceed 25, and at 15 of the 28 localities, the total population included less than 10% dinoflagellates. Chlorophyceae other than Desmidiales dominated with 84.3% in an unnamed Price County lake, but contributed less than 25% to the total in 23 of 28 localities and less than 10% in 12 of those lakes. Diatoms showed a similar pattern (50% in 1 lake, 25% in 23 lakes, 10% in 15 lakes), and the Chlorococcales registered percentages of less than 10 in 25 of the 28 study sites and never exceeded 23.0% of the total plankton population.

In each of the five alkaline bog lakes, one group of organisms accounted for over 50% of the total euplankton population. Thus diatoms registered percentages of 74.6 and 63.8 in Hegmeister and Cedar lakes respectively, Dinophyceae registered a 72.7 reading in Bullhead Lake, 'other Chlorophyceae' accounted for 54.3% of the Bog Lake euplankton, and Cyanophyceae contributed 75.7% to the total Mystery Lake euplankton. Only in Mystery Lake, however, was a conspicuous surface bloom of algae present. The Chlorococcales, like the euglenoid algae, were of little consequence, appearing in only 2 lakes and never accounting for over 1.7% of the total population.

Additional comments

Alkaline bog lakes potentially offer two distinct chemical environments for algal communities (see Table 2). The

open water of the study sites under consideration had pH values of 7.7-9.1 as compared to bog mat pH values of 4.4-7.3. With one exception, all mat pH values were less than 6.0. In addition, the open waters contained 1.6 to over 3.8 times as much Ca^{++} as did mat waters, had substantially less free CO_2 as compared to mat waters, and with one exception, had noticeably greater total alkalinity readings than did mat waters.

These chemical differences, however, apparently are not convincingly reflected by the biological data which, for the most part, indicate that a similar algal flora occurs both in the open water and the mat. Thus in only one of 32 cases did a significant difference occur in the population densities of desmids associated with two different hosts in a given lake (Table 8), and in that instance, both hosts were growing in open water. Moreover, in 4 of the 6 instances where a complete absence of significant differences occurred in aufwuchs community composition between hosts, one host came from the mat and the other from the lake. In none of the component algal groups in Table 8 did significant differences occur in over half of the possible pairwise comparisons, and the same is true for the total population pairwise analyses. Finally, the occurrence of significant differences seems to be more or less uniformly distributed among comparisons involving 2 lake hosts, 2 mat hosts, or one lake host and one mat host.

The only noticeable difference between the desmid communities of the open water and those of the mat appeared to be qualitative in nature. Of the 11 desmid genera detected during this study, 9 occurred in the mat samples and 5 were confined to that environment. Only 6 genera, in contrast, occurred in the open waters, and only 2 of these (one planktonic, one benthic) were confined to that environment. The full significance of this difference has yet to be assessed for Wisconsin waters (see, however, Woelkerling & Gough, 1975).

The chemical environment of the closed bogs analyzed differed from that of the acid bogs and alkaline bogs in having decidedly higher levels of the various nitrogen species, in containing generally higher levels of total phosphorus and SO_4, and in having mostly lower pH levels. Ten of the twelve closed bogs had pH readings of 4.0-4.9; the highest recorded value was 5.9. This contrasts with ranges of 7.1-9.1 in the open waters of alkaline bogs and 5.6-7.0 in the open waters of acid bogs. However, the mats of the alkaline bogs, with one exception, had a comparable pH range [4.4-5.7 (-7.3)] to those of the closed bogs. The similarities in the aufwuchs communities of closed bogs and alkaline bogs leave some uncertainties as to the extent to which pH or the other chemical parameters measured control population density and community composition. The absence of an open water area in closed bogs excludes comparisons of euplankton communities.

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WISCONSIN DESMIDS. III. DESMID COMMUNITY COMPOSITION AND DISTRIBUTION IN RELATION TO LAKE TYPE AND WATER CHEMISTRY

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Abstract

This investigation summarizes quantitative data on the generic composition of the euplankton and aufwuchs desmid communities of 61 Wisconsin lakes, and analyzes the information with respect to 1) the role of the various genera in terms of frequency, density, and relative importance, 2) the suitability of various lake types for harboring desmid communities, and 3) the relationships between chemical parameters and desmid distribution. The genera *Staurastrum, Cosmarium,* and *Closterium* are of wide occurrence, appear to play major roles in the communities of all lake types, and are the most tolerant of varying chemical conditions. Most euplankton genera are of importance only in acid bogs, but aufwuchs genera generally are more widely distributed. Both the euplankton and the aufwuchs communities appear to be composed of 1-4 desmid assemblages, each with a differing range of importance values. Based on biological criteria, acid bogs appear to be the most suitable lake type for harboring desmid communities and calcareous spring ponds the least suitable type. High generic diversity of desmids appears to be correlated with low conductivity, calcium and alkalinity levels, pH values of 5.1-7.0, and the presence of free CO_2. The evidence attending various hypotheses concerning water chemistry and desmid distribution appears contradictory, and further studies are needed to help clarify the situation.

Previous articles in this series have considered the role of desmids (Desmidiales, Chlorophyta) as a group in the euplankton and aufwuchs communities of selected acid bog lakes, alkaline bog lakes, and closed bogs (Woelkerling 1976), and of selected soft water lakes, hard water lakes, and calcareous spring ponds (Cough & Woelkerling, 1976) in Wisconsin. Although qualitative data on the occurrence of the various desmid genera has been included for the 61 study sites encompassed by these investigations, other aspects of desmid community composition and distribution have yet to be considered. This paper summarizes quantitative information on the generic composition of the euplankton and aufwuchs desmid communities in selected Wisconsin lakes and analyzes the data with respect to the role of the various genera in terms of frequency, density, and relative importance, the suitability of various lake types for harboring desmid communities, and the relationships between chemical parameters and desmid occurrences. The significance of these results is also considered in connection with current hypotheses concerning water chemistry and desmid distribution.

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Materials and Methods

The data presented here have been gathered during the course of summer studies on the 61 Wisconsin lakes (Fig. 1) discussed in the first two parts of this series. Geographical, chemical, and biological information for these localities is summarized in the tables of those papers, and the methods utilized in gathering, processing, and analyzing the data already have been outlined elsewhere (Woelkerling, 1976). In addition to the above mentioned data, detailed quantitative records (based on Sedgwick-Rafter cell analyses) have been kept on the generic composition of the desmid component of both the euplankton community and the aufwuchs communities associated with the various macrophytes at each locality. These data are summarized in Tables 1 and 6 in the present study.

The relative importance of a particular genus in lakes of a given type has been assessed by determining importance values using the formula

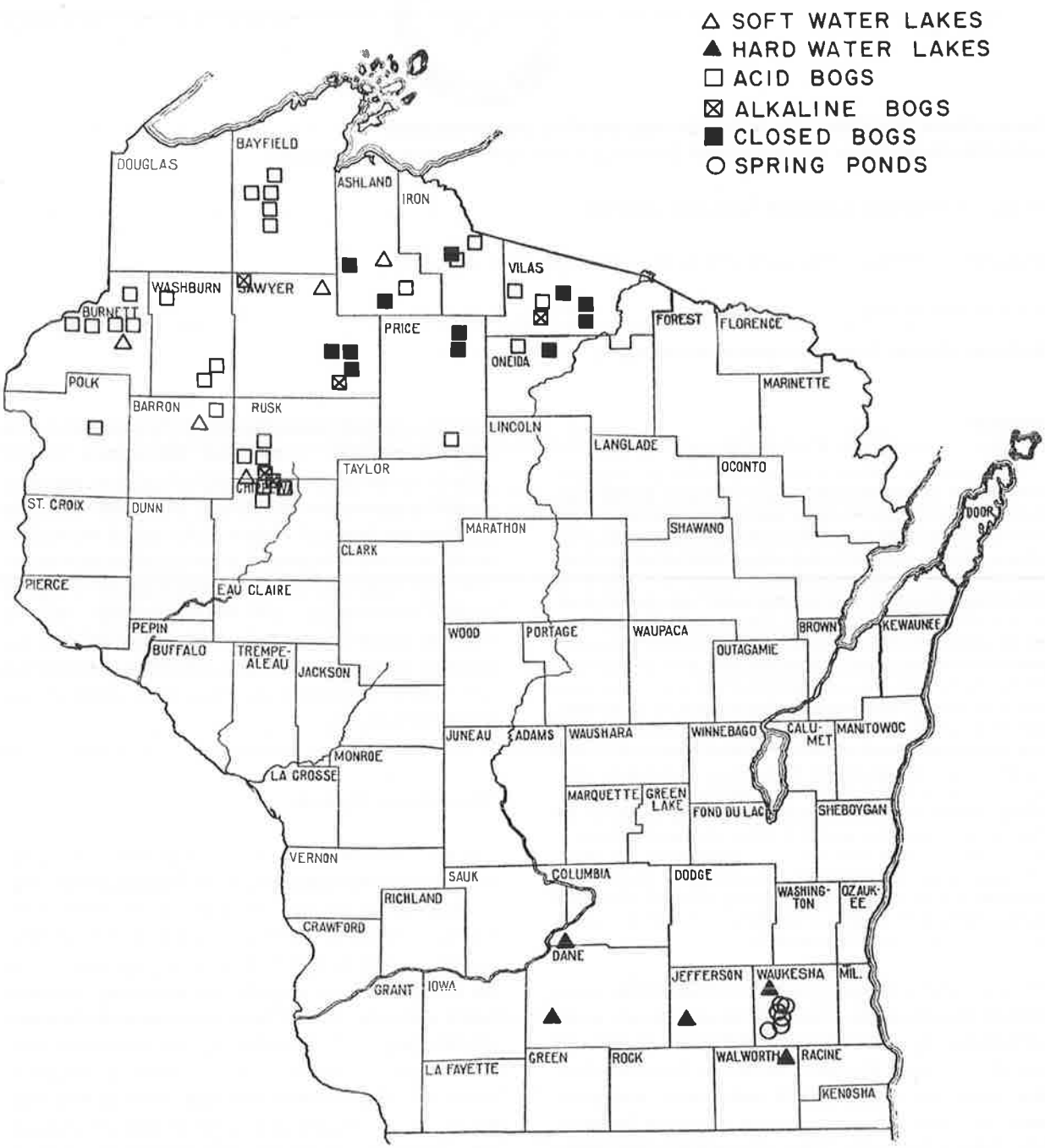

Fig. 1. Location of Study Sites within Wisconsin.

(1) $I.V. = (3F_A + 2RD_R + RD_U)/6$

where I.V. is the importance value in units, F_A is the absolute frequency of the genus in a given lake type, RD_R is the mean relative density of the genus in those lakes where it occurs, and RD_U is the mean relative density in all lakes of the type in question. Absolute frequencies are defined by the formula

(2) $F_A = (A/B)100$

where F_A is the absolute frequency as a percentage, A is the number of lakes in which a taxon occurs, and B is the total number of lakes under consideration. The ratio A/B is multiplied by 100 to express F_A as a percentage. Relative density is defined by the formula

$$(3) \quad RD = (C/D)100$$

where RD is the relative density as a percentage, C is the mean population density, and D is the mean total desmid population density. I.V. values range from 0-100; the higher the reading, the greater is the apparent importance of the taxon.

The formula for I.V. has been derived on the rationale that F_A is the most important criterion since it summarizes presence/absence data. Such data are considered more reliable (in terms of importance) than standing crop determinations from which RD_R and RD_U values are calculated. The RD_R value, in turn, is given more weight than the RD_U value since the former provides a better indication of the relative role of the taxon in those lakes where it occurs. The RD_U values have been included to insure some measurement of all localities of a given type and to reduce emphasis of taxa with prominent populations in only one or several of the total number of lakes of a given type.

Relative frequencies (F_R) have been employed in comparing the importance of a particular genus from one lake type to another and are defined by the formula

$$(4) \quad F_R = (G/H)100$$

where F_R is relative frequency as a percentage, G is het number of lakes in which a particular desmid occurs, and H is the total number of occurrences of all desmid taxa in those lakes. Higher F_R values indicate greater apparent importance than lower F_R values.

Absolute frequencies (Formula 2) have been employed in assessing the potential of particular taxa to occur in and to be restricted to lakes of a given type. Special attention has been paid to those genera present in acid bog lakes and absent in one or more of the other lake types.

Four biological criteria have been utilized to help assess the suitability of a particular lake type for harboring desmid communities. These include:

A. The mean absolute density of the total desmid population (i.e. $AD_M = \Sigma T/N$ where AD_M is the absolute mean density, ΣT is the total desmid population density for all localities, and N is the number of localities) for lakes of the type in question;
B. The total number of desmid genera present in lakes of type in question;
C. The number of desmid 'assemblage orders' present in lakes of the type in question; and
D. The number of genera present in each assemblage order.

In general, higher numerical values for each of these criteria mean a greater apparent suitability for harboring desmids. The first two criteria are self-explanatory; the latter two represent an outgrowth of a hypothesis on desmid community structure (based on importance values) which is outlined below in the discussion on euplankton community composition.

The overall suitability of a lake type has been assessed by assigning ranks to each of the lakes for each of the above four criteria. The highest value of a given criterion received a rank of 1, the next highest 2, etc. Tied values received rank numbers equal to ½, ⅓, etc. the sum of the relevant integers. (For further details on assigning rank numbers, consult Wilcoxon & Wilcox, 1964). The sum of the rank numbers for all criteria then represents an index of a lake type's suitability for harboring desmids; the lower the rank number total, the greater is the suitability of the lake type. Results of the suitability analyses are summarized in Table 5 and Table 10.

Results and Discussion

Euplankton Community Composition

Of the nineteen desmid genera encountered in the euplankton (Table 1), *Staurastrum* is by far the most widely distributed, and it assumes primary quantitative importance more frequently than any other desmid genus. Taxa of *Staurastrum* occurred in 36 of the 49 euplankton communities analyzed (the 12 closed bogs lack open water by definition). It was the only genus recorded from the plankton of calcareous spring ponds and hard water lakes and was the sole desmid genus present in the plankton of 3 of the five soft water lakes. It contributed at least 25% to the total desmid population in the five alkaline bogs and accounted for over 80% of the total in three of those localities. Among the 28 acid bogs studied, *Staurastrum* occurred in 24 cases, accounted for at least 50.0% of the total desmid population in 10 localities, and contributed 25.0% or more to the total desmid population in 18 plankton communities.

Six other desmid genera occurred in 12 or more of the 49 plankton communities. Of these, *Xanthidium* was restricted to acid bog lakes, *Arthrodesmus* and *Bambusina* appeared only in acid bogs and alkaline bogs, *Closterium* and *Desmidium* occurred only in acid bogs and soft

Table 1. The percentage composition of the euplankton desmid populations at the study sites.

Data expressed as % of the total desmid population in column 3.

Locality	Lake Type	Total Desmid Population Density (# organisms/ml)	Taxon																			
			Arthrodesmus	Bambusina	Closterium	Cosmarium	Desmidium	Euastrum	Gonatozygon	Hyalotheca	Micrasterias	Netrium	Penium	Phymatodocis	Pleurotaenium	Sphaerozosma	Spondylosium	Staurastrum	Tetmemorus	Triploceras	Xanthidium
A	Spring Pond	$5.30x10^{-1}$	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0	--	--	--
B	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
C	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
D	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
E	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
F	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Beulah	Hard Water	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Brunner's	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Fish	" "	$2.0x10^{0}$	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0	--	--	--
Fowler	" "	Absent	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Ripley	" "	$3.0x10^{0}$	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0	--	--	--
Ike	Soft Water	$2.30x10^{1}$	--	--	12.5	50.0	--	--	--	--	--	--	--	--	--	--	--	37.5	--	--	--
Pine	" "	$1.62x10^{1}$	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0	--	--	--
Zielke	" "	$1.74x10^{1}$	--	--	--	--	--	--	--	--	--	--	-	--	--	--	--	100.0	--	--	--
15-12	" "	$1.25x10^{1}$	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0	--	--	--
20-12A	" "	$1.53x10^{1}$	--	--	--	--	100.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--

Table 1 continued

Locality	Lake Type	Total Desmid Population Density (# organisms/ml)	Taxon																			
			Arthrodesmus	Bambusina	Closterium	Cosmarium	Desmidium	Euastrum	Gonatozygon	Hyalotheca	Micrasterias	Netrium	Penium	Phymatodocis	Pleurotaenium	Sphaerozosma	Spondylosium	Staurastrum	Tetmemorus	Triploceras	Xanthidium
26-9	Acid Bog	$1.07x10^{0}$	40.0	--	20.0	--	--	--	--	--	20.0	--	--	--	--	--	--	20.0	--	--	--
13-2d	" "	$1.36x10^{1}$	--	--	1.6	3.1	6.3	1.6	23.4	12.5	1.6	3.1	--	--	1.6	1.5	--	43.7	--	--	--
11-5	" "	$1.63x10^{-1}$	100.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Evelyn	" "	$4.08x10^{-1}$	--	--	100.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Unnamed (Price)	" "	$5.10x10^{0}$	--	--	4.2	25.0	4.2	--	--	--	--	--	--	--	4.2	--	--	41.6	--	--	20.8
Round	" "	$2.74x10^{2}$	37.3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	62.7	--	--	--
Saxton	" "	$1.46x10^{1}$	--	--	--	--	--	2.3	--	--	--	--	--	--	--	--	--	97.7	--	--	--
School	" "	$1.04x10^{1}$	49.2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	50.8	--	--	--
Spruce	" "	$2.39x10^{0}$	12.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	68.7	--	18.8	--
Unnamed (Vilas)	" "	$5.10x10^{-1}$	--	16.7	--	--	--	--	--	50.0	--	--	--	--	--	--	--	33.3	--	--	--
Washburn:																					
Unnamed-1	" "	$3.14x10^{0}$	5.4	5.4	5.9	21.6	2.7	10.8	--	--	--	2.7	--	--	--	2.7	--	35.2	--	--	8.1
Unnamed-2	" "	$2.69x10^{1}$	3.2	25.4	--	4.8	12.7	4.8	--	9.5	--	1.6	1.6	--	1.6	--	1.6	31.6	--	--	1.6
Unnamed-3	" "	$1.96x10^{0}$	8.7	4.3	4.3	4.3	17.4	--	--	13.0	--	4.3	--	--	4.3	--	--	30.8	--	4.3	4.3
Bog	Alkaline Bog	$4.76x10^{0}$	14.3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	85.7	--	--	--
Bullhead	" "	$1.02x10^{0}$	33.3	--	--	33.4	--	--	--	--	--	--	--	--	--	--	--	33.3	--	--	--
Cedar	" "	$2.10x10^{0}$	--	--	--	75.0	--	--	--	--	--	--	--	--	--	--	--	25.0	--	--	--
Hegmeister	" "	$1.02x10^{0}$	--	16.7	--	--	--	--	--	--	--	--	--	--	--	--	--	83.3	--	--	--
Mystery	" "	$5.1x10^{-1}$	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0	--	--	--

Table 1 continued

Locality	Lake Type	Total Desmid Population Density (# organisms/ml)	Taxon																		
			Arthrodesmus	Bambusina	Closterium	Cosmarium	Desmidium	Euastrum	Gonatozygon	Hyalotheca	Micrasterias	Netrium	Penium	Phymatodocis	Pleurotaenium	Sphaerozosma	Spondylosium	Staurastrum	Tetmemorus	Triploceras	Xanthidium
Trout	Acid Bog	$8.16x10^{-2}$	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100.0
7-9d	" "	$5.95x10^{1}$	--	0.7	13.7	--	82.0	--	--	1.4	--	--	--	--	--	--	--	2.2	--	--	--
17-5	" "	$1.18x10^{0}$	14.3	--	7.1	14.3	14.3	--	--	--	35.8	7.1	--	--	--	--	--	--	--	--	7.1
7-2	" "	$1.97x10^{0}$	18.1	--	--	27.3	--	--	--	9.1	--	--	--	--	--	--	--	27.3	--	9.1	9.1
33-14(Bayfield)	" "	$1.42x10^{1}$	3.0	6.0	--	17.9	11.9	4.5	--	--	--	1.5	--	--	--	--	--	55.2	--	--	--
1-16c	" "	$1.10x10^{0}$	--	7.7	--	--	--	--	--	--	--	7.7	--	--	--	--	--	76.9	--	--	7.7
6-10d	" "	$7.65x10^{0}$	--	5.6	13.9	13.9	52.6	2.8	--	--	--	--	--	2.8	--	2.8	--	5.6	--	--	--
9-2	" "	$4.41x10^{1}$	4.8	2.4	1.2	6.0	14.3	2.4	--	--	4.8	--	--	--	--	--	--	53.4	--	--	10.7
10-6	" "	$1.74x10^{1}$	5.9	--	2.9	14.7	32.4	8.8	--	--	--	--	--	--	--	--	--	23.5	--	--	11.8
16-2	" "	$1.19x10^{1}$	3.6	7.2	--	17.6	3.6	--	--	3.6	--	--	--	--	--	7.2	--	50.0	--	--	--
17-4	" "	$1.60x10^{1}$	6.1	3.0	3.0	27.3	--	--	--	--	--	--	--	--	--	--	--	42.4	3.0	--	15.2
33-14	" "	$1.98x10^{0}$	--	--	--	--	--	--	--	--	--	--	--	--	--	--	25.0	75.0	--	--	--
Larrabee	" "	$5.10x10^{-1}$	16.7	--	--	16.7	--	--	--	--	--	--	--	--	--	--	16.7	49.9	--	--	--
Leo Joerg	" "	$2.11x10^{1}$	1.0	16.8	11.9	16.8	18.7	3.0	--	3.0	1.0	1.0	--	--	--	--	2.0	14.9	--	--	9.9
2-8	" "	$5.10x10^{0}$	--	--	--	8.3	--	16.7	--	--	8.3	--	--	--	4.2	--	--	16.7	--	45.8	--

Table 2. Importance values of euplankton desmid genera within lakes of a particular type

Genus	Spring Ponds	Hard Water	Soft Water	Acid Bog	Alkaline Bog
Arthrodesmus	0	0	0	38.9	29.5
Bambusina	0	0	0	24.9	16.1
Closterium	0	0	14.6	29.0	0
Cosmarium	0	0	28.3	34.9	41.7
Desmidium	0	0	46.7	33.1	0
Euastrum	0	0	0	20.3	0
Gonatozygon	0	0	0	10.0	0
Hyalotheca	0	0	0	19.4	0
Micrasterias	0	0	0	16.7	0
Netrium	0	0	0	15.9	0
Penium	0	0	0	2.4	0
Phymatodocis	0	0	0	3.0	0
Pleurotaenium	0	0	0	10.2	0
Sphaerozosma	0	0	0	8.3	0
Spondylosium	0	0	0	11.0	0
Staurastrum	46.2	60.0	79.4	63.0	82.8
Tetmemorus	0	0	0	3.0	0
Triploceras	0	0	0	14.0	0
Xanthidium	0	0	0	28.5	0

water lakes, and *Cosmarium* was present in all 3 of the above lake types. All six genera contributed over 50% to the total desmid plankton population of at least one of the study sites. The remaining 12 genera were detected only in acid bog lakes and occurred in less than 25% of the euplankton samples analyzed.

The importance values (I.V.) of the various genera within the desmid euplankton communities of each of the five lake types are summarized in Table 2. These I.V. readings suggest the possibility that up to four desmid assemblages, each with a different range of I.V. readings, may exist within the euplankton communities. In all five lake types, a single genus – *Staurastrum* – occupies the first assemblage order and has I.V. readings at least 24.1 units greater than any other desmid. Thus the first order assemblage is sharply delimited from the lesser orders.

In spring ponds and hard water lakes, the lesser assemblage orders are absent. The second order in both soft water lakes and alkaline bogs is occupied by a single genus – *Desmidium* in the first lake type and *Cosmarium* in the second lake type. In acid bogs, however, the second assemblage order is occupied by a group of five genera including *Arthrodesmus, Closterium, Cosmarium, Desmidium,* and *Xanthidium.*

A similar situation exists in the third and fourth assemblage orders. In soft water lakes the third and fourth orders are occupied by *Cosmarium* and *Closterium* respectively. In alkaline bogs these orders are occupied by *Arthrodesmus* and *Bambusina* respectively. In both of these lake types, the various assemblage orders appear sharply delimited from each other and are separated by I.V. readings of at least 12 units.

In acid bog lakes, in contrast, assemblages of the second and succeeding levels all contain groups of genera and are not as distinctly separated from one another in terms of I.V. figures. Thus *Bambusina* (I.V. = 24.9) occupies a transition zone between the 5 genera of the second order mentioned above (I.V. readings of 28.5-38.9) and the four genera (*Euastrum, Hyalotheca, Micrasterias, Netrium*) present in the third order (I.V. readings of 15.9-20.3). Similarly *Triploceras* (I.V. = 14.0) lies in the transition zone between the third and fourth orders, the latter containing seven genera (*Gonatozygon, Penium, Phymatodocis, Pleurotaenium, Sphaerozosma, Spondylosium,* and *Tetmemorus*) with I.V. readings of 2.4 to 11.0.

It cannot be emphasized too strongly that the data which suggested the hypothesis concerning the existence of possible desmid assemblages in euplankton communities comes from a limited number of lakes in one geographic region. Moreover, the conclusions are based on an arbitrary method of determining generic importance. Further studies on additional lakes in this region and/or on lakes elsewhere may result in considerable modification or complete rejection of the hypothesis.

Table 3. The relative frequencies for euplankton desmid genera within lakes of particular types

Genus	Spring Ponds	Hard Water	Soft Water	Acid Bog	Alkaline Bog
Arthrodesmus	0	0	0	11	20
Bambusina	0	0	0	7	10
Closterium	0	0	14	8	0
Cosmarium	0	0	14	10	20
Desmidium	0	0	14	8	0
Euastrum	0	0	0	6	0
Gonatozygon	0	0	0	1	0
Hyalotheca	0	0	0	5	0
Micrasterias	0	0	0	4	0
Netrium	0	0	0	5	0
Penium	0	0	0	1	0
Phymatodocis	0	0	0	1	0
Pleurotaenium	0	0	0	3	0
Sphaerozosma	0	0	0	2	0
Spondylosium	0	0	0	2	0
Staurastrum	100	100	58	16	50
Tetmemorus	0	0	0	1	0
Triploceras	0	0	0	2	0
Xanthidium	0	0	0	7	0

The same applies to the use of desmid assemblages elsewhere in this paper.

Based on relative frequency (F_R) values (Table 3), the majority of desmid genera are of no importance outside of acid bog lakes. In all six cases where a genus occurs in two or more lake types, the lowest F_R value, and thus the least important role for that genus, occurs in conjunction with acid bog lakes. *Cosmarium,* for example, plays a more significant role in the alkaline bogs studied (F_R = 20) than in the soft water lakes studied (F_R = 14), and it plays a more important role in soft water lakes than in acid bog lakes (F_R = 10). Similarly *Staurastrum* is of far less importance in acid bog euplankton communities (F_R = 16) where it is one of 19 genera present than in soft water (F_R = 58) or alkaline bog (F_R = 50) communities where it is one of only 4 genera present or in spring ponds (F_R = 100) or hard water lakes (F_R = 100) where it is the only genus present. It follows, then, that among lake types, the relative importance of a given genus decreases as the number of genera in the community increases.

The absolute frequency data (Table 4) suggest that certain genera found only in acid bogs during this study have a higher potential of being found in other lake types than do certain other genera. Thus *Gonatozygon, Penium, Phymatodocis,* and *Tetmemorus* all were of rare occurrence (F_A's of 4, F_R's of 1) and could be present in other lake types in such small numbers that they were missed in the collection and/or analysis solely by chance. Because of their apparent rarity and consequent low impor-

Table 4. The absolute frequencies for euplankton desmid genera within lakes of particular types

Genus	Spring Ponds	Hard Water	Soft Water	Acid Bog	Alkaline Bog
Arthrodesmus	0	0	0	61	40
Bambusina	0	0	0	43	20
Closterium	0	0	20	46	0
Cosmarium	0	0	20	57	40
Desmidium	0	0	20	46	0
Euastrum	0	0	0	36	0
Gonatozygon	0	0	0	4	0
Hyalotheca	0	0	0	29	0
Micrasterias	0	0	0	25	0
Netrium	0	0	0	29	0
Penium	0	0	0	4	0
Phymatodocis	0	0	0	4	0
Pleurotaenium	0	0	0	18	0
Sphaerozosma	0	0	0	14	0
Spondylosium	0	0	0	14	0
Staurastrum	17	40	80	86	100
Tetmemorus	0	0	0	4	0
Triploceras	0	0	0	14	0
Xanthidium	0	0	0	43	0

Table 5. Summary of data relating to the suitability of particular lake types for harboring euplankton desmid communities

Criterion	Spring Ponds		Hard Water		Soft Water		Acid Bog		Alkaline Bog	
	Value	Rank	Value	Rank	Value	Rank	Value	Rank	Value	Rank
Mean Absolute Population Density	1.06×10^{-1}	5	1.00×10^{0}	4	1.69×10^{1}	2	1.91×10^{1}	1	1.88×10^{0}	3
Total # desmid Genera present	1	4.5	1	4.5	4	2.5	19	1	4	2.5
Number of assemblage Orders present	1	4.5	1	4.5	4	2	4	2	4	2
Number of genera Present in each Assemblage order:										
1	1	3	1	3	1	3	1	3	1	3
2	0	4.5	0	4.5	1	2.5	5	1	1	2.5
3	0	4.5	0	4.5	1	2.5	4	1	1	2.5
4	0	4.5	0	4.5	1	2.5	7	1	1	2.5
Rank Total		30.5		29.5		17		10		18
Suitability Rank		5		4		2		1		3

tance (I.V. readings of 2.4-10), genera such as these offer little value as potential biological indicators.

Certain other genera, in contrast, appear to have a higher potential of being confined solely to acid bogs. Thus *Xanthidium* (F_A = 43), *Euastrum* (F_A = 36), *Hyalotheca* (F_A = 29), and *Netrium* (F_A = 29) all have reasonably high acid bog F_A values and do not occur (i.e. F_A = 0) in any of the other lake types. This suggests that these taxa may be characteristic of acid bog euplankton communities and, therefore, may have good potential value as biological indicators of acid bog lakes. Again, caution must be exercised in carrying such generalizations too far since the data bank forming the basis for these observations involves only 61 lakes in one geographic region. Further studies may require modification of these hypotheses. Moreover, the absence of any one or several of these taxa does not eliminate the possibility of the locality being an acid bog. The presence of one or more, however, appears to be a good potential indicator of acid bog conditions.

Data relating to the suitability of a particular lake type for harboring an euplankton desmid community are summarized in Table 5. Based on these criteria, acid bog lakes are far more suitable for harboring desmids in the euplankton than are soft water lakes or alkaline bog lakes, and these two lake types, in turn, are much more suitable than are spring ponds or hard water lakes. The relationships between the relative biological suitability of a lake type for harboring desmids and the factors in the chemical environment are discussed in Section 3 below.

Aufwuchs Community Composition

Within the 61 study lakes, the aufwuchs communities of 107 macrophyte hosts were analyzed (Table 6), including 10 from spring ponds, 19 from hard water lakes, 12 from soft water lakes, 35 from acid bogs, 16 from alkaline bogs, and 15 from closed bogs. Since, as determined in parts 1-2 of this series on Wisconsin Desmids, each of these hosts has the potential to harbor a unique algal association, the desmid community of each macrophyte is considered as a distinct entity, even though the hosts may have come from the same locality. The macrophytes of the spring ponds studied did not harbor desmid communities and will not be considered further.

Among the 23 genera recorded from the aufwuchs communities analyzed during this investigation (Table 6), *Cosmarium* and *Staurastrum* appear to be the two most widely distributed taxa and often are the two most conspicuous taxa present; both were found in all five lake types which harbored aufwuchs desmids. Plants of *Cosmarium* occurred in 71 of the 97 aufwuchs samples analyzed. It was the sole genus present in 11 cases, accounted for at least 50% of the desmid population in 32 instances, and contributed 25% or more to the total desmid population in 48 communities. *Staurastrum* was recorded from 60 macrophytes, but was the sole aufwuchs genus present on only two occasions. It contributed over 50% of the total desmid population to 13 aufwuchs communities and over 25% to 31 aufwuchs communities.

Closterium was the only other genus recorded from all five lake types and appeared in 39 of 97 samples. In two samples, it was the sole desmid present, in five samples it dominated with over 50% of the desmid population, and in eleven samples it accounted for 25% of more of the desmid population. Two other genera occurred in at least one-quarter of the total number of aufwuchs communities. *Euastrum,* with 32 occurrences, was found in all lake types except for hard waters. *Netrium,* with 28 occurrences, was detected in acid bogs, alkaline bogs, and soft water lakes. Both genera contributed over 50% to the total desmid population in at least one aufwuchs community.

The remaining 18 genera occurred in less than 25% of the samples analyzed and for the most part were found in only two or three of the lake types. None occurred in hard water lakes. Four genera (*Docidium, Gonatozygon, Spinoclosterium, Spirotaenia*) were confined to acid bog lakes, and one genus (*Roya*) was detected only in soft water lakes.

The importance values of the various desmid genera in the aufwuchs communities of each of the five lake types are summarized in Table 7. These I.V. readings suggest the possibility that the aufwuchs communities, like the euplankton communities, contain up to 4 desmid assemblage orders of varying importance. In hard water lakes only two desmid assemblages occur. The first order contains *Cosmarium* (I.V. = 81.8), and the second order includes *Closterium* and *Staurastrum* (I.V. = 16.0-18.3). The closed bogs as a group harbored 3 desmid assemblages, the first order containing only one genus (*Staurastrum,* I.V. = 49.1), the second order including seven genera (*Bambusina, Closterium, Cosmarium, Cylindrocystis, Euastrum, Netrium, Penium*) with I.V. readings of 17.6-34.3, and the third order having four genera (*Arthrodesmus, Desmidium, Hyalotheca, Tetmemorus*) with I.V. readings of 5.7-12.1.

The remaining 3 lake types all contain 4 desmid assemblages. In soft water lakes the first order includes only

Table 6. The percentage composition of the aufwuchs desmid populations at the study sites of the various lake types. Date expressed as a % of the total desmid population in the right hand column.

A. Data For Hard Water Lakes

County	Locality	Host	Closterium	Cosmarium	Staurastrum	Total Desmid Population Density org/mg host dry wt
Dane	Bruner's	Ceratophyllum	--	---	--	Absent
	Pond	Myriophyllum	12.1	87.9	--	3.02×10^3
		Potamogeton	--	100.0	--	1.39×10^3
	Fish Lake	Ceratophyllum	--	---	--	Absent
		Myriophyllum	--	93.9	6.1	1.96×10^3
		Nuphar	--	100.0	--	3.20×10^1
		Utricularia	--	94.5	5.5	5.94×10^3
Jefferson	Ripley	Myriophyllum	--	81.0	19.0	2.73×10^2
		Nuphar	--	---	--	Absent
		Potamogeton	--	100.0	--	7.10×10^1
		Utricularia	3.4	73.7	22.9	1.10×10^4

Table 6 continued

A. Data For Hard Water Lakes

County	Locality	Host	Closterium	Cosmarium	Staurastrum	Total Desmid Population Density org/mg host dry wt
Walworth	Beulah	Anacharis	--	100.0	--	2.20×10^{1}
		Myriophyllum	--	100.0	--	3.70×10^{1}
		Potamogeton	--	100.0	--	1.60×10^{1}
		Utricularia	--	100.0	--	7.70×10^{1}
Waukesha	Fowler	Anacharis	--	---	--	Absent
		Chara	16.0	68.0	16.0	3.69×10^{2}
		Myriophyllum	27.6	72.4	--	4.61×10^{2}
		Potamogeton	--	100.0	--	5.61×10^{2}

Table 6 continued

B. Data for Soft Water Lakes

County	Locality	Host	Closterium	Cosmarium	Desmidium	Euastrum	Hyalotheca	Micrasterias	Netrium	Pleurotaenium	Roya	Sphaerozosma	Spondylosium	Staurastrum	Triploceras	Xanthidium	Total Desmid Population Density org/mg host dry wt
Sawyer	Ike	Potamogeton	---	33.0	--	--	-	-	-	67.0	-	--	-	--	-	-	2.14×10^4
		Utricularia	22.7	59.2	--	4.5	-	-	-	4.5	9.1	--	-	--	-	-	4.86×10^4
Chippewa-Rusk	Pine	Hygroamblystegium	3.2	35.7	--	20.6	6.5	3.2	-	1.8	-	12.9	-	12.9	3.2	-	1.87×10^4
		Potamogeton	---	56.6	--	7.5	7.5	-	1.5	--	-	7.5	-	19.4	-	-	1.82×10^4
		Sphagnum	---	62.5	12.5	18.8	-	-	-	--	-	--	-	6.2	-	-	1.73×10^4
		Utricularia	2.2	37.3	4.4	12.1	9.9	-	2.2	1.1	-	9.9	-	19.8	-	1.1	3.96×10^4
Ashland	Zielke	Nitella	25.0	25.0	--	50.0	-	-	-	--	-	--	-	--	-	-	2.39×10^4
		Utricularia	100.0	--	--	--	-	-	-	--	-	--	-	--	-	-	4.74×10^4
Burnett	Lk 15-12	Equisetum	---	60.5	--	12.1	3.0	-	-	6.1	-	--	-	15.1	-	3.0	1.04×10^4
		Utricularia	1.5	34.7	1.5	18.5	1.5	-	-	3.1	-	7.7	1.5	25.5	1.5	-	4.78×10^4
Barron	Lk 20-12A	Riccia	---	60.0	--	--	-	-	-	--	-	20.0	-	20.0	-	-	2.74×10^4
		Utricularia	13.6	40.9	4.5	--	-	9.1	-	--	-	--	-	31.9	-	-	4.93×10^4

Table 6 continued

C. Data for Acid Bog Lakes

County	Locality	Host	Arthrodesmus	Bambusina	Closterium	Cosmarium	Cylindrocystis	Desmidium	Docidium	Euastrum	Gonatozygon	Hyalotheca	Micrasterias	Netrium	Penium	Pleurotaenium	Spinoclosterium	Spirotaenia	Sphaerozosma	Spondylosium	Staurastrum	Tetmemorus	Triploceras	Xanthidium	Desmid Population Density
Ashland	Trout	Sphagnum	--	18.2	--	--	--	9.1	--	--	--	9.1	--	9.1	9.1	--	--	--	--	--	45.4	--	--	--	9.16×10^2
Barron	Lk 7-9d	Sphagnum	12.5	--	--	--	--	--	--	--	--	--	--	12.5	25.0	--	--	--	--	--	37.5	--	12.5	--	1.73×10^2
		Utricularia	7.7	7.7	15.3	7.7	--	7.7	--	--	--	--	--	7.7	--	--	--	--	--	--	46.2	--	--	--	4.24×10^3
Bayfield	Lk 7-5	Sphagnum	--	--	--	--	--	--	--	--	--	42.8	--	--	14.3	--	--	--	--	--	28.6	14.3	--	--	4.45×10^2
	Lk 7-2	Sphagnum	--	6.3	6.3	6.2	--	--	--	--	--	--	6.2	50.0	21.9	--	--	--	--	--	--	--	3.1	--	2.15×10^3
	Lk 33-14	Utricularia	--	4.3	--	23.9	--	2.2	2.2	15.0	--	--	2.2	4.3	2.2	2.2	--	--	--	--	41.3	--	--	2.2	3.49×10^3
	Lk 1-16c	Utricularia	--	--	25.0	41.8	--	--	--	8.3	--	--	--	8.3	--	--	--	--	--	--	8.3	--	--	8.3	2.18×10^3
	Lk 6-10d	Utricularia	--	--	3.7	33.4	--	--	--	7.4	3.7	--	--	3.7	3.7	--	--	--	7.4	--	33.3	--	--	3.7	2.06×10^3
Burnett	Lk 9-2	Utricularia	2.0	--	21.5	23.5	--	2.0	--	7.8	2.0	--	--	2.0	--	3.9	--	--	--	11.8	23.5	--	--	--	9.81×10^3
	Lk 10-6	Utricularia	--	--	17.1	31.4	--	7.1	--	12.9	--	--	--	1.4	1.4	1.4	--	--	--	2.9	24.3	--	--	--	1.45×10^4
	Lk 16-2	Utricularia	2.4	3.9	3.9	43.9	--	2.4	--	3.9	2.4	2.4	2.4	--	--	--	--	--	--	7.3	22.0	--	--	--	5.87×10^3
	Lk 17-4	Sphagnum	8.3	--	75.0	8.4	--	--	--	--	--	--	--	--	--	8.3	--	--	--	--	--	--	--	--	8.23×10^2
		Utricularia	3.4	--	6.8	37.5	--	--	1.1	2.3	2.3	--	1.1	1.1	2.3	1.1	--	--	--	--	36.4	--	2.3	2.3	1.63×10^4
	Lk 33-14	Sphagnum	--	--	62.5	--	--	--	--	--	--	--	--	6.2	--	--	--	25.0	--	--	--	6.3	--	--	8.62×10^2
Chippewa	Larrabee	Utricularia	20.0	--	--	33.3	--	6.7	--	13.3	--	--	--	6.7	--	--	--	--	--	--	20.0	--	--	--	2.21×10^3

Table 6 continued

C. Data for Acid Bog Lakes

County	Locality	Host	Arthrodesmus	Bambusina	Closterium	Cosmarium	Cylindrocystis	Desmidium	Docidium	Euastrum	Hyalotheca	Micrasterias	Netrium	Penium	Pleurotaenium	Spinoclosterium	Spirotaenia	Sphaerozosma	Spondylosium	Staurastrum	Tetmemorus	Triploceras	Xanthidium	Desmid Population Density
	Leo Joerg	Brasenia	--	10.7	--	64.3	--	3.6	--	10.7	--	--	--	--	--	--	7.1	--	--	--	--	--	3.6	8.15×10^2
		Sphagnum	--	14.3	14.3	14.3	--	--	--	14.3	--	--	42.8	--	--	--	--	--	--	--	--	--	--	3.21×10^2
		Utricularia	--	3.3	13.3	26.8	--	3.3	--	10.0	--	3.3	--	--	--	--	--	--	--	40.0	--	--	--	4.01×10^3
	Lk 2-8	Utricularia	--	18.2	4.5	9.1	--	11.4	--	27.2	2.3	4.5	--	--	4.5	--	--	--	4.5	9.1	2.3	--	2.3	2.97×10^3
Iron	Lk 26-9	Sphagnum	--	2.0	5.9	52.9	11.8	--	--	--	--	--	5.9	17.6	--	--	--	--	--	3.9	--	--	--	1.50×10^3
		"Moss"	--	--	--	4.9	7.3	--	--	--	--	--	4.9	4.9	--	--	--	--	--	78.0	--	--	--	6.66×10^3
	Lk 13-2d	Potamogeton	--	20.0	6.7	13.2	--	20.0	--	6.7	--	--	--	--	--	--	--	--	--	26.7	--	--	6.7	7.92×10^2
		Sphagnum	--	--	--	57.1	--	--	--	14.3	--	--	--	--	--	--	--	--	--	28.6	--	--	--	2.10×10^2
		Utricularia	--	3.4	8.6	15.5	--	3.4	--	12.1	--	--	1.7	--	3.4	--	--	--	--	51.9	--	--	--	1.10×10^4
Oneida	Lk 11-5	Sphagnum	13.8	--	--	7.7	--	--	--	1.5	--	67.8	1.5	1.5	--	--	--	--	--	6.2	--	--	--	8.87×10^3
Polk	Evelyn	Utricularia	--	--	50.0	20.0	--	--	--	--	--	--	10.0	--	--	--	--	--	--	10.0	--	--	10.0	1.33×10^3
Price	Unnamed	Sphagnum	--	--	--	40.0	--	--	--	--	--	20.0	20.0	--	--	--	--	--	--	--	20.0	--	--	2.74×10^2
Rusk	Round	Utricularia	41.1	--	--	--	--	--	--	--	--	--	1.5	--	--	--	--	--	--	57.4	--	--	--	8.31×10^3
	Saxton	Sphagnum	--	--	--	--	--	--	--	--	--	--	20.0	--	--	--	--	--	--	80.0	--	--	--	1.69×10^2
	School	Utricularia	31.6	--	26.4	11.8	--	--	--	--	--	--	--	--	1.3	--	--	--	1.3	27.6	--	--	--	6.58×10^3
Vilas	Spruce	Sphagnum	11.1	--	11.1	11.2	--	--	--	--	11.1	--	11.1	--	--	--	--	--	--	11.1	11.1	11.1	11.1	9.30×10^2

Table 6 continued

C. Data for Acid Bog Lakes

County	Locality	Host	Arthrodesmus	Bambusina	Closterium	Cosmarium	Cylindrocystis	Desmidium	Docidium	Euastrum	Gonatozygon	Hyalotheca	Micrasterias	Netrium	Penium	Pleurotaenium	Spinoclosterium	Spirotaenia	Sphaerozosma	Spondylosium	Staurastrum	Tetmemorus	Triploceras	Xanthidium	Desmid Population Density
	Unnamed	Sphagnum	45.6	18.1	--	--	--	--	--	--	--	--	4.5	--	4.5	--	--	--	--	--	27.3	--	--	--	2.20×10^3
Washburn	Unnamed(1)	Potamogeton	--	--	20.0	20.0	--	--	--	--	--	--	--	--	--	20.0	20.0	--	--	--	20.0	--	--	--	5.08×10^2
	Unnamed(2)	Utricularia	7.9	3.1	9.2	12.3		21.5		15.4	--	--	--	1.5	1.5	4.6	--	--	--	1.5	20.0	--	--	1.5	1.90×10^3
	Unnamed(3)	Sphagnum	2.8	17.2	8.6	8.6	2.8	5.7		2.8	--	--	8.6	8.6	8.6	--	--	--	--	--	22.9	--	2.8	--	2.80×10^3

Table 6 continued

D. Data for Alkaline Bog Lakes

County	Locality	Host	Arthrodesmus	Closterium	Cosmarium	Cylindrocystis	Desmidium	Euastrum	Micrasterias	Staurastrum	Xanthidium	Total Desmid Population Density
Rusk	Bog Lake	Potamogeton	--	--	14.3	---	--	--	--	85.7	--	2.5×10^2 org/mg d.w.
Sawyer	Bullhead Lake	Chara	--	--	21.4	---	--	21.4	--	57.2	--	4.65×10^2
		Nojas	--	--	80.0	---	--	--	--	20.0	--	4.28×10^1
		Potamogeton	--	--	85.7	---	--	--	--	14.3	--	2.09×10^2
		Utricularia(Lk)	3.8	--	38.5	---	--	11.5	--	46.2	--	1.97×10^3
		Utricularia (Mat)	--	--	10.0	---	10.0	--	10.0	60.0	10.0	1.32×10^3
Chippewa	Cedar Lake	Ceratophyllum	--	42.9	14.2	---	--	--	--	42.9	--	8.33×10^2
Sawyer	Hegmeister Lk	Myriophyllum	--	--	---	---	--	--	--	100.0	--	6.26×10^1
		Potamogeton A	--	--	---	---	--	--	--	---	--	---
		Potamogeton B	--	--	100.0	---	--	--	--	---	--	3.83×10^1
		Potamogeton C	--	--	---	---	--	--	--	---	--	---
		Sphagnum A	--	--	100.0	---	--	--	--	---	--	3.46×10^1
		Sphagnum B	--	--	---	100.0	--	--	--	---	--	2.05×10^1
		Utricularia	20.0	20.0	60.0	---	--	--	--	---	--	1.53×10^3
Vilas	Mystery Lake	Carex	--	11.1	66.7	---	--	--	--	22.2	--	6.96×10^2
		Sphagnum	--	--	11.1	---	--	--	11.1	77.8	--	7.29×10^2

Table 6 continued

E. Data for Closed Bogs

County	Locality	Host	Arthrodesmus	Bambusina	Closterium	Cosmarium	Cylindrocystis	Desmidium	Euastrum	Hyalotheca	Netrium	Penium	Staurastrum	Tetmemorus	Population Density
	1	Sphagnum A	--	--	---	---	--	--	---	--	100.0	---	--	--	6.06×10^{1}
		Sphagnum B	--	--	---	---	50.0	--	---	--	33.3	---	16.7	--	6.29×10^{2}
	2	Utricularia	--	--	100.0	---	--	--	---	--	---	---	--	--	2.94×10^{2}
	3	Sphagnum	--	--	---	---	--	--	---	--	---	---	100.0	--	5.25×10^{2}
	4	Sphagnum	--	--	---	---	--	--	---	--	---	---	---	--	---
	5	Sphagnum	--	--	---	62.1	37.9	--	---	--	---	---	---	--	1.12×10^{3}
	6	Sphagnum	--	--	---	---	--	25.0	---	--	---	50.0	---	25.0	2.40×10^{2}
	7	Sphagnum	--	12.5	12.5	12.5	--	--	---	6.3	---	---	56.2	--	9.40×10^{2}
	8	Sphagnum	--	--	---	100.0	--	--	---	--	---	---	---	--	1.12×10^{3}
		Potamogeton	--	--	25.0	50.0	--	--	---	--	---	---	25.0	--	1.44×10^{2}
	9	Sphagnum	--	33.3	---	---	--	--	33.3	--	---	---	33.4	--	1.93×10^{2}
	10	Sphagnum	25.0	--	---	---	--	--	12.5	--	---	---	62.5	--	1.85×10^{2}
	11	Sphagnum	--	--	---	---	--	--	100.0	--	---	---	---	--	8.15×10^{1}
		Carex	--	16.7	---	33.3	--	--	16.7	--	---	---	33.3	--	2.22×10^{2}
	12	Sphagnum	--	--	---	---	--	--	---	---	---	---	100.0	--	1.75×10^{1}

Table 7. Importance values of aufwuchs desmid genera within lakes of a particular type

Genus	Hard Water	Soft Water	Acid Bog	Alkaline Bog	Closed Bog
Arthrodesmus	0	0	26.5	10.7	12.1
Bambusina	0	0	25.6	0	17.6
Closterium	16.0	39.3	39.7	18.5	26.8
Cosmarium	81.8	67.0	50.6	62.7	34.3
Cylindrocystis	0	0	6.7	37.4	22.9
Desmidium	0	14.3	23.0	6.4	12.1
Docidium	0	0	3.6	0	0
Euastrum	0	42.9	29.7	12.4	26.6
Gonatozygon	0	0	6.4	0	0
Hyalotheca	0	23.1	11.8	0	5.7
Micrasterias	0	10.7	19.1	10.2	0
Netrium	0	9.2	39.1	0	30.2
Penium	0	0	23.3	0	20.7
Pleurotaenium	0	30.8	16.5	0	0
Roya	0	7.2	0	0	0
Spinoclosterium	0	0	8.3	0	0
Spirotaenia	0	0	8.5	0	0
Sphaerozosma	0	26.1	4.0	0	0
Spondylosium	0	4.5	10.3	0	0
Staurastrum	18.3	42.5	55.3	59.3	49.1
Tetmemorus	0	0	10.9	0	12.1
Triploceras	0	9.4	9.3	0	0
Xanthidium	0	9.3	16.5	6.4	0

Cosmarium (I.V. = 67.0), but in acid bogs and alkaline bogs both *Staurastrum* and *Cosmarium* occur in the first order. The I.V. range in acid bogs is 50.6-55.9 and in alkaline bogs 59.3-62.7. The second and succeeding orders of soft water lakes and acid bogs all contain more than one genus. In soft water lakes the second order includes *Closterium, Euastrum,* and *Staurastrum* (I.V. 39.3-42.9), the third order contains *Hyalotheca, Pleurotaenium,* and *Sphaerozosma* (I.V. 23.1-30.8), and the fourth order contains *Desmidium, Micrasterias, Netrium, Roya, Spondylosium, Triploceras,* and *Xanthidium* (I.V. 4.5-14.3). The second order assemblage in acid bogs includes *Closterium* and *Netrium* (I.V. 39.1-39.7), the third order contains *Arthrodesmus, Bambusina, Desmidium, Euastrum,* and *Penium* (I.V. 23.0-29.7), and the fourth order includes the remaining 12 genera (I.V. 3.6-16.5, see Table 7). *Micrasterias* (I.V. = 19.5) occupies a transition zone between the third and fourth orders in acid bogs.

In alkaline bogs, the second and third orders have only one genus each (*Cylindrocystis* [I.V. = 37.4] in 2, *Closterium* [I.V. = 18.5] in 3), a situation which contrasts to that of the other lake types. The fourth order, however, is occupied by an assemblage of 5 genera including *Arthrodesmus, Desmidium, Euastrum, Micrasterias,* and *Xanthidium* (I.V. = 6.4-12.4).

Based on relative frequency values (Table 8), *Closterium, Cosmarium* and *Staurastrum* are the three most important genera in all lake types except acid bogs, where *Netrium* replaces *Closterium* as the third most important taxon. *Closterium* and *Cosmarium* reach their maximum F_R values in hard water lakes while *Staurastrum* attains maximum relative importance in alkaline bogs. *Netrium,* in contrast, has its highest F_R value in acid bogs and was not detected in hard water lakes or alkaline bogs.

The maximum relative importance (based on F_R values) for two genera (*Closterium, Cosmarium*) occurs in hard water lakes, for five other genera (*Hyalotheca, Pleurotaenium, Roya, Sphaerozosma, Triploceras*) in soft water lakes, for 8 genera (*Docidium, Gonatozygon, Micrasterias, Netrium, Penium, Spinoclosterium, Spirotaenia, Xanthidium*) in acid bogs, and for 4 genera (*Bambusina, Cylindrocystis, Euastrum, Tetmemorus*) in closed bogs. *Staurastrum* is the only genus to reach a maximum F_R in alkaline bogs, although *Arthrodesmus* had maximum F_R values of 6 for both acid and alkaline

Table 8. The relative frequencies for aufwuchs desmid genera within lakes of particular types

Genus	Hard Water	Soft Water	Acid Bog	Alkaline Bog	Closed Bog
Arthrodesmus	0	0	6	6	3
Bambusina	0	0	6	0	9
Closterium	17	11	9	9	9
Cosmarium	63	17	12	37	16
Cylindrocystis	0	0	1	3	6
Desmidium	0	6	6	3	3
Docidium	0	0	1	0	0
Euastrum	0	13	7	6	14
Gonatozygon	0	0	2	0	0
Hyalotheca	0	3	2	0	3
Micrasterias	0	3	4	3	0
Netrium	0	3	10	0	6
Penium	0	0	6	0	3
Pleurotaenium	0	8	4	0	0
Roya	0	2	0	0	0
Spinoclosterium	0	0	0.5	0	0
Spirotaenia	0	0	1	0	0
Sphaerozosma	0	8	0.5	0	0
Spondylosium	0	2	2	0	0
Staurastrum	20	13	12	30	25
Tetmemorus	0	0	2	0	3
Triploceras	0	3	2	0	0
Xanthidium	0	3	4	3	0

Table 9. The absolute frequencies for aufwuchs desmid genera within lakes of particular types

Genus	Hard Water	Soft Water	Acid Bog	Alkaline Bog	Closed Bog
Arthrodesmus	0	0	40	13	7
Bambusina	0	0	43	0	20
Closterium	21	58	63	19	20
Cosmarium	79	92	80	75	33
Cylindrocystis	0	0	9	6	13
Desmidium	0	25	40	6	7
Docidium	0	0	6	0	0
Euastrum	0	67	51	13	27
Gonatozygon	0	0	11	0	0
Hyalotheca	0	42	14	0	7
Micrasterias	0	17	29	13	0
Netrium	0	17	69	0	13
Penium	0	0	40	0	7
Pleurotaenium	0	50	29	0	0
Roya	0	8	0	0	0
Spinoclosterium	0	0	3	0	0
Spirotaenia	0	0	6	0	0
Sphaerozosma	0	42	3	0	0
Spondylosium	0	8	17	0	0
Staurastrum	26	67	83	63	53
Tetmemorus	0	0	14	0	7
Triploceras	0	17	14	0	0
Xanthidium	0	17	29	6	0

bogs. Similarly *Desmidium* and *Spondylosium* had identical maxima in acid bogs and soft water lakes.

The absolute frequency data (Table 9) suggest that *Closterium, Cosmarium,* and *Staurastrum* are 'weedy' taxa with moderate to high F_A values in all five lake types. Similarly, the six genera (*Docidium, Gonatozygon, Roya, Spinoclosterium, Spirotaenia, Tetmemorus*) found in only one lake type exhibit the potential for weediness since they all have low F_A values (3-14) and thus could have been missed in collection or analysis of samples by chance alone.

The biological indicator potential (in terms of lake type) for all of the above genera appears low since the first three are ubiquitous and the remaining ones are of apparent infrequent occurrence and have low I.V. readings (3.6-10.9). Indeed, the absolute frequency data offer few clues as to which aufwuchs genera, if any, may have biological indicator potential. *Pleurotaenium* appears to be characteristic only of soft water lakes and acid bogs where it has F_A values of 50 and 29 respectively, whereas it has F_A values of 0 in the other lake types. The remaining genera appear to be distributed over three or more lake types and/or have low F_A's, thus showing little apparent potential as indicators. Whether particular species within

Table 10. Summary of data relating to the suitability of particular lake types for harboring aufwuchs desmid communities

	Hard Water		Soft Water		Acid Bog		Alkaline Bog		Closed Bog	
Criterion	Value	Rank	Value	Rank	Value	Rank	Value	Rank	Value	Rank
Mean Absolute Population Density	1.33×10^3	3	2.60×10^4	1	3.66×10^3	2	5.13×10^2	4	3.85×10^3	5
Total # desmid genera present	3	5	14	2	22	1	9	4	12	3
Number of assemblage orders present	2	5	4	2	4	2	4	2	3	4
Number of genera present in each assemblage order:										
1	1	4	1	4	2	1.5	2	1.5	1	4
2	2	3.5	3	2	2	3.5	1	5	7	1
3	-	5	3	3	5	1	1	4	4	2
4	-	4.5	7	2	12	1	5	3	-	4.5
Rank Total		30		16		12		23.5		23.5
Suitability Rank		5		2		1		3		3

Table 11. Range of chemical conditions under which desmid genera occurred in Wisconsin lakes. Chemical tolerance range for each genus.

Genus	Conductivity	pH	CO_2	O_2	PO_4-P	Total P
Arthrodesmus	14-112	4.2-8.6	1-21	2-15	<.005-.104	.02-.16
Bambusina	14-96	4.0-9.1	0-21	2-17	.012-.147	.02-1.40
Closterium	15-490	4.0-8.8	0-21	2-15	<.005-.468	.02-1.13
Cosmarium	16-490	4.0-8.8	0-21	2-15	<.005-.747	.02-1.61
Cylindrocystis	17-50	4.3-6.7	(4)	(10)	.024-.967	.03-1.90
Desmidium	14-53	5.6-7.0	0-21	2-15	.019-.446	.04-2.12
Docidium	14-18	5.7-5.9	10-16	5-6	.028-.048	.04-.06
Euastrum	14-56	4.0-7.0	0-21	2-13	<.005-.519	.02-1.40
Gonatozygon	17-23	5.9-6.6	3-16	5-10	.028-.048	.04-.12
Hyalotheca	16-50(-180?)	4.3-7.0	2-20	6-15	.001-.147	.02-.20
Micrasterias	14-28	5.7-7.0	3-16	5-13	.026-.072	.03-.22
Netrium	14-48	4.7-7.0	0-21	2-15	.012-.967	.02-1.90
Penium	14-53(-180?)	5.6-6.8	0-21	4-11	.025-.051	.04-2.12
Pleurotaenium	14-56	5.6-7.0	3-21	4-12	<.005-.058	.02-.11
Phymatodocis	(15)	(6.5)	(0)	(11)	(.026)	(.06)
Roya	(56)	(6.9)	(6)	(7)	(<.005)	(.02)
Spinoclosterium	(18)	(5.7)	(21)	(2)	(.019)	(.04)
Spirotaenia	14-24	5.7-6.3	7-10	6-10	.028-.058	.04-.07
Sphaerozosma	15-22	5.7-7.0	0-21	2-12	.019-.058	.04-.11
Spondylosium	14-28	5.6-7.0	3-21	4-12	.025-.058	.04-.12
Staurastrum	14-520	4.0-9.1	0-28	2-17	<.005-.967	.02-1.40
Tetmemorus	14-39	5.6-6.8	3-16	5-12	.023-.052	.04-.09
Triploceras	17-38	5.8-7.0	3-16	5-15	.001-.058	.02-.11
Xanthidium	14-48(-180?)	5.6-7.0	2-21	2-13	.001-.058	.02-.11

these genera exhibit more restricted distributions and/or have greater indicator potential remains to be determined.

Data relating to the suitability of a particular lake type for harboring an aufwuchs desmid community are summarized in Table 10. As was the case for euplankton communities, acid bog lakes appear to be the most suitable type for aufwuchs desmids, and soft water lakes are the second most suitable. Following these, alkaline bogs and closed bogs appear to have a similar degree of suita-

Table 11 continued

Genus	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	Cl^{-}	$SO_4^{=}$
Arthrodesmus	0-15.7	<2.0-7.6	<0.5-2.2	<1.0-20.4	2-28	3-12
Bambusina	0-17.8	<2.0-6.8	<0.5-2.2	<1.0-10.2	2-13(-26?)	1-31(-69?)
Closterium	0-63	<2.0-5.5	<0.5-3.7	<1.0-11.4	2-27	3-40
Cosmarium	0-63	<2.0-55	<0.5-2.4	<1.0-10.2	2-27	1-40)139?)
Cylindrocystis	0.3-3.4	<2.0-3.1	<0.5-2.2	<1.0-5.1	7-15	4-25(139?)
Desmidium	0-7.6	<2.0-4.7	<0.5-6.6	<1.0-10.2	9-18(26?)	1-21
Docidium	1.0-2.0	(<2.0)	<0.5-1.4	<1.0-1.7	4-9	3-6
Euastrum	0-9.1	<2.0-5.2	<0.5-2.2	<1.0-20.4	2-28	3-31(-69?)
Gonatozygon	0.9-1.3	(2.0)	<0.5-1.8	<1.0-1.7	3-9(26?)	4-7
Hyalotheca	0-6.2	<2.0-2.2	<0.5-2.1	<1.0-7.3	2-39	3-21
Micrasterias	0.3-4.8	(<2.0)	<0.5-1.8	<1.0-1.7	3-10)26?)	3-7
Netrium	0-8.0	<2.0-3.7	<0.5-2.2	<1.0-5.1	3-15	3-25
Penium	0-6.4	<2.0-4.7	<0.5-6.6	<1.0-4.2	2-39	3-21
Pleurotaenium	0-9.1	<2.0-5.2	<0.5-2.1	<1.0-10.2	2-18	1-8
Phymatodocis	(0)	(2.1)	(2.0)	1.0	(3)	(6)
Roya	(9.1)	(5.2)	(2.0)	(2.2)	(2)	(6)
Spinoclosterium	(2.2)	(2.5)	(2.2)	(<1.0)	(3)	(6)
Spirotaenia	2.0-3.7	(<2.0)	<0.5-0.6	(<1.0)	(4)	3-4
Sphaerozosma	0-3.2	<2.0-2.5	<.5-2.2	<1.0-2.7	3-18	3-6
Spondylosium	0-4.8	<2.0-2.2	<.5-1.6	<1.0-1.8	2-5(-26?)	3-8
Staurastrum	0-50	<2.0-37.7	<0.5-3.7	<1.0-83.1	2-140	1-40)-69?)
Tetmemorus	0.9-3.7	(<2.0)	<0.5-1.8	<1.0-10.2	3-13	1-6
Triploceras	1.0-3.7	(<2.0)	<0.5-2.1	<1.0-5.1	3-18	4-6
Xanthidium	0-8.0	<2.0-2.5	<0.5-2.2	<1.0-10.2	2-39	1-10

bility, and hard water lakes show the least suitability. Spring ponds, with a total absence of aufwuchs desmids, also appear unsuitable.

Chemical Considerations in Wisconsin Lakes

The relative suitability of lakes of a given type to harbor desmid communities may be governed in part by the range of chemical conditions present and in part by the ability of various desmids to survive under those conditions. The occurrence of desmid genera in the 61 Wisconsin localities in relation to chemical parameters is summarized below; the bearing these results have on various

Table 11 continued

Genus	NO_2-N	NO_3-N	NH_3-N	Org-N	Total-N	Total Alkalinity
Arthrodesmus	<.002-.021	<.04-.27	<.03-.27	.24-1.64	.33-1.97	0-41
Bambusina	<.002-.62	.04-2.21	<.03-.26	.27-6.60	.38-7.34	0-50
Closterium	.002-.04	<.04-.95	<.03-.20	.36-3.64	.54-4.83	0-324
Cosmarium	<.002-.058	<.04-3.22	<.03-1.62	.44-3.64	.54-4.83	0-324
Cylindrocystis	.004-.06	<.04-3.22	<.03-1.62	.66-12.63	.67-13.30	0-1
Desmidium	<.002-.12	.04-3.44	<.03-2.26	.27-6.14	.38-11.96	0-6
Docidium	<.002-.005	.04-.08	.03-.05	1.03-1.07	1.10-1.20	0-1
Euastrum	<.002-.62	.04-2.21	<.03-.27	.44-6.60	.54-7.42	0-19
Gonatozygon	.002-.006	.04-.09	<.03-.05	.92-1.07	1.06-1.20	0-2
Hyalotheca	.002-.02	.04-.45	<.03-.27	.24-1.96	.33-2.52	0-6
Micrasterias	<.002-.013	<.04-.13	<.03-.27	.66-1.31	.67-1.58	0-6
Netrium	<.002-.06	.04-.29	<.03-.32	.72-12.63	.81-13.30	0-18
Penium	<.002-.12	.04-3.44	.03-2.26	.8-6.14	.96-11.96	0-4
Pleurotaenium	<.002-.013	.04-.13	<.03-.15	.27-1.29	.38-1.58	0-19
Phymatodocis	(.004)	(.06)	(.04)	(1.85)	(1.95)	(0)
Roya	(.004)	(.10)	(<.03)	(.44)	(54)	(19)
Spinoclosterium	(.004)	(.08)	(<.03)	(.81)	(.89)	(2)
Spirotaenia	<.002-.008	.04-.10	.03-.26	1.03-1.05	1.10-1.42	1-6
Sphaerozosma	.002-.013	.05-.13	<.03-.15	.72-1.85	.81-1.95	0-2
Spondylosium	<.002-.014	.04-.11	.03-.27	.73-1.23	.98-1.42	0-6
Staurastrum	<.002-.62	<.04-2.72	<.03-.70	.34-12.63	.33-13.30	0-247
Tetmemorus	<.002-.008	.04-.10	.03-.26	.24-1.07	.33-1.42	0-6
Triploceras	.004-.013	.04-.14	<.03-.26	.24-1.29	.33-1.58	0-6
Xanthidium	<.002-.013	.04-.15	<.03-.27	.27-1.85	.38-1.95	0-18

hypotheses concerning desmid distribution and water chemistry then will be considered.

The range in chemical conditions under which the various desmid genera occurred is summarized in Table 11. To determine overall relative tolerance of the genera, the extent of the range (i.e. the difference between maximum and minimum values) of each parameter for each genus was calculated from Table 11. Then the genera were ranked for each parameter, with the widest range given a rank of 1, the next widest a rank of 2, etc. The ranks for each genus were then summed and relative tolerance ratings assigned, the lowest rank sum receiving a

tolerance rating of 1, the second lowest 2, etc. These results appear in Table 12.

Considering relative tolerance to all chemical parameters simultaneously, *Staurastrum* appears to be by far the most tolerant of the desmid genera encountered. Its ability to survive a wide range of chemical conditions may account, in part, for its prominence in the euplankton and/or aufwuchs of all six lake types in terms of frequency, density, and importance values. *Cosmarium,* with the second highest tolerance rating, and *Closterium,* with the fifth highest tolerance rating, occurred in the euplankton and/or aufwuchs communities of all lake types except for spring ponds. *Bambusina* (tolerance rating of 3) was one of the more prominent desmids in the 3 types

Table 12. Tolerance Ranges and Tolerance Ratings of Desmid Genera.

Genus	Conductivity		pH		CO_2		O_2		PO_4 - P	
	Range	Rank	Range	Rank	Range	Rank	Range	Rank	Range	Rank
Arthrodesmus	98	4	4.4	5	20	10	13	5	.104	9
Bambusina	85	5	5.1	1.5	21	5.5	15	1.5	.135	8
Closterium	475	2	4.8	3.5	21	5.5	13	5	.468	5
Cosmarium	474	3	4.8	3.5	21	5.5	13	5	.747	3
Desmidium	39	8.5	1.4	10.5	21	5.5	13	5	.427	6
Docidium	4	19	0.2	19	6	19	1	19	.020	18.5
Euastrum	42	6.5	3.0	7	21	5.5	11	8.5	.519	4
Gonatozygon	6	18	0.7	18	13	16.5	5	18	.020	18.5
Hyalotheca	34	10	3.7	6	18	13	9	12	.146	7
Micrasterias	14	15	1.3	13.5	13	16.5	8	14	.046	13
Netrium	14	15	2.3	8	21	5.5	13	5	.955	2
Penium	39	8.5	1.2	16	21	5.5	7	16.5	.026	17
Pleurotaenium	42	6.5	1.4	10.5	18	13	8	14	.058	11
Sphaerozosma	7	17	1.3	13.5	21	5.5	10	10.5	.039	14
Spondylosium	14	15	1.4	10.5	18	13	8	14	.033	15
Staurastrum	506	1	5.1	1.5	28	1	15	1.5	.967	1
Tetmemorus	25	12	1.2	16	13	16.5	7	16.5	.029	16
Triploceras	21	13	1.2	16	13	16.5	10	10.5	.058	11
Xanthidium	30	11	1.4	10.5	19	11	11	8.5	.058	11

Genus	Na^+		Cl^-		SO_4^{2-}		Rank Total	Tolerance Rating
	Range	Rank	Range	Rank	Range	Rank		
Arthrodesmus	20.4	2.5	26	5.5	9	10.5	139.0	8
Bambusina	10.2	7.5	11	13	30	4	95.5	3
Closterium	11.4	4	25	7.5	37	3	95.5	5
Cosmarium	10.2	7.5	25	7.5	39	1.5	78.0	2
Desmidium	10.2	7.5	9	15	20	7	105.0	4
Docidium	1.7	18	5	18	3	17	316.0	19
Euastrum	20.4	2.5	26	5.5	28	5	97.5	6
Gonatozygon	1.7	18	6	17	3	17	298.5	18
Hyalotheca	7.3	11	37	3	18	8.5	163.0	10
Micrasterias	1.7	18	7	16	4	15	235.5	14
Netrium	5.1	12.5	12	12	22	6	119.5	7
Penium	4.2	14	37	3	18	8.5	138.5	9
Pleurotaenium	10.2	7.5	16	9	7	12	184.0	12
Sphaerozosma	2.7	15	15	10.5	3	17	232.0	15
Spondylosium	1.8	16	3	19	5	13.5	249.0	16
Staurastrum	83.1	1	138	1	39	1.5	37.0	1
Tetmemorus	10.2	7.5	10	14	5	13.5	251.5	17
Triploceras	5.1	12.5	15	10.5	2	19	229.0	13
Xanthidium	10.2	7.5	37	3	9	10.5	166.0	11

Table 12 continued

Genus	Total N		Total Alkalinity		Ca^{++}		K^+	
	Range	Rank	Range	Rank	Range	Rank	Range	Rank
Arthrodesmus	1.64	10	41	5	15.7	5	2.2	8.5
Bambusina	6.96	5	50	4	17.8	4	2.2	8.5
Closterium	4.29	7.5	324	1.5	63	1.5	3.7	3.5
Cosmarium	4.29	7.5	324	1.5	63	1.5	2.4	5
Desmidium	11.58	3	6	12.5	7.6	10	6.6	1.5
Docidium	.10	19	1	19	1.0	18	1.4	19
Euastrum	6.88	6	19	6.5	9.1	6.5	2.2	8.5
Gonatozygon	.14	18	2	17.5	.4	19	1.8	16
Hyalotheca	2.19	9	6	12.5	6.2	12	2.1	13
Micrasterias	.91	16	6	12.5	4.5	14	1.8	16
Netrium	12.49	2	18	8.5	8.0	8.5	2.2	8.5
Penium	11.0	4	4	16	6.4	11	6.6	1.5
Pleurotaenium	1.20	13	19	6.5	9.1	6.5	2.1	13
Sphaerozosma	1.14	14	2	17.5	3.2	15	2.2	8.5
Spondylosium	.44	17	6	12.5	4.8	13	1.6	18
Staurastrum	12.97	1	247	3	50	3	3.7	3.5
Tetmemorus	1.09	15	6	12.5	2.8	16	1.8	16
Triploceras	1.25	12	6	12.5	2.7	17	2.1	13
Xanthidium	1.57	11	18	8.5	8.0	8.5	2.2	8.5

Genus	Total P		NO_2 - N		NO_3 - N		NH_3 - N		Org-N	
	Range	Rank	Range	Rank	Range	Rank	Range	Rank	Range	Rank
Arthrodesmus	.14	11	.019	10	.023	19	.27	8	1.40	11
Bambusina	1.38	6	.618	2	2.17	5.5	.26	11.5	6.33	3
Closterium	1.11	8	.02	9	.95	7	.20	15	3.28	7
Cosmarium	1.59	4	.056	8	3.22	3	1.62	3	3.20	8
Desmidium	2.08	1.5	.118	4	3.40	1.5	2.26	1	5.86	5
Docidium	.02	19	.003	19	.04	18	.02	18.5	.04	19
Euastrum	1.38	6	.618	2	2.17	5.5	.27	8	6.16	4
Gonatozygon	.08	15.5	.004	18	.05	17	.02	18.5	.15	18
Hyalotheca	.18	10	.018	11	.41	8	.27	8	1.72	9
Micrasterias	.19	9	.013	13	.13	10	.27	8	.65	16
Netrium	1.88	3	.06	7	.25	9	.32	5	11.91	2
Penium	2.08	1.5	.12	6	3.40	1.5	2.23	2	5.34	6
Pleurotaenium	.09	13	.13	5	.09	13	.15	16.5	1.02	14
Sphaerozosma	.07	17	.011	14.5	.08	14	.15	16.5	1.13	12
Spondylosium	.08	15.5	.014	12	.07	15	.24	13	.50	17
Staurastrum	1.38	6	.618	2	2.72	4	.70	4	12.29	1
Tetmemorus	.05	18	.006	17	.06	16	.23	14	.83	15
Triploceras	.09	13	.009	16	.10	12	.26	11.5	1.05	15
Xanthidium	.09	13	.011	14.5	.11	11	.27	8	1.58	10

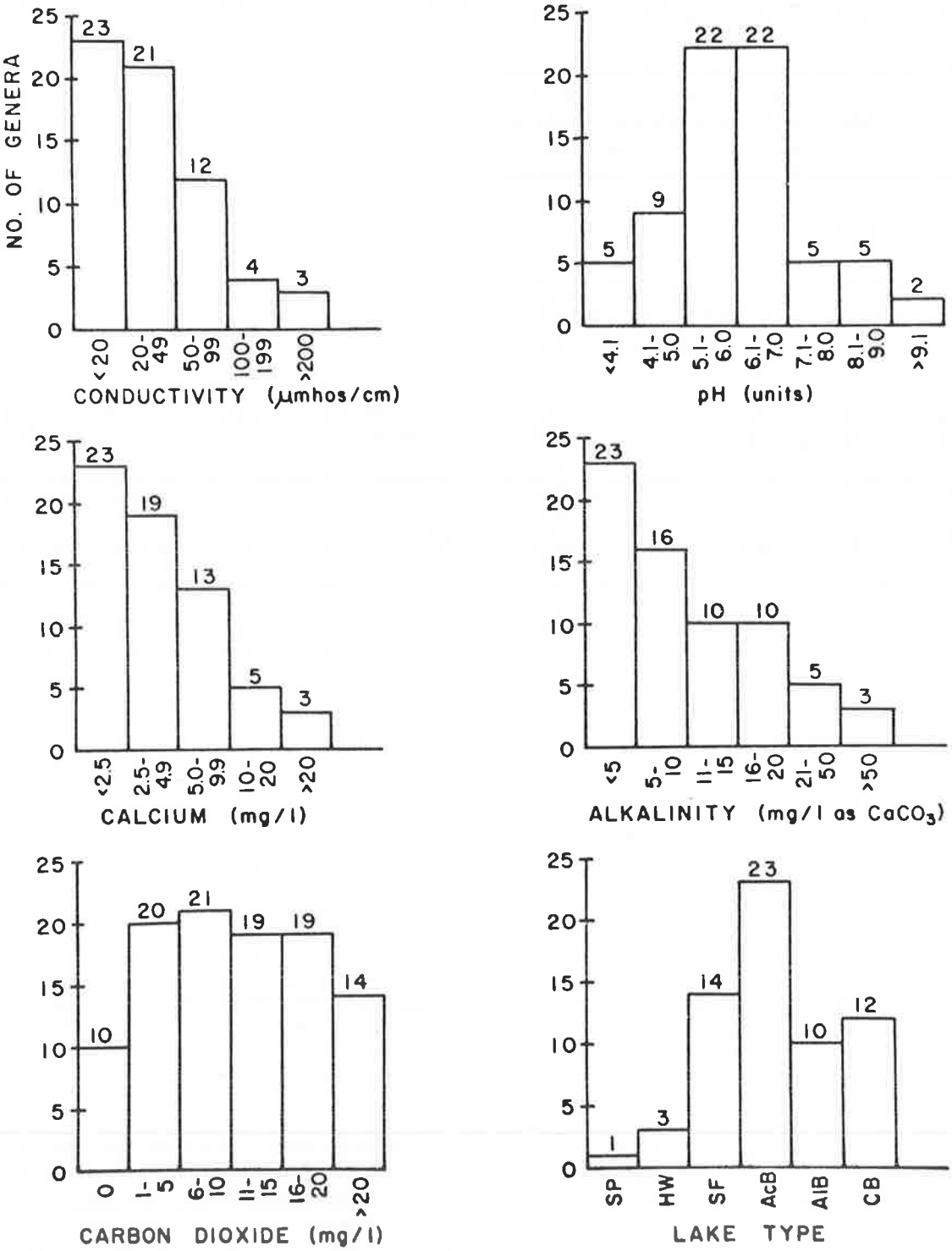

Fig. 2. Relationships between the occurrence of desmid genera and particular environmental parameters. (Numbers on top of each bar indicate the number of desmid genera present.)

of bog environments, and *Desmidium* (tolerance rating of 4) was among the more prominent desmids of soft water lakes and acid bogs. It also occurred in closed bogs and alkaline bogs.

The five least tolerant genera were detected in only 1 or 2 lake types, one of which was the acid bog. In most cases these genera did not play a prominent role in terms of frequency, density or relative importance. It was not possible to calculate tolerance ratings for *Phymatodocis, Roya,* and *Spinoclosterium* because of their presence at only 1 locality. Similarly, overall tolerance ratings could not be computed for *Cylindrocystis* and *Spirotaenia* because of incomplete data or very low levels of certain chemical species at all localities where the taxa were recorded.

Apparent correlations exist between the number of desmid genera present at a locality and the levels of certain chemical parameters in that locality (Fig. 2). Thus the greatest number of genera occur when conductivity levels are under 20 μmhos/cm, the pH is 5.1-7.0, calcium levels are less than 2.5 mg/l, alkalinity readings are below 5 mg/l (expressed as $CaCO_3$), and CO_2 levels are 1-20 mg/l. Five or fewer genera, in contrast, were detected in waters where conductivity levels exceeded 100 μmhos/cm, and/or pH readings were over 7.0, and/or calcium levels surpassed 10 mg/l, and/or alkalinity readings were greater than 20 mg/l. Similarly only 10 genera were recorded from waters where carbon dioxide levels of 0 mg/l occurred.

Of the six lake types covered in these investigations, the chemical environments (Table 13) of acid bogs most nearly correspond to the apparent optima for the occurrence of desmids. This assessment supports the suitability rating of acid bogs based on biological criteria (Table 5, 10) and concurs with the observed qualitative richness of desmid genera in acid bogs (Table 4, 9). Conversely, the chemical environments of spring ponds and hard water lakes differ sharply from the apparent chemical optima for the occurrence of desmids, and this correlates with their low biological suitability rating (Table 5, 10) and the paucity of desmid genera present.

Apparent correlations also occur between the number of desmid genera present and the levels of Mg^{++}, K^{+}, Na^{+}, Cl^{-}, and $SO_4^{=}$ in the water (see Table 11). All of these ions, however, contribute to the conductivity levels which have been discussed above. In general, higher levels of the various ions correspond to the occurrence of fewer desmid genera.

Meaningful relationships between levels of the various nitrogen and phosphorous species and the occurrence of desmid genera are difficult to detect because the chemical readings reflect only the amounts present in the water and do not necessarily take into account any nitrogen or phosphorous bound up in biological tissues or in the sediments.

Desmid Distribution and Water Chemistry

The apparent correlation between desmid distribution and certain factors in the chemical environment has been recognized for many years, and a number of hypotheses (see Hutchinson 1967, pgs. 330-333 and Prescott 1946, pgs. 667-670 for reviews) have been offered to account for the observed situation. The most widely accepted views suggest that calcium concentrations (or calcium and magnesium concentrations), or pH–conductivity relations, or pH–bicarbonate–CO_2 relations govern desmid distributions.

A number of investigators (e.g. Hutchinson, 1967; Hutchinson & Pickford, 1932; Strom, 1921; Wade, 1957) have postulated that desmids are calciphobic and that desmid diversity and abundance decrease as calcium concentrations increase. Thus, environments with low calcium levels (e.g. acid bogs, soft water lakes) presumably favor desmid development while environments with high calcium levels (e.g. spring ponds, hard water lakes) presumably retard desmid development.

Other studies (e.g. Mevius, 1924; Ruttner, 1963) suggest that total electrolyte content in conjunction with pH control the distribution of many organisms, including desmids, by affecting the permeability of the plasmalemma. According to this hypothesis, alkaline pH's greatly increase plasmalemma permeability. Increased permeability in environments where electrolyte content (as measured by conductivity) is high results in the cells being flooded by excess ions, and this, in turn, causes death. Such flooding does not occur in situations where conductivity levels are high but pH values are acidic because of reduced plasmalemma permeability. Similarly ionic flooding does not occur in situations where conductivity levels are low, regardless of pH. Thus, hard water lakes and spring ponds (alkaline pH, high conductivity) are supposedly unsuitable for desmid development in comparison with soft water lakes and acid bogs (acid pH, low conductivity).

A third hypothesis (Moss, 1972, 1973a-c) suggests that desmid distribution is controlled by the availability of free CO_2 for photosynthesis. At acidic pH levels, most carbon available for photosynthesis will be in the form of

Table 13. Summary of water chemistry conditions in the various lake types.

All values expressed as mg/l except for conductivity (μmhos/cm) and pH (units). N.A. = data not available.

Parameter	Spring Ponds		Hard Water Lakes		Soft Water Lakes		Acid Bogs		Lake Samples Alkaline Bogs		Mat Samples Alkaline Bogs		Closed Bogs	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Conductivity	520-619	584	228-490	375	16-56	32	14-61(180?)	27	37-103	79	41-78	59	30-429	104
pH	7.3-7.5	7.4	8.30-8.80	8.58	6.5-7.0	6.8	5.6-7.0	6	7.1-9.1	8.0	4.4-7.3	5.7	4.0-5.9	4.5
CO_2	24-32	29	N.A.	N.A.	3-6	4	0-21	8	0-10	4	40-54	45	N.A.	N.A.
O_2	4.0-9.0	7.7	N.A.	N.A.	7-13	11	2-15	9	9-17	12	2-11	4	N.A.	N.A.
PO_4-P	.014-.030	.020	.014-.051	.023	<.005-.072	.040	.011-.058	.033	<.005-.104	.051	.017-.095	.068	.015-.967	.310
Total P	.03-.06	.04	.01-.08	.04	.02-.22	.09	.02-.12	.06	.02-.13	.08	.03-.16	.25	.04-2.12	.85
NO_2-N	.002-.021	.010	.000-.032	.007	.004-.013	.009	<.002-.014	.06	.003-.021	.011	.002-.036	.019	.01-.62	.09
NO_3-N	2.35-2.94	2.61	<.04-.39	.12	.07-.28	1.36	<.04-.27	.08	<.04-.27	.06	.04-1.94	.60	.16-3.44	1.02
NH_3-N	.05-.23	.14	<.03 .12	N.A.	<.03-.15	.07	<.03-.27	.06	<.03-.70	N.A.	.04-.94	.29	<.03-2.26	.44
Org. N	.34-.66	.56	.64-1.48	.96	.44-1.31	.97	.24-1.85	.90	.34-1.36	.77	.72-3.53	1.9	.95-12.63	3.96
Total N	3.07-3.63	3.34	.76-1.53	1.12	.54-1.58	1.18	.33-1.95	1.06	.39-2.25	1.00	.80-6.43	2.91	1.19-13.30	5.52
Total Alkalinity	247-290	271	110-324	196	1-19	8	0-21	2	14-50	38	12-39	20	0-17	1
Ca^{++}	50-74	66	35-63	48	2.7-9.1	5.0	0-99	3	7.5-20.8	14.8	<2.0-12.0	8.7	2.3-12.3	5.7
Mg^{++}	25-43	36	N.A.	N.A.	N.A.	N.A.	<2.0-2.5	N.A.	<2.0-7.6	5.1	<2.0-7.9	4.5	<2.0-5.2	3.2
K^{+}	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	<.5-2.2	N.A.	<.5-1.9	1.0	<.5-2.1	1.4	<.5-6.6	2.1
Na^{+}	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	<1.0-11.5	N.A.	<1.0-4.8	2.4	<1.0-4.7	3.1	<1.0-83.1	14.8
Cl^{-}	21-32	26	13-27	18	2-18	7	2-39	6	4-28	10	5-8	6	2-140	27
$SO_4^{=}$	27-32	29	3-30	18	6-14	8	1-12	5	3-8	6	3-35(92?)	17.7	7-40	21

free CO_2 (see Hutchinson, 1957, p. 657). At alkaline pH levels, more and more of the carbon becomes bound as bicarbonate or carbonate and less and less remains as free CO_2 under most circumstances (an important exception occurs in calcareous spring ponds; its bearing on this hypothesis is discussed below). Assuming most desmids require free CO_2 (i.e., they cannot utilize HCO_3^-) for photosynthesis, acidic environments with a ready source of free CO_2 (e.g., acid bogs) would favor desmid development whereas alkaline environments with low or non-existent free CO_2 (e.g., hard water lakes) would retard desmid development.

In addition to the above three hypotheses, a fourth idea, developed in conjection with experimental work on *Sphagnum* (Clymo, 1973), merits consideration. Clymo (*op. cit.*) found that alkaline pH's (7.6) acting in concert with high levels of calcium (100 mg/l) caused the death of *Sphagnum* plants, whereas high pH or high calcium alone did not adversely affect the plants. Similarly, low pH and low calcium in concert did not adversely affect *Sphagnum* growth. If desmids as a group respond similarly to varying combinations of pH and Ca^{++}, then environments with high pH and Ca^{++} (e.g., spring ponds, hard water lakes) would retard desmid development whereas environments low in either or both pH and Ca^{++} (e.g., acid bogs with surrounding *Sphagnum* mats) would tend to favor desmid development.

The available field and laboratory data do not provide a clear indication as to which of the above hypotheses, if any, most accurately accounts for observed desmid distributions. Field data collected during the investigations of Wisconsin lakes show an inverse relationship between calcium levels and desmid diversity (Fig. 2C) and thus supports the hypothesis that most desmids may be calciphobic. Tassigny (1971), working with axenic cultures of four desmids, found the growth was markedly reduced in the three species normally found in oligotrophic environments (see Moss, 1973c for definitions of oligotrophy and eutrophy) when calcium levels were increased. The species normally found in eutrophic environments prospered equally well at all calcium levels. Thus Tassigny's results also suggest that most desmids are calciphobic. Moss (1972), however, concluded from laboratory experiments on a variety of algae (including 11 desmids) that calcium concentration (range of 0.02-100.0 mg/l) does not affect the growth of desmids regardless of their natural distribution and that, consequently, experimental evidence does not support the hypothesis that most desmids are calciphobic. The current evidence regarding relationships between calcium levels and desmid distribution therefore appears to be contradictory.

The second hypothesis implicating pH-conductivity relations as a controlling factor in desmid distribution is also attended by apparently contradictory evidence. The Wisconsin field studies, which confirm the observations of a number of earlier investigators, indicate that a marked reduction in desmid diversity occurs in environments (e.g., spring ponds, hard water lakes) with alkaline pH's and conductivity levels over 100 μmhos/cm. Desmid diversity is greatest where pH values are acidic and conductivity levels are low (acid bogs, soft water lakes). Intermediate diversities occur under acidic conditions with increased conductivity levels (alkaline bogs, closed bogs). A drastic reduction in desmid diversity occurs when pH values go above 7.0, a condition which Ruttner (1963) states is almost invariably accompanied by increased conductivities in natural environments. Experiments conducted by Moss (1973a) on three desmids, however, suggest that conductivity levels in excess of 100 μmhos/cm when combined with alkaline pH readings do not always adversely affect survival and growth rates. Indeed, Moss (1973a, p. 168) concludes that '...the possibility of toxicity of high ionic content has been experimentally eliminated.'

The third hypothesis – that desmid distribution is controlled by availability of free carbon dioxide – gains support from the experimental studies of Moss (1972, 1973a-c). Based on extensive laboratory investigations, Moss presumably eliminated calcium concentrations and conductivity-pH relations as control factors in desmid distribution, assumed that most desmids require free CO_2 for photosynthesis, and, using known pH-bicarbonate-CO_2 relations (see Hutchinson 1957, p. 657), concluded that pH indirectly governs desmid distribution by controlling the amount of free CO_2 available. Thus the desmid flora should reach its greatest diversity in environments with readily available free CO_2 and should be comparatively depauperate in environments poor in free CO_2, regardless of calcium concentrations or conductivity levels.

Field data gathered during the course of investigations of Wisconsin desmid communities apparently do not support CO_2 availability as the sole factor in controlling desmid distributions. Thus 10 genera (Table 11) were encountered in situations where free CO_2 levels apparently were 0. Included were genera (e.g., *Cosmarium, Staurastrum*) found in a number of lake types and genera (e.g., *Phymatodocis, Sphaerozosma*) confined to one or

two lake types. Moreover, the six Wisconsin spring ponds all had plentiful levels of CO_2 (which supposedly makes them conducive to desmid development), but their desmid flora was the most depauperate of all six lake types studied. Indeed, plants of only one genus (*Staurastrum*) were encountered in only one of the six ponds. Thus field observations are not supportive of the hypothesis that CO_2 levels alone govern desmid distribution.

The recent experimental work of Clymo (1973) on *Sphagnum* suggests the possibility that alkaline pH values in concert with high (ca. 100 mg/l) calcium concentrations may affect desmids adversely. This combination of factors exists in Wisconsin spring ponds and hard water lakes where the desmid diversities are low. Similarly, the open waters of alkaline bog lakes (pH 7.1-9.1; Ca^{++} 7.5-20.8) have a much less diverse flora than the mats (pH 4.4-7.3; $Ca^{++} < 2.0$-12.0) [see Woelkerling, 1976]. In acid bogs and soft water lakes, pH is acidic, Ca^{++} levels are low (Table 13), and desmid diversity is high. All this data support the experimental observations of Clymo (1973). The work of Moss (1972), however, indicates that at least some desmids naturally present in acid waters with low Ca^{++} levels can also survive and grow in alkaline waters with Ca^{++} levels up to 100 mg/l. Thus the hypothesis that alkaline pH and high Ca^{++} levels act in concert to adversely affect desmid diversity also is attended by apparently contradictory evidence.

Concluding Remarks

The problem of accounting for observed desmid distributions in natural environments appears complex and has not been resolved. All hypotheses involving apparent correlations between certain chemical parameters and desmid diversity have both favorable and unfavorable evidence associated with them, and obviously more research is needed.

Part of the current dilemma stems from attempts to extract sweeping generalizations from experiments on an extremely limited number of taxa. To conclude, for example, that high conductivity levels do not adversely affect desmids (Moss, 1973a, p. 164, 168) on the basis of experiments on only three of the thousands of described species seems, to these investigators at least, to be exceedingly presumptuous. Meaningful conclusions can be drawn, it seems, only from far more broadly based experimentation. Carefully planned laboratory studies are needed on a wide variety of desmids to determine to what extent, if any, various species are calciphobic, to elucidate to what extent, if any, ionic content (i.e., conductivity) affects desmids, to establish whether none, some, most, or all desmids require free CO_2 for photosynthesis, and to gain insight into the role, if any, played by pH.

While the above chemical parameters are most commonly implicated in explaining desmid distributions, other factors also could be involved. Thus little is known about the effects of other chemical parameters. For example, to what extent, if any, is bicarbonate toxic to desmids? Moss (1973a, p. 164 and Fig. 4) found, for instance, that the growth of two desmids was suppressed when 420 mg/l $NaHCO_3$ was added to the cultures. Likewise, little is known about the ability of desmids to utilize the various nitrogen species (see, however, Moss, 1973b), and more work is needed.

The role of various biological factors also remains largely unexplored. Little is known about the ability of desmids to compete with other algae for available nutrients. Perhaps the environments of acid bogs give desmids a greater competitive advantage than do those of hard water lakes or spring ponds. There also is a paucity of information on desmid-bacterial relations. Perhaps desmids are favored by an association with bacteria which are largely restricted to certain types of environments. These and many other questions must be answered before the problem of explaining desmid distributions is finally resolved.

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SEDGWICK-RAFTER CELL COUNTS: A PROCEDURAL ANALYSIS

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Abstract

Information in the existing literature on some aspects of the collection and statistical analysis of Sedgwick-Rafter cell data appears contradictory, confusing, or absent. Using data from an experimental phytoplankton population as a basis, an investigation of S-R cell procedure has been undertaken with the following conclusions: 1) settling time depends upon the type of preservation and the composition of the sample; 2) the field counting technique gives more accurate data and is less time consuming than the strip counting technique; 3) making fewer counts on each of a greater number of S-R cells gives more accurate results than making a greater number of counts on one or several S-R cells; 4) nonparametric methods offer a more convenient and nearly as efficient a means of detecting statistically significant differences as compared with parametric methods. A method is presented for optimally allocating counts within and among S-R cells for getting an estimator with the greatest precision in the least time.

Introduction

The use of Sedgwick-Rafter (S-R) cells for estimating the standing crop of phytoplankton and in measuring algal growth rates by counting cell divisions appears to be widespread, and descriptions of the techniques involved have been included in a number of methodological handbooks and review papers (e.g., APHA 1971, Guillard 1973, Lund & Talling 1957, Welch 1948). According to the APHA (1971, page 734), the S-R cell offers the advantage of being '...easily manipulated and provides reasonably reproducible information...'; it suffers, however, from the limitation that the high magnifications needed for counting nannoplankton and ultraplankton are difficult to achieve with ordinary microscopes due to S-R cell design, and other procedures (see Guillard 1973, Schwoerbel 1970) have been proposed for these purposes.

During preliminary work on the role of desmids (Desmidiales, Chlorophyta) in Wisconsin lake communities, it quickly became apparent that the directions given in the methodological handbooks for S-R cell use are not explicit in some respects and that information on these points from other sources appears contradictory, or confusing, or altogether absent. Among questions that have arisen are the following:

1. Should at least 15 minutes settling time be allowed prior to counting (APHA 1971) or is 3-5 minutes sufficient (Guillard 1973)?
2. Does the field counting technique yield results that are better than, comparable to, or poorer than strip counting data in terms of accuracy and efficiency?
3. If the field counting technique is employed, how many S-R cells should be examined and how many fields per cell should be counted? (The APHA (1971) states that 10 or more random fields should be counted but makes no mention of the number of S-R cells to be examined; Welch (1948) recommends counting at least 10 fields in each of 2 cells; McAlice (1971) suggests examining 30 fields in each of 3 cells; Kutkuhn (1958) proposes enumerating 10 fields in each of 4 cells, and Guillard (1973, page 300) says: 'Count enough fields to get the precision desired.')
4. What is the most efficient way of obtaining S-R data

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given arbitrarily defined standards of accuracy or arbitrarily set time limits for the examination of individual samples? McAlice (1971) considers only time but not accuracy in his cost analysis, and to our knowledge, no one else has undertaken a complete cost analysis.

Another problem concerns methods used to detect statistically significant differences between two or more samples. Those apparently few investigators (e.g., Ballentine 1953, Gilbert 1942, Littleford *et al.* 1940) who have employed statistical evaluations have used parametric procedures on the assumption that the distribution of the data is approximately normal. Kutkuhn (1958), McAlice (1971), and Serfling (1949), however, have demonstrated that this assumption cannot always be made. Furthermore, transforming data to approximate a normal distribution apparently is not always possible (Kutkuhn 1958, page 73). In view of these facts, the question arises as to whether nonparametric procedures, which are less distribution-dependent, offer a satisfactory alternative to parametric procedures for detecting statistically significant differences.

The present study has been undertaken 1) to gather information which hopefully will help to answer the four questions raised above concerning S-R cell use and 2) to discuss the use of parametric and nonparametric procedures in testing S-R cell data for statistical significance.

II. Materials and Methods

The experimental population employed in this investigation has been prepared by mixing aliquots of three unicellular desmids *(Micrasterias laticeps* Nordstedt, *Netrium digitatus* (Ehrenberg) Itzigsohn and Rothe, *Staurastrum leptacanthum* Nordstedt), one filamentous desmid (*Sphaerozosma* sp.), and one colonial chlorococcalean alga (*Scenedesmus quadricauda* (Turpin) Breb.) and then preserving the mixture with Lugol's solution (H_2O-1000 ml.; I_2-10 gm.; KI-5 gm.) or with FAA (10:7:2:1::95% ethanol:distilled water:formalin:acetic acid). All taxa represent clonal isolates from Wisconsin lakes.

Using pipettes with a bore diameter of 1 mm., aliquots of the test population were extracted from the preserved sample (which was constantly being mixed with a magnetic stirrer) and were pipetted into S-R cells according to directions given in APHA (1971). Once the algae had settled, data were obtained at 100x total magnification by the field counting method using a Whipple micrometer (APHA op. cit.). Five randomly selected (see Guillard 1973, page 300) Whipple grid areas were tallied in each of 100 different S-R cells for a total of 500 counts. Each count included the total population and the numbers of individual plants (a filament or colony is one plant) of each of the five component taxa. Organisms touching or crossing the upper and the right hand boundaries of the Whipple grid were included in the tallies while those touching or crossing the lower or left hand boundaries were excluded from the tallies.

In this study, the time required to prepare a S-R cell for counting (excluding settling time; see discussion below)

Table 1. List of mathematical symbols.

Symbol	Definition
A	Estimated component of variance due to differences among S-R cells
CV	Coefficient of variation
k	Number of available S-R cells
M	Settling time for a S-R cell
m	Number of fields counted per S-R cell
m*	Integer just smaller than the calculated value of m
m* + 1	Integer just larger than the calculated value of m
n	Number of S-R cells studied
p	Half-width of confidence interval, expressed as fraction of mean
s	Time required for preparing, filling and cleaning a S-R cell
s_f	Time required for filling a S-R cell
T	Total time spent for a S-R cell analysis of a population
t	Time required for making a single Whipple grid tally
$t_{.05,n-1}$	Student's t at 5% significance level with n-1 degrees of freedom
V	Estimated variance of mean
W	Estimated component of variance due to differences among counts within S-R cells
$\bar{x}$	Mean of nm measurements
$\sigma^2_{\bar{x}}$	True variance of mean
σ^2_A	True component of variance due to differences among S-R cells
σ^2_W	True component of variance due to differences among counts within S-R cells

averaged 1 min; the time required to clean an S-R cell after use (see Guillard 1973, page 297 for cleaning instructions) averaged 2 min; and the time required to examine one Whipple grid area also averaged 2 min. Since similar times were required in counting raw plankton samples from Wisconsin lakes (unpublished data), the above times have been employed in making efficiency determinations.

The coefficient of variation (CV) of the mean has been employed as a statistical measure of the accuracy and reproducibility of a given counting regime. A low CV means greater accuracy and reproducibility than a high CV. A detailed summary of mathematical formulae and calculations appears in Appendix I at the end of the paper and a complete list of mathematical symbols appears in Table 1.

III. Procedural Results

A. Settling Time & Counting Technique

Settling time appears to depend upon the type of fixative used and upon the type of algae present. The iodine in Lugol's solution apparently facilitates settling (Guillard 1973), probably because of its high atomic weight and by speeding gas release from cells, whereas FAA does not appear to offer such advantages. In tests conducted on the experimental population and on some raw plankton samples from Wisconsin lakes, plants preserved with Lugol's solution required a maximum settling time of 7 min. while FAA preserved material required a maximum settling time of 10 min. Waiting for 15 min as recommended by APHA (1971) appears unnecessary in the samples tested. Observations made during these experiments suggest that taxa with large surface to volume ratios (e.g., certain species of *Staurastrum*) or taxa with gas vacuoles (e.g., certain Cyanophyta) settled more slowly than most other taxa.

Superficially, the strip counting technique would appear to offer more reliable results than the field counting technique since a much greater area of the S-R cell is counted. Closer investigation, however, reveals that the field counting technique is not only far less time consuming but is also more reliable (i.e., it results in a smaller coefficient of variation).

Consider the nature of a strip count involving the use of a Whipple grid whose width is 0.7 mm. at 100x magnification (this equals the grid width for the microscope employed in this study). Since the length of an S-R cell is 50 mm., each strip contains 71.4 Whipple grid areas, and if one follows APHA recommendations, 2-4 strips or 142.8-285.6 Whipple grid areas would be counted. Assuming 2 minutes are required to count each Whipple grid area, the counting of two strips would take 286 minutes (4 hours, 46 minutes) and the counting of four strips would take 571 minutes (9 hours, 31 minutes). In contrast, a field counting technique involving two Whipple grid tallies on each of 12 different S-R cells takes only 84 minutes (1 hour, 24 minutes), including the time necessary to prepare (1 minute) and clean (2 minutes) each slide. Moreover, the coefficient of variation (CV) for the above field counting regime on the experimental population examined during this study was 5.83%, while the comparable CV for the strip counting method was 13.33% for a 2 strip count and 13.27% for a 4 strip count (see Table 2).

Thus, the 2/12 field counting method requires less than a third (0.29) the time and gives a CV less than one half (0.43) as large as the two-strip counting technique. Therefore, the former appears to be by far the preferred method.

Table 2. Coefficients of variation (CV) of the mean of the experimental population for various combinations of n and m.

n	m	nm	CV	Comments
1	10	10	14.9	
1	24	24	13.9	
1	71.4	71.4	13.5	
1	142.8	142.8	13.3	
1	285.6	285.6	13.3	
2	10	20	10.5	Recommended by Welch (1948)
2	12	24	10.3	
3	30	90	8.0	Recommended by McAlice (1971)
4	6	24	7.9	
4	10	40	7.4	Recommended by Kutkuhn (1958)
5	5	25	7.3	
6	4	24	7.0	
8	3	24	6.4	
10	2	20	6.4	
10	3	30	5.8	
12	2	24	5.8	
15	1	15	6.5	
15	2	30	5.2	
15	3	45	4.7	
20	1	20	5.7	
24	1	24	5.2	

B. The Counting Regime

Since, as indicated above, recommendations for S-R cell counting regimes vary considerably in the existing literature, studies have been undertaken to develop a general procedure for deciding upon a particular counting regime and to determine which, if any, of the recommended schemes is to be preferred based on a comparison of coefficients of variation of the mean.

A S-R counting regime has two components: n, the number of slides studied, and m, the number fields per slide counted. To determine the coefficient of variation for a given combination of n and m, it is necessary to estimate the variance of the mean, V, which is given by the expression

(1) $V = A/n + W/nm$

where A is that component of the variance due solely to differences in algal densities among the various S-R cells and W is that component of the variance due solely to differences in the counts within a given S-R cell (Cochran 1953, chapter 10; see appendix I for further details on A and W). Once V has been determined, the coefficient of variation can be calculated from the formula

(2) $CV = 100\sqrt{V}/\bar{x}$

where $\bar{x}$ is the mean of the nm measurements.

Using $A = 8.06$, $W = 21.6$, and $\bar{x} = 21.5$ (calculated for the experimental population with $n = 100$ and $m = 5$ as described under 'Materials and Methods'), the CV values for different combinations of n and m have been calculated and are summarized in Table 2. The results strongly indicate that, in general, making fewer counts on each of a greater number of S-R cells gives more accurate results (based on CV values) than making a large number of counts on one or several S-R cells. Consider, for example, making a total of 24 counts. The CV value for 24 counts on one S-R cell is 13.9, for 6 counts on 4 cells, CV = 7.9; and for 2 counts on 12 cells, 5.8. The analysis also indicates that the regimes recommended by Kutkuhn (1958), McAlice (1971), and Welch (1948) provide less reliable data than does a regime involving 2 counts on each of 12 S-R cells. Moreover, the Kutkuhn and McAlice schemes involve total counts of 40 and 90 respectively, and this

Table 3. Cost analyses giving optimum n and m with time or precision limiting and with $t = 2$ minutes ($A = 8.06$, $W = 21.6$, $\bar{x} = 21.5$, $s = 3$, and $M = 10$).

	T	CV	p	m	n
$(k - 1)s \geq M$ or $k \geq 5$					
	63	6.7	.16	2	9
	126	4.8	.10	2	18
$k = 2$					
	59	7.6	.21	4	5
	158	4.6	.10	4	14
$k = 1$					
	63	9.9	.42	4	3
	294	4.6	.10	4	14

[a] The limiting value, time or precision, is underlined. If time, T, is limiting, it is made as close to 60 minutes as possible with balanced sampling. Precision is measured by the quantity p, where the 95% confidence limits are $\bar{x} \pm p\bar{x}$. If precision, p, is limiting, it is made as close to .10 as possible.

means that they require much more time to gather data than does a 2/12 regime.

McAlice (1971) got m = 25 from Table 3 of Brooks (1955) and increased this to m = 30 to insure detection of less frequently occurring species. The increasing m from 25 to 30 is of questionable value not only because of the difficulties involved in getting reliable data at the species level (see Kutkuhn 1958) but also because McAlice (1971) himself recommends the technique only for taxon populations $\geqslant 10^5$ cells/l. Moreover, the detection of taxa depends on the total number of fields examined (i.e. nm), not just on m, and increasing n will, therefore, have the same effect as increasing m with the added advantage of increasing precision. The use of Table 3 of Brooks (1955) is discussed below in connection with part *C*, efficiency.

A and W, and, hence, CV will vary for different samples and different techniques. However, greater variability in algal density among the S-R cells (or relatively larger A) will only increase the advantage of studying more slides. On the other hand, less variability in algal density among the S-R cells (or relatively smaller A) would favor using fewer slides. But the experimental population was well mixed, making unlikely, for all practical purposes, the drastic reduction in A that would be necessary to favor studying only 2 to 4 S-R cells, as recommended in the literature.

C. Efficiency

The cost of estimating algal density with S-R cells in terms of time and accuracy depends not only upon the values of A and W but also upon the following factors:

1. The desired precision of the mean (e.g., the value of CV);
2. The time required for preparing and cleaning of S-R cells (denoted by 's');
3. The time required for making an individual Whipple grid tally (denoted by 't');
4. The time available for making the total number of counts (denoted by 'T'; T = ns + nmt); and
5. The settling time (denoted by 'M').

Based on results of work on the experimental population

Table 4. Cost analyses giving optimum n and m with time or precision limiting and with t = 1 minute (A = 8.06, W = 21.6, $\bar{x}$ = 21.3, s = 3, and M = 10).

	T	CV	p	m	n
(k - 1)s $\geq$ M or k $\geq$ 5					
	60	5.7	.13	3	10
	90	4.7	.10	3	15
k = 2					
	64	6.3	.16	7	6
	124	4.5	.10	7	12
k = 1					
	57	9.2	.39	6	3
	228	4.6	.10	6	12

[a] The limiting value, time or precision, is underlined. If time, T, is limiting, it is made as close to 60 minutes as possible with balanced sampling. Precision is measured by the quantity p, where the 95% confidence limits are $\bar{x} \pm p\bar{x}$. If precision, p, is limiting, it is made as close to .10 as possible.

as well as on some raw plankton samples from Wisconsin lakes, values of s = 3 minutes (i.e., 1 minute for filling and 2 minutes for cleaning), t = 2 minutes, and M = 10 minutes appear to be reasonable estimates. Moreover, if $k \geq 1 + M/s_f$ where k is the number of S-R cells available and s_f is the filling time, the settling time can be ignored (see Appendix I for further details and for cases where M cannot be ignored.).

Knowing the values for s, t, A, and W, and assuming M can be ignored, the optimum value of m can be determined from the equation

(3) $m = \sqrt{Ws/At}$

Commonly the integer value of m will equal one. However, A and W, and hence m, will vary with different techniques of S-R cell preparation and with samples of differing composition as shown in Appendix I. It is important, therefore, to get data that allow estimating both A and W to see if the optimum m changes substantially. Consequently one should consider making m = 2 even when formal analysis gives m = 1 so as to allow some measure of variation within slides.

McAlice (1971) selected an initial m of 25 by consulting Table 3 of Brooks (1955). This implies that McAlice used only one S-R cell (k = 1) and thus could not use his 15 min settling time productively. Our results indicate that settling time can be ignored (and thus efficiency increased) if $k \geq 1 + M/s_f$ as shown above. McAlice implies he had a W/A ratio between 10.5 and 184.2. For our experimental population W/A = 2.7, and (based on our values for M, s, and t), Table 3 of Brooks (1955) gives a range for m of 1 to 4; and this is consistent with our results and recommendations. Thus, the difference between McAlice's recommendation of m = 30 and our recommendation of m = 2 or 3 stems from our assuming more than 1 S-R cell is available and from our having greater variability among S-R cells. Our Table 7 allows for choosing the optimum m for any number of S-R cells and for a range of W/A ratios.

The value of n, unlike m, is dependent upon both CV and T, and hence one cannot arbitrarily set limits on both precision (CV) and time (T). If time is the more important and, therefore, limiting factor, the optimum value of n for a specified T is given by the equation

(4) $n = T/(s + mt)$

whereas if precision is the more important and, therefore, limiting factor, the optimum n is given by the equation

(5) $n = (A + W/m)/V$

where $V = (\bar{x} \cdot CV/100)^2$ for a specified value of CV. An alternative way of determining n where precision is defined in terms of confidence intervals rather than CV is presented in Appendix I. Tables 3 and 4 summarize results of cost analyses for the experimental population given different restrictions of time and precision.

IV. Parametric vs. Nonparametric Tests

The choice of parametric or nonparametric procedures in testing for statistically significant differences depends both upon the nature of the data and upon the relative advantages and limitations of the two approaches. As a basis for discussion, consider the data in Table 5, which

Table 5. Summary of S-R cell data for five samples from the experimental population using a m = 2, n = 12 counting regime. Samples 1 to 3 were taken from the original population; samples 4 and 5 were taken from the original population after dilution and concentration, respectively.

Sample and organism	Sums of two counts on each Sedgwick-Rafter cell											
	1	2	3	4	5	6	7	8	9	10	11	12
Sample 1												
Micrasterias	3	3	3	3	0	4	0	2	1	3	5	0
Netrium	1	2	1	1	1	1	1	4	1	2	2	0
Scenedesmus	22	37	17	23	13	21	32	27	22	21	26	17
Sphaerozosma	2	4	5	5	2	2	0	2	3	4	4	2
Staurastrum	8	9	7	16	10	13	15	11	6	12	12	11
TOTAL	36	55	33	52	26	41	48	46	33	42	49	30

Table 5 continued

Sample 2												
Micrasterias	3	2	4	3	5	2	3	4	1	4	4	4
Netrium	0	0	0	0	1	0	2	2	2	1	0	1
Scenedesmus	16	29	26	22	24	28	26	21	29	42	32	18
Sphaerozosma	3	1	2	2	1	1	3	1	2	2	6	2
Staurastrum	19	9	6	17	12	16	15	8	8	19	16	13
TOTAL	41	41	38	44	43	47	49	36	42	68	58	38
Sample 3												
Micrasterias	1	1	5	2	1	4	12	1	2	2	2	2
Netrium	2	0	1	0	0	1	1	1	2	0	0	0
Scenedesmus	34	22	31	27	29	27	18	23	29	26	15	17
Sphaerozosma	5	2	2	3	7	5	1	5	7	1	4	3
Staurastrum	9	9	13	14	16	9	8	11	13	13	13	9
TOTAL	48	34	52	46	53	46	30	41	53	42	34	31
Sample 4												
Micrasterias	1	1	0	1	2	1	1	3	0	2	2	2
Netrium	0	0	0	0	0	0	1	0	2	1	0	0
Scenedesmus	3	5	10	9	10	7	9	13	10	12	11	11
Sphaerozosma	1	2	1	2	1	0	2	3	2	0	1	0
Staurastrum	2	11	7	2	3	5	4	5	4	2	3	5
TOTAL	7	19	18	14	16	13	17	24	18	17	17	18
Sample 5												
Micrasterias	5	2	8	6	1	5	2	2	1	1	5	3
Netrium	0	3	1	1	1	0	0	1	1	1	1	1
Scenedesmus	35	26	21	25	23	30	29	22	21	34	32	32
Sphaerozosma	7	7	6	7	6	5	4	3	2	3	3	3
Staurastrum	7	19	18	20	13	17	13	14	9	9	14	13
TOTAL	54	57	54	59	44	57	48	42	34	48	55	52

was generated from the experimental population by means of a $m = 2$, $n = 12$ counting regime, and assume one wishes to know whether significant differences occur among the population densities of the samples for the total population and for each organism.

Because parametric procedures are applicable only to

approximately normally distributed data, and because such data cannot always be assumed for S-R cell work (Kutkuhn 1958, McAlice 1971, Serfling 1949), tests such as the Lilliefors test (Conover 1971, p. 302) must first be conducted to determine if the data are normally distributed. For cases where the test indicates non-normal distribution, efforts can be made to transform the data to an approximately normal distribution (see Kutkuhn 1958, McAlice

Table 6. Results of parametric and nonparametric analyses of data in Table 5.

	Lilliefors test			Probabilities associated with test statistics	
				True status of null hypothesis that no differences exist	
Organism	Best transformation[a]	Probability	Statistical test[b]	True[c]	False[d]
Micrasterias	logarithm (x + 2)	>>.20	Parametric	.093	.011
			Nonparametric	.071	.036
Netrium	logarithm (x + .1)	>.20	Parametric	.052	.069
			Nonparametric	.11	.11
Scenedesmus	logarithm (x + .1)	>>.20	Parametric	.52	$5.6 \cdot 10^{-11}$
			Nonparametric	.48	$6.7 \cdot 10^{-6}$
Sphaerozosma	logarithm (x + 1)	>.20	Parametric	.14	.000016
			Nonparametric	.099	.00019
Staurastrum	logarithm (x + .1)	>>.20	Parametric	.41	$4.2 \cdot 10^{-9}$
			Nonparametric	.35	$1.7 \cdot 10^{-5}$
TOTAL	logarithm (x + .1)	>>.20	Parametric	.43	$9.5 \cdot 10^{-4}$
			Nonparametric	.67	$2.3 \cdot 10^{-6}$

[a] Lilliefors tests were made on 36 observations from a single population (samples 1, 2, and 3 of Table 5) using the original data and the following transformations: $\sqrt{x}$, $\sqrt{x + .5}$, $\sqrt{x + 1}$, $\ln(x + .1)$, $\ln(x + .5)$, $\ln(x + 1)$, $\ln(x + 2)$. Under "Best transformation" is the transformation giving the closest approximation to a normal distribution.

[b] The parametric test is the one-way analysis of variance with data transformed using the transformation listed under "Best transformation." The nonparametric test is the Kruskal-Wallis test, with the probability associated with the test statistic (corrected for ties) estimated using a chi-square approximation.

[c] Analysis based on samples 1-3 in Table 5, all of which represent aliquots of the same population.

[d] Analysis based on samples 3-5 in Table 5, each of which represents a different population.

1971), but such transformations are not always possible (e.g., Kutkuhn 1958, page 73), especially in cases where the means approach zero. For the samples in Table 5, transformations appear to be possible in all cases, once the proper transformation functions have been determined (see Table 6).

Nonparametric procedures, in contrast, are less distribution-dependent. As a result they offer two distinct advantages: 1) they can be used for a wider range of data, and 2) they can be applied directly without any preliminary testing or transforming. Furthermore, the nature of the data may be such that nonparametric tests are the only ones which can be applied.

Where the data are approximately normally distributed or can be transformed, the choice between nonparametric or parametric tests for S-R cell analysis also involves a consideration of the asymptotic relative efficiency (A.R.E.) of particular nonparametric tests with their parametric counterparts. If only two samples are involved, one can test for statistically significant differences by using either the parametric t-test or the nonparametric Mann-Whitney test (or the Wilcoxon rank sum test). If more than two samples are involved, one can test for statistically significant differences by using either the parametric F test or the nonparametric Kruskal-Wallis test. In both cases, the A.R.E. of the nonparametric test relative to the parametric test for normally distributed data is 0.955 (Conover 1971, pages 235 and 262). Roughly this means that if a parametric test of a given power and level of significance requires 96 observations on each population, the nonparametric test of the same power and level of significance would require 100 observations on each population. Thus, nonparametric tests are almost as powerful as their parametric counterparts.

Analyzing the same data (Table 5) parametrically and nonparametrically illustrates the above point (see Table 6). As shown there, results of nonparametric tests agree with those of parametric tests in all cases in showing or not showing significance at the 5% and 1% levels. When the null hypothesis that no differences exist among samples

Table 7. Summary of equations to be used in cost analyses for various conditions of k.

Equation for	$k = 1$	$k > 1$ but $(k - 1)s < M$	$k > 1$ but $(k - 1)s \geq M$
$T =$	$n(s + M) + nmt$	$M - 2(k - 1)s + ns + nmt$	$ns + nmt$
$V =$	$A/n + W/nm$	$A/n + W/nm$	$A/n + W/nm$
$m =$	$\sqrt{W(s + M)/At}$	The larger of the quantities $\sqrt{Ws/At}$ or $[M/(k - 1) - s]/t$	$\sqrt{Ws/At}$
n (time limiting)	$T/(s + M + mt)$	$[T - M + 2(k - 1)s]/(s + mt)$	$T/(s + mt)$
n (precision, defined by CV, limiting)	$(A + W/m)/V$	$(A + W/m)/V$	$(A + W/m)/V$
n (precision, defined by confidence interval, limiting)	$t^2_{.05,n-1}\ (A + W/m)/(p\bar{x})^2$	$t^2_{.05,n-1}\ (A + W/m)/(p\bar{x})^2$	$t^2_{.05,n-1}\ (A + W/m)/(p\bar{x})^2$

is true (i.e., among samples 1-3 in Table 5), the probabilities from the nonparametric and the parametric tests are similar and indicate no significant differences. When the null hypothesis that no differences exist among samples is not true (i.e., among samples 3-5 in Table 5), the probabilities from the nonparametric tests are all larger than those from the parametric tests. Thus, the nonparametric test is more conservative. However, for probabilities in the range .05-.01 (e.g., for *Micrasterias* and *Netrium* in Table 6) the tests give equivalent results. The only dramatic differences occur for probabilities much less than .001 (e.g., for *Scenedesmus* and *Staurastrum* in Table 6), but since both tests give overwhelming evidence of real differences among the samples, the differences in probabilities are of no practical importance.

Assuming normally distributed data, two conclusions can be drawn from the above: 1) nonparametric tests are nearly as effective as parametric tests in detecting significant differences; and 2) nonparametric tests are slightly more conservative than parametric tests; i.e., any significant difference detected by a nonparametric test will also probably be detected by the parametric counterpart, whereas in a few borderline cases only the parametric test will show significant differences.

In view of the facts that nonparametric procedures can be applied in all situations without testing for the presence of approximately normal distributions and without attempting to make transformations, and because they are nearly as efficient as their parametric counterparts (indeed, they can be even more efficient where the data is not normally distributed; see Conover 1971), nonparametric tests generally appear to be more satisfactory than parametric tests for analyzing Sedgwick-Rafter cell counts.

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Appendix I

This appendix presents details for the derivation of the formulae used in the main body of the paper. In addition, it provides a method for determining which integer to use when the calculated m is not a whole number, and it indicates how a cost analysis can be performed when the number of Sedgwick-Rafter cells, k, is limited. The mathematical symbols used are summarized in Table 1. The material presented, though independently derived, is an extension of that in Cochran (1953, chapter 10).

A. Derivation of Formulae

Let n be the number of slides studied, m, the number of

counts made on each slide, and x_{ij}, count j on slide i, where $j = 1, ..., m$, and $i = 1, ..., n$. One can use the mean of all the counts,

$$\bar{x} = \sum_{i=1}^{n} \sum_{j=1}^{m} x_{ij}/nm,$$

to estimate the density of algae if the volume represented is known. The variance of the mean is a measure of the precision of the estimator. The smaller the variance, the better the estimator. The variance of the mean is

$$\sigma^2_{\bar{x}} = \sigma^2_A/n + \sigma^2_W/nm \quad (1)$$

where σ^2_A is that component of the variance due solely to differences among densities on different slides and σ^2_W is that component of the variance due solely to differences among counts within a given slide (Cochran, 1953). Using a preliminary set of data (x_{ij}; $i = 1, ..., n$; $j = 1, ..., m$), one can estimate the components of variance with statistics from an analysis of variance testing for differences among the slides:

$$W = \hat{\sigma}^2_W = MS_W \quad (2)$$

$$A = \hat{\sigma}^2_A = (MS_A - MS_W)/m \quad (3)$$

where

$$MS_W = \sum_{i=1}^{n} \sum_{j=1}^{m} (x_{ij} - \bar{x}_i)^2/(nm - n) \quad (4)$$

with

$$\bar{x}_i = \sum_{j=1}^{n} x_{ij}/m \quad (5)$$

and

$$MS_A = \sum_{i=1}^{n} (\bar{x}_i - \bar{x})^2/(n - 1) \quad (6)$$

are mean squares measuring variation within and among slides respectively (Sokal and Rohlf, 1969). Using the estimator of variance components one can estimate the variance of the mean by

$$V = A/n + W/nm \quad (7)$$

The coefficient of variation can then be determined from

$$CV = 100\sqrt{V}/\bar{x} \quad (8)$$

If the total number of counts to be made, nm, is fixed and the relative costs of making a slide and of making a count on a slide are ignored, the variance of $\bar{x}$ is minimized by making n as large as possible or, equivalently, making m as small as possible, i.e., $m = 1$. Setting $m = 1$, however, will not always give the most precise estimator of algal density if time is limited.

To determine the best choice of n and m the cost, in time, of collecting the data must be considered. Let T be the total time spent studying a sample; then

$$T = ns + nmt \quad (9)$$

where s is the time needed to make a slide and t is the time required to make a count on a slide. In practice, slides need a minimum settling time, M, before counting can begin. Thus, after the first slide is made one must wait at least M units of time before starting to count. If this time can be used to make additional slides (i.e., if $(n-1)s \geqslant M$), M can be ignored in the cost equation, and this has been done in equation 9.

If one assumes $(n-1)s \geqslant M$, then the optimum choice of m and n is such as to minimize V (equation 7) and T (equation 9) simultaneously. To obtain the desired minimization, equation 7 indicates that m and n should be made larger and equation 9 indicates the reverse. Also, if the total number of counts, nm, is fixed, equation 7 indicates that n should be increased and equation 9 indicates the opposite. Clearly a compromise is necessary.

If the total time for analysing a sample is fixed, T is constant, and using equation 9, n can be expressed as a function of m, namely $n = T/(s + mt)$. Substituting this expression for n in equation 7 gives

$$V = [A(s + mt) + W(s + mt)/m]T. \quad (10)$$

To get the value of m which minimizes the estimated variance of the mean, V, the derivative of V with respect to m is set equal to zero, and the equation is solved for m:

(11) $dV/dm = (At - Wsm^{-2})/T = 0$

and

(12) $m = \sqrt{Ws/At}$

Substituting expression 12 in d^2V/dm^2 shows that the positive root of Ws/At minimizes V.

Thus, the best m is independent of both V and T and depends only upon two ratios, namely the within to among slide variation and the time needed for making a slide to the time needed for making a count. Equation 12 is intuitively reasonable, since the number of counts per slide, m, increases as either the variability within a slide, W, or the cost of making a new slide, s, increases.

Once m is known, the value of n can be determined by solving equation 9 for n if a given time, T, is specified, i.e.,

(13) $n = T/(s + mt)$

or by solving equation 7 for n if a given degree of precision, V, is specified, i.e.,

(14) $n = (A + W/m)/V.$

An alternative way of having precision determine n is to use confidence intervals rather than coefficients of variation. The number of slides, n, must be such as to give 95% confidence limits on the mean approximately equal to $\bar{x} \pm p\bar{x}$, where p is an arbitrary number, e.g., p = .1. If the data are approximately normally distributed, the 95% confidence limits are $\bar{x} \pm t_{.05,\, n-1}\ s_{\bar{x}}$, where $t_{.05,\, n-1}$ is Student's t at the 5% significance level with n − 1 degrees of freedom and $s_{\bar{x}}$ is the standard deviation of the mean (Sokal and Rohlf, 1969). Estimating $s_{\bar{x}}$ by $\sqrt{V}$ gives

(15) $p\,\bar{x} = t_{.05,\, n-1}\ \sqrt{V}$

or

(16) $V = p^2\,\bar{x}^2/t^2_{.05,\, n-1}$

Substituting expression 16 in equation 7 and solving for n gives

(17) $n = t^2_{.05,\, n-1}\ (A + W/m)/(p^2\,\bar{x}^2).$

Substituting values of Student's associated with different values of n until the right-hand expression of equation 17 approximately equals the n of Student's t gives the required n.

B. The Integer Value of 'm'

Since practical considerations dictate that the same number of counts, m, be made on each Sedgwick-Rafter cell, it will be necessary to convert the calculated value of m (equation 12) to either the integer just smaller, m*, than or just larger, m* + 1, than m itself. The choice of m* or m* + 1 depends on which minimizes the estimated variance of the mean, V. Let V_0 and V_1 be the variances obtained by substituting m* and m* + 1 respectively into equation 10. If $V_0 < V_1$ the integer m* is preferred, whereas if $V_0 > V_1$ the integer m* + 1 is preferred. These relations are equivalent to choosing m* if m* (m* + 1) is greater than Ws/At and m* + 1 otherwise.

C. Cost Analysis for a Limiting 'k'

In cases where the number of available Sedgwick-Rafter cells, k, is limited such that (k − 1)s < M, the settling time, M, cannot be used fully to make new slides. Therefore, M must be taken into consideration in computing the cost in time of analyzing a sample, and equation 9 must be modified accordingly. If only one S-R cell is available (k = 1), the settling time can be included in the cost of making a slide, and equation 9 becomes

(18) $T = n(s + M) + nmt$

and the cost analysis is as in part A of the appendix with s + M substituted for s.

If k > 1 but (k − 1)s < M, equation 9 becomes

(19) $T = s + M - (k-1)s + k(mt + s) - ks$
$+ (n/k - 1)[\text{Positive}\,(M - (k-1)(mt + s)) + k(mt + s)]$

where the function 'Positive' takes on the value zero or [M − (k − 1) (mt + s)] if the latter expression is negative or positive, respectively. The function Positive [(M − (k − 1) (mt + s)] represents time wasted to allow for settling in the interval between the end of counting and refilling one batch of k slides and the start of counting and refilling the next batch. Optimization requires that this time either be eliminated or put to use.

Since the time cannot be eliminated because the slides must settle, and since the time cannot be used to make additional slides because k is limited, the only alternative

is to spend the time making more counts on each of the available slides. Therefore, m must be made large enough to make the function Positive $[M-(k-1)(mt+s)]$ zero, that is

(20) $$M-(k-1)(mt+s) \leqslant o$$

or

(21) $$m \geqslant [M/(k-1)-s]/t.$$

Hence, one need only consider the simpler version of the cost function represented by equation 19 where Positive $[M-(k-1)(mt+s)]$ is zero:

(22) $$T+M-2(k-1)s+ns+nmt$$

Equation 22, however, is equivalent to equation 9 with T replaced by $T-M+2(k-1)s$. Therefore, the optimum m is the same as before and can be computed from equation 12 with the restriction that m must also satisfy equation 21.

A summary of the sequence of equations to be used for various conditions of k appears in Table 7.

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MASTOPHOROPSIS CANALICULATA (HARVEY IN HOOKER) GEN. ET COMB. NOV. (CORALLINACEAE, RHODOPHYTA) IN SOUTHERN AUSTRALIA

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Mastophoropsis canaliculata (Harvey in Hooker) gen. et comb. nov. (Corallinaceae, Rhodophyta) is restricted to south-eastern Australian waters. It is unique among Corallinaceae in possessing an erect, tenacular, branched, taeniform, non-geniculate thallus which produces multiporate tetrasporangial conceptacles. Based on a detailed morphological and anatomical study, including an examination of the designated lectotype, this taxon is referred to the tribe Phymatolitheae in the subfamily Melobesioideae and its relationships to other non-geniculate Corallinaceae are discussed. A simplified microtechnique procedure involving decalcification with nitric acid, resin embedding and staining serially mounted sections with $KMnO_4$ also is outlined. X-ray microanalysis of surface tissues indicates that calcification occurs largely as $CaCO_3$ and that various structures contain substantially differing amounts of Ca.

Setchell (1943), in his treatment of the Mastophoroideae (Corallinaceae, Rhodophyta), established the genus *Metamastophora* for two southern African and three southern Australian species, the latter including *M. flabellata* (Sonder) Setchell—the type species, *M. canaliculata* (Harvey in Hooker) Setchell, and *M. plana* (Sonder) Setchell. Because specimens of only one (*M. flabellata*) of the five species were available to Setchell, he regarded his "outline" as tentative and recognized the need for further detailed studies. As an apparent consequence, Johansen (1976, p. 232) placed *Metamastophora* among a group of poorly known or unclearly understood genera of the Corallinaceae.

During the initial phases of morphosystematic and ecological investigations of non-geniculate Australian Corallinaceae, the type and other specimens of *M. canaliculata* became available for study, and examination of the material has led to the conclusion that this taxon must be removed from *Metamastophora* and the Mastophoroideae and placed in the Melobesioideae as the type and only known species of *Mastophoropsis* gen. nov. This report provides a morphosystematic account of *Mastophoropsis canaliculata* (Harvey in Hooker) comb. nov. and considers its relationships to other genera of non-geniculate Corallinaceae. Details of a simplified microtechnique procedure utilizing resin embedding are also included.

MATERIALS AND METHODS

MICROTECHNIQUE

Formalin fixed, alcohol preserved and dried material all were decalcified in 0·6 N nitric acid. Following dehydration through 30, 60, 90 and 100% ethanol at 10 min intervals, material

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was transferred to epoxy propane for 90 min and then embedded in Spurr's resin (vinylcyclohexene dioxide, 5 g; diglycidyl ether of polypropylene glycol, 3·5 g; nonenyl succinic anhydride, 13 g; dimethylaminoethanol, 0·2 g) according to the following schedule:

(1) 1:1:: epoxy propane:Spurr's resin—12 h or overnight.
(2) Spurr's resin —8 h.
(3) Fresh Spurr's resin —12 h or overnight.

Material of suitable size was then placed in "boats". Fresh Spurr's resin was added to the "boats" and allowed to harden at 70°C for 12–24 h. Sections 6–12 μm thick were cut with a steel knife, placed serially on slides, stained for 10–20 min in 2% aqueous $KMnO_4$, and mounted in Eukitt (MgF: O. Kindler, Freiburg, W. Germany).

The above procedure provides permanent, serial mounts without the use of the mercury containing Sousa's solution (Adey & Adey, 1973; Cabioch, 1971a; Johansen, 1973;—see Suneson, 1937 for formula) and without employing chloronated acids for decalcification (Gordon et al., 1976; Lebednik, 1977) which, if used after formalin preservation, can lead to the production of bis-chlormethylether, a potentially powerful carcinogen. Comparisons of material decalcified in nitric acid alone and in the commonly used Pyrenyi's solution (Cabioch, 1971a; Chamberlin, 1977; Mason, 1953;) which contains chromic acid and ethanol in addition to nitric acid indicate that 0·6 N nitric acid alone was as effective as Pyrenyi's solution and resulted ultimately in tissue sections of equal quality.

Attempts to employ freeze microtome sections (see Chamberlin, 1977; Dawson, 1960) proved unsatisfactory; either sections were too thick, or the more delicate tissues (e.g. conceptacle roofs) were easily damaged during sectioning or subsequent processing.

SCANNING ELECTRON MICROSCOPY AND X-RAY MICROANALYSIS

Dried specimens were mounted on stubs with "dag 915" (Acheson Colloids Co., Plymouth, England), shadowed with carbon or with gold–palladium during rotation through 360° in an Edward's "Speedivac" 12E6 vacuum evaporator, and examined in a Siemens ETEC-Autoscan scanning electron microscope at 20 kV. X-ray microanalysis was carried out on both carbon and silver coated tissues using an Edax energy dispersive analyser Si(Li) detector with the above SEM unit at 20 kV. Further X-ray microanalysis details are provided in the results section (Table III).

MASTOPHOROPSIS GEN. NOV.

DIAGNOSIS

Thallus non-geniculatus, haptero basili affixus, axibus ascendentibus ramosis complanatis dorsiventralibus. Thallus constitutus est medulla non-coaxiali filamentosa multistratosa biextrorsa, et cortice dorsali cellulis elongatis gradatim ascendenti et epithallis unistratosis non-pigmentiferis dorsalibus ventralibusque. Meristema subepitheliale in apicibus ramorum. Conjunctiones cellularum praesentes; conjunctiones secundariae non-visae. Structurae reproductivae dorsaliter natae; conceptacula tetrasporangialia multiporosa, tecta conceptaculorum cellula 4 plo crassiora, cellulis-pororum absentibus; primordia conceptaculorum in perithallo adventitia.

Thallus non-geniculate, anchored by a basal holdfast and producing ascending, branched, flattened, dorsiventral axes; structurally composed of filaments forming a multistratose, biextrorse, non-coaxial medulla, a dorsal, ascending cortex with progressively elongate cells, and unistratose non-pigmented dorsal and ventral epithallia. Meristem sub-epithallial in the cortex. Cell fusions present; secondary pit connections not apparent. Reproductive structures borne on dorsal surface; tetrasporic conceptacles multiporate with conceptacle roofs more than four cells thick and lacking pore cells; conceptacle primordia arising in the meristem.

Type Species: *Mastophoropsis canaliculata* (Harvey in Hooker) comb. nov. Basionym: *Mastophora canaliculata* Harvey in Hooker 1860: 310.

OBSERVATIONS

TYPIFICATION, DISTRIBUTION

Harvey (1860) did not specify a holotype but based his protologue on a series of plants from Tasmania (collected by C. Stuart) and Port Fairy, Victoria (collected by W. H. Harvey). Most of the syntypes were assigned number 443 in

Harvey's Algae Australiae Exsiccatae (Harvey 1860), including four (two Tasmanian, two Victorian) of the seven syntypes in TCD. The best preserved of the four (a Tasmanian specimen) has been chosen as lectotype (Fig. 1). All seven TCD syntypes possess tetrasporic conceptacles. Additional isotypes occur in MEL and the Mitchel Library in Sydney, and still others may exist in other herbaria (Ducker, 1977; Blackler, 1977; May, 1977).

The species appears to be restricted geographically to south-eastern Australian waters. Collections are known from Cape Lannes, Nora Crena, Port McDonnell, and Robe in South Australia; from Port Fairy, Port Phillip Bay, Warratah Bay, Warrnambool and Waterloo Bay (Wilson's Promontory) in Victoria; and from an unspecified locality in Tasmania. Except for one plant in a mid-littoral tidepool in a cave entrance (Cape Lannes) and a population of 21 epilithic plants gathered from a depth of 10 m (Waterloo Bay), all collections originated from the drift, and it seems likely that this taxon normally grows in deeper waters. Specimens have been obtained in March, April, May, August, September and October suggesting that it probably occurs throughout the year. Pertinent systematic data including synonomy and a list of specimens examined is summarized in Table I.

TABLE I. Pertinent systematic data on *Mastophoropsis canaliculata* (Harvey in Hooker) comb. nov.

Synonomy & References:

Mastophora canaliculata Harvey in Hooker, 1860: 310. De Toni, 1905: 1776; 1924: 695. Guiler, 1952: 87. Harvey, 1863: XXXI, pl. 263. Lucas, 1909: 56; 1913: 163. Lucas & Perrin, 1947: 391, Fig. 198. Printz, 1929: 47, pl. 73, Figs. 10–12. Reinbold, 1898: 54. Rosanoff, 1866: 13. Sonder, 1880: 20.

Metamastophora canaliculata (Harvey in Hooker) Setchell, 1943: 132. May 1965: 357.

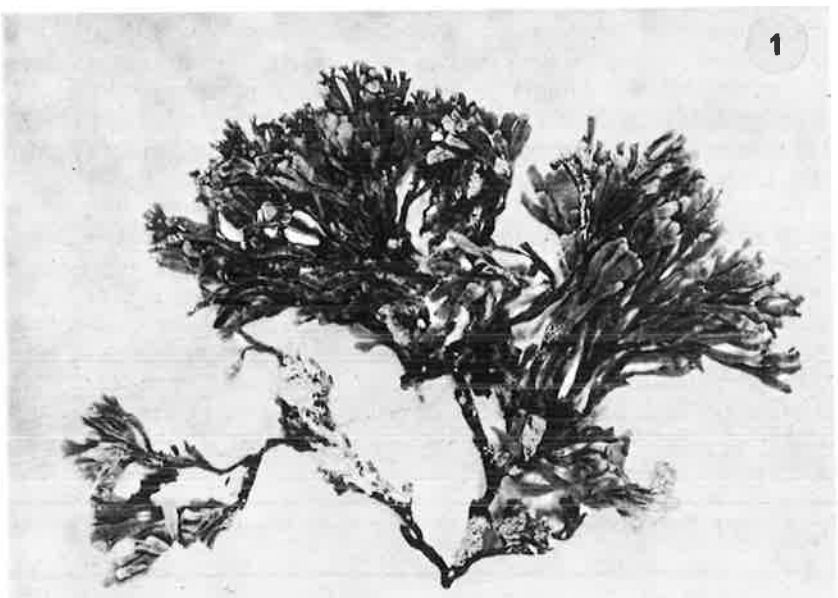
Type Locality: Tasmania.

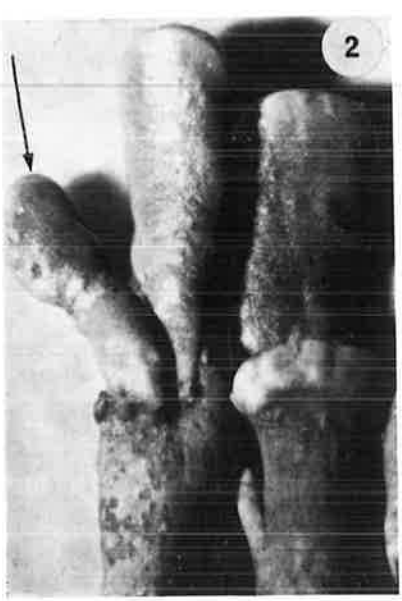
Type: TCD. See text and Fig. 1.

Specimens examined: ADU—A 10,901a; A 11,019B; A 18,975; A 21,525; A 22,916; A 23,001. LTB (current location of author's personal herbarium)—WJW 182; WJW 10,264—a total of 21 plants in 2 populations. MEL—516730; 516731; 516732; 516733; 516734; 516735; 516736; 516737. MELU—4595; G.K. 4235. TCD—Nine unnumbered specimens on two different sheets; annotations attached. UWA—2550.

EXTERNAL MORPHOLOGY

One to several non-geniculate, compressed to flattened erect axes arise from an irregularly discoid to applanate holdfast and produce moderately to profusely branched plants up to 15 cm tall (Fig. 1). Lateral branches normally arise apically in an irregular and/or dichotomous to polychotomous manner, but adventitious branches can arise from the dorsal surface, usually just posterior to points of wounding or severed axes (Fig. 2). Lower portions of axes are of relatively uniform width and rarely exceed 2·5 mm, while apical portions commonly are slightly to moderately expanded, reaching widths up to 7 mm near points of polychotomy. Tips of ultimate laterals commonly are slightly or moderately flabelliform and up to 5 mm broad (Fig. 3). A complete summary of vegetative morphological and anatomical measurements appears in Table II.





FIGS 1–3. *Mastophoropsis canaliculata*. Fig. 1. Lectotype specimen in TCD. ×1·5. Fig. 2. Adventitious branch (arrow) near apex of severed axis. ×14. Fig. 3. Flabelliform and linear branch apices with concentric channel-like markings on dorsal surface. ×16.

Both dorsal and ventral surfaces of younger axes commonly but not invariably are traversed by a series of minute, concentric, anteriorily convex channel like markings (Figs 3, 5) from which the specific epithet is derived. Whether these markings delimit successive zones of growth behind the apices remains uncertain. Some axes also possess ventral ridge like thickenings about the apices and lateral margins (Fig. 4). While apical ridges appear to be the result of $CaCO_3$ deposits (see below), the lateral ridges represent the thickened margins of axes. Although axes commonly become more or less laterally involute upon drying (Fig. 4), they are almost always flat in living or liquid preserved specimens. Axes may also possess more or less median vein-like markings (Fig. 5) which arise at varying distances behind the apices, usually broaden towards the base (sometimes encompassing the entire axis width), and occasionally become costellate on older axes. In dried plants veins are usually more conspicuous ventrally than dorsally and are differentiated from surrounding tissues by a distinctly darker colour. The transverse channels, apical and lateral ridges, and median veins all occur unpredictably and in varying combinations and thus appear to have little systematic significance.

TABLE II. Summary of morphological and anatomical measurements of vegetative structures of *Mastophoropsis canaliculata*

Character	Unit	Range*
Plant height†	cm	5–15
Lower axis width	mm	1–3
Upper axis width	mm	(1–) 2–4 (–7)
Branch tip width	mm	(0·75–) 1–3 (–5)
Medulla: Cell length (l.s.)	μm	12–30 (–40)
Cell diameter (l.s.)	μm	5–9 (–12)
L/D	ratio	(1·75) 2–5 (–7·5)
Dorsal cortex:		
Meristematic cells: Length (l.s.)	μm	5–12
Diameter (l.s.)	μm	3–12
L/D	ratio	0·5–1·5 (–2)
Elongating cells: Length (l.s.)	μm	10–20
Diameter (l.s.)	μm	5–12
L/D	ratio	1·5–3·5
Ventral cortex:		
Cell length (l.s.)	μm	8–20
Cell diameter (l.s.)	μm	5–10
L/D	ratio	1–4
Dorsal epithallium (t.s.)		
Cell diameter	μm	5–12
Cell height	μm	4–9
H/D	ratio	0·3–1 (–1·5)
Ventral epithallium (t.s.)		
Cell diameter	μm	(5–) 8–15
Cell height	μm	(5–) 8–15
H/D	ratio	(0·5–) 1–1·7

* Extreme range values are given in parentheses.
† Based on entire, fertile plants.

FIGS 4–6. *Mastophoropsis canaliculata*. Fig. 4. Ventral view of branch tips showing apical ridges of $CaCO_3$. ×5. Fig. 5. Ventral view of older axes with median vein-like markings. ×7. Fig. 6. Group of tetrasporic conceptacles near branch tip. ×14.

Active deposition of calcium carbonate appears to be confined to the branch apices, which commonly are whitish in colour and sometimes possess distinct ventral and/or dorsal calcareous ridges (Fig. 4). Branch tips appear more or less uniformly calcified, but older axes commonly become roughened and irregularly foveate, apparently as a consequence of partial loss of the $CaCO_3$ deposits. Veins likewise appear to be relatively depleted of $CaCO_3$ deposits and the holdfast and lowermost axes of many plants appear totally devoid of surface deposits. These calcium-poor regions generally appear distinctly darker red in colour than areas with greater calcium concentrations.

TABLE III. X-ray microanalysis ratios indicating relative surface calcium content in various *Mastophoropsis* tissues

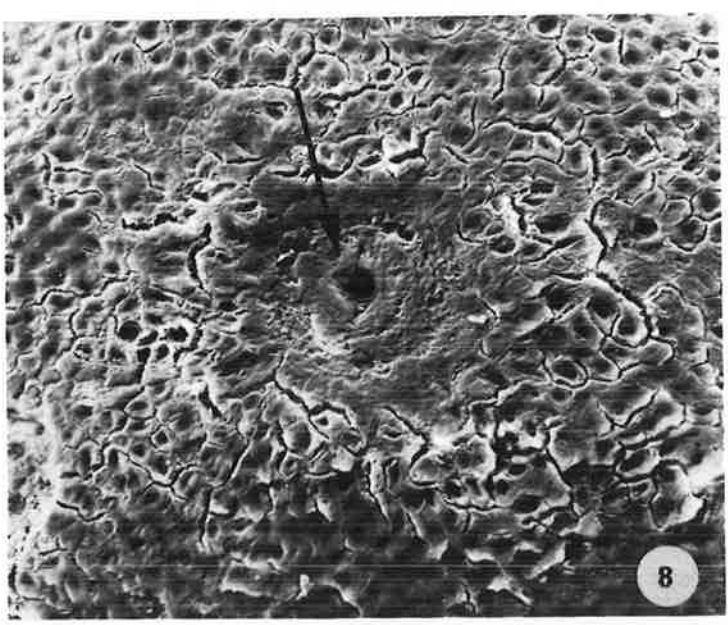
Specimen coating	Branch tip	Lamina	Vein
Carbon*	12·56 [0·43]	10·04 [0·36]	6·94 [0·11]
Silver†	0·246 [0·023]	0·190 [0·031]	0·124 [0·005]

* Means of 6 values ($S_{\bar{x}}$ given in brackets) of peak: background ratio. Ca (Kα) window centred at 3660 eV, background at 3380 eV, both 260 eV; 100 s counts; irradiated area of 105·6 μm^2.

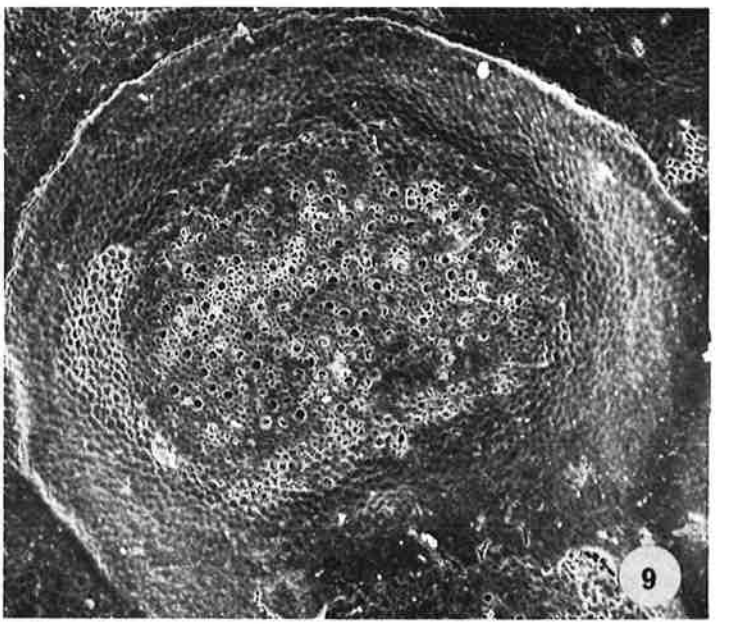
† Means of 6 values ($S_{\bar{x}}$ given in brackets) of Ca: Ag (peak: background) ratio. Ca(Kα) window centred at 3660 eV, Ag (Lα) window centred at 2980 eV, background window centred at 3460 eV, all 220 eV; 100 s counts; irradiated area of 105·6 μm^2.

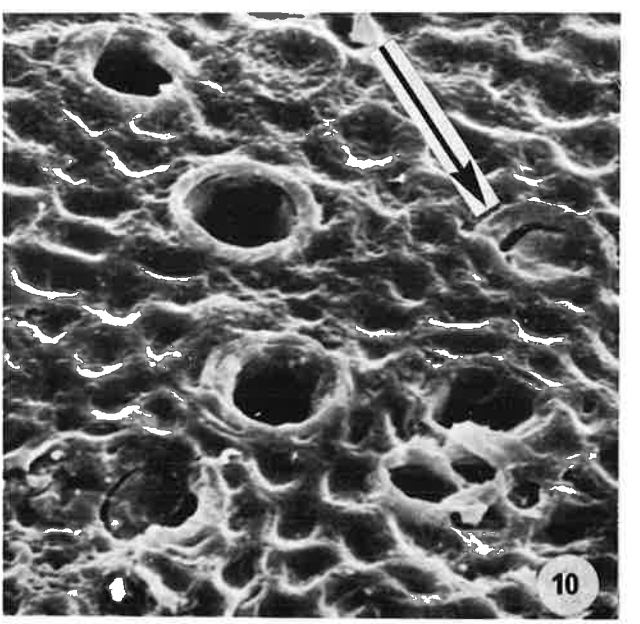
Results of X-ray microanalyses (Table III) of branch apices, laminae (non-vein portions of axes) and veins confirm these observations. The carbonate deposits are almost exclusively $CaCO_3$ (magnesium levels are very low) and based on mean values per μm^2, older axes contain only 75–80% of the surface Ca^+ deposit found at the branch apices, and veins contain only 50–55% of the surface Ca^+ found in branch apices. Assuming these tissues all were calcified at the time of their formation, subsequent decalcification may have resulted from localized secretion of hydrogen ions (K. S. Rowan, personal communication), but the source and function of such an activity has yet to be documented experimentally. Decalcification is also known to take place during geniculum maturation and conceptacle formation in the articulated Corallinaceae (Johansen, 1974), but precise mechanisms apparently are not understood.

Gametic and tetrasporic conceptacles arise solely on the dorsal surface and occur singly or in small clusters near the branch apices and/or along the younger axes. In some cases, conceptacles become so crowded as to appear partially fused with one another (Fig. 6). Conceptacles vary in outline from circular to irregularly ellipsoidal to angular, are up to 1000 μm in maximum breadth and protrude conspicuously (up to 450 μm) above the surrounding thallus surface. Table IV summarizes numerical data relating to reproductive structures. Gametic conceptacles are more or less conoidal and possess a single apical pore which is circular to triangular in surface view (Figs 7, 8). Tetrasporic conceptacles, in contrast, are more or less frustoidal, with a multiporate top surface (Fig. 9). The pores (Fig. 10) are irregularly disposed, are blocked initially by mucilaginous plugs, possess a distinct rim, and appear to have polygonal side walls. It is the presence of multiporate tetrasporic conceptacles (with sporangial plugs;



FIGS 7, 8. Conceptacles of *Mastophoropsis canaliculata*. Fig. 7. SEM of female conceptacle showing several patches (arrows) where epithallium has deteriorated. ×185. Fig. 8. Pore of female conceptacle. Note trianguloid shape of pore (arrow) and cracks in $CaCO_3$ layer. ×425.





FIGS 9, 10. Conceptacle of *Mastophoropsis canaliculata*. Fig. 9. Multiporate tetrasporic conceptacle. Note frustoidal shape. ×130. Fig. 10. Pores of tetrasporic conceptacle. Note plug (arrow). ×1450.

see below) which necessitates transfer of this taxon from the genus *Metamastophora* and the Mastophoroideae into the Melobesioideae. It should be noted that Harvey's illustration (1863, pl. 263, Fig. 3) of an apparent *Mastophoropsis* plant shows uniporate conceptacles and is based on a **TCD** specimen of J. E. Wood from MacDonnell Bay. Re-examination of this plant, however, has revealed that it is a carposporic specimen of *Metamastophora flabellata* (Sonder) Setchell rather than a tetrasporic plant of *Mastophoropsis canaliculata*. Professor H. B. S. Womersley (unpublished annotation dated 8.X.1958 on **ADU**, A21525) previously has noted the occurrence of multiporate tetrasporic conceptacles in *Mastophoropsis*.

INTERNAL ANATOMY

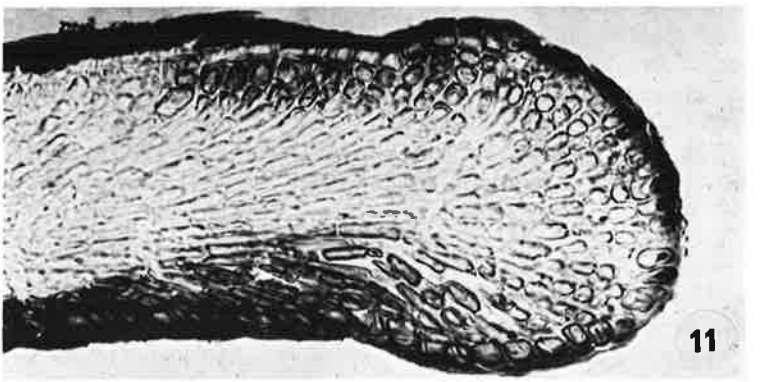
The ascending non-geniculate branches possess a multiaxial, dorsiventral organization (Figs 11–13) with a core of medullary filaments composed of more or less cylindrical elongate cells up to 12 μm broad and 40 μm long (see Table II for summary of measurements). Dorsally, the medulla intergrades into an overlying cortex (4–6, rarely more, cells thick) composed of filaments which arch outwards and ultimately lie more or less perpendicular to the central medulla. The dorsal cortex, which is overlain by a unistratose epithallium, consists of a sub-epithallial meristem of 2–3 cell layers and region of cell elongation of a similar number of cell layers. Meristem cells are more or less isodiametric or broader than long (Table II) and are mostly 5–10 μm in length; elongating cells are 1·5–3·5 diameters long, are generally 10–20 μm in length, and usually become progressively elongate at increasing distances behind the meristem. All cortical cells possess numerous chloroplasts. The dorsal epithallium, in contrast is devoid of chloroplasts. Most epithallial cells are distinctly transversely rectangular in section and generally 0·3–1 diameters high.

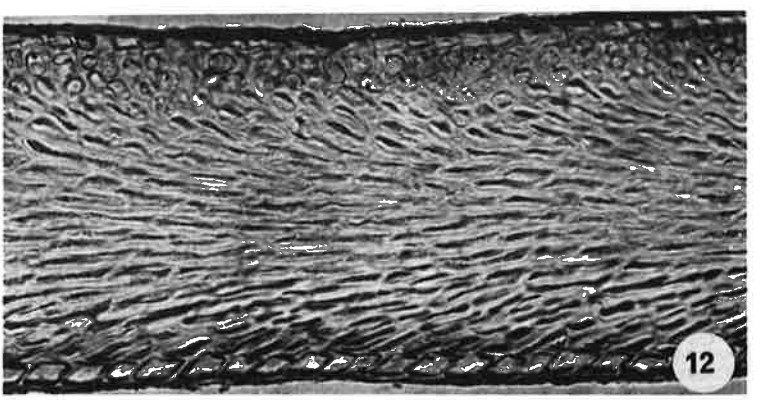
The ventral cortex, in contrast to the dorsal cortex, is poorly defined and generally composed of 1–2 cell layers lying mostly at acute angles to the medulla rather than perpendicular to it (Fig. 12). Ventral cortical cells are more or less cylindrical rather than ovoid and commonly differ from medullary cells only in position and somewhat shorter length. Few chloroplasts are present. The ventral epithallium, however, is quite distinct and consists of a single layer of non-pigmented cells which appear quadrate or somewhat angustate-rectangular in section and are mostly 1·0–1·7 diameters high (Table II).

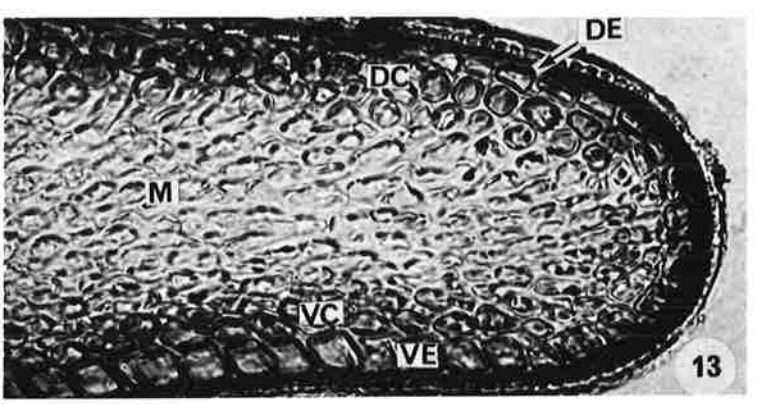
Transition from the larger ventral epithallial cells to the smaller, comparatively transversely-rectangular dorsal epithallial cells occurs along the lateral margins either gradually or abruptly (Fig. 13).

Meristematic activity within vegetative tissues appears to be confined to the sub-epithallial cells of the dorsal cortex which like both dorsal and ventral epithallia appear to be devoid of both secondary pit connections and cell fusions. Partial fusions of adjacent cells occur, however, in the elongated cells of the cortex and in the medulla. Secondary pit connections, in contrast, apparently do not occur either in the cortex or medulla.

Only mature conceptacles (see Table IV for a summary of data on numeric attributes) were observed during this study; early developmental stages were not encountered in the material examined. Based on the investigation of numerous mature sporangial conceptacles, however, several points appear evident with







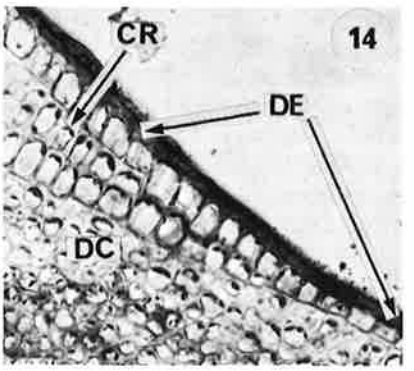
FIGS 11–13. Internal Anatomy. Fig. 11. Paradermal section through branch tip showing multiaxial nature. ×350. Fig. 12. Longitudinal section through older axis. ×350. Fig. 13. Transverse section of older axis showing transition from dorsal epithallium to ventral epithallium. ×360. DE, dorsal epithallium; VE, ventral epithallium; DC, dorsal cortex; VC, ventral cortex; M, medulla.

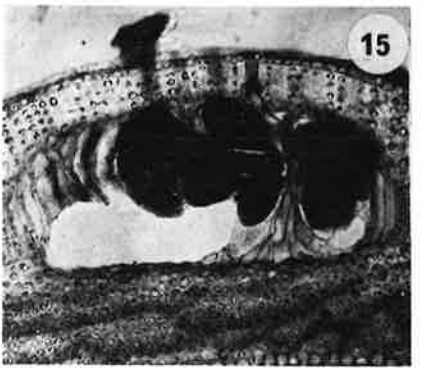
respect to their ontogeny. Throughout development, the vegetative dorsal epithallium remains intact and forms the surface layer of cells in the conceptacle roof. Breaks or disruptions to epithallial tissue occur only in mature or scenescent conceptacles (Fig. 7). Secondly, conceptacles develop from a meristem which is distinct from the cortical meristem of vegetative tissue (see below). This concepticular meristem originates either in the uppermost cell layer of the vegetative cortex or from the epithallium itself (Fig. 14). The possibility of an epithallial origin is raised because epithallial cells around the basal margin enlarge vertically and in some cases appear to divide, producing two cells (Fig. 14). The basal derivative ultimately takes on the appearance of a cortical meristematic cell and probably undergoes subsequent divisions. The apical derivative retains all the characteristics of an epithallial cell. Further detailed studies are required to provide more definitive evidence, especially because of the commonly held viewpoint (Dixon, 1973) that surface epithallial cells (so-called "cap cells") never divide.

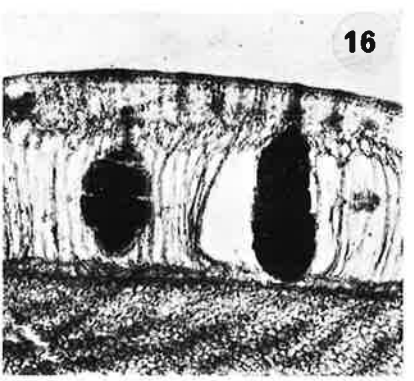
Mature sporangial conceptacles (Figs 15–16) are composed of a roof, a chamber containing a variable number of tetrasporangia, and a floor. The roof consists of four structures, including the unistratose epithallium at the surface. Epithallial cells lack chloroplasts and develop neither secondary pits nor cell fusions. Beneath the epithallium lies a meristematic region composed of 1–6 layers of more or less square or elliptical cells (t.s.) with a height diameter ratio of 0·5–1·5. These cells contain a few chloroplasts; secondary pits do not occur, but cell fusions develop in moderate abundance. Beneath the meristem lies a region of elongation comprising 1–4 layers of angustate-rectangular cells (t.s.) which generally become longer at greater distances behind the meristem and have height diameter ratios up to 5·5 (Fig. 14). Cells in this region possess numerous chloroplasts, lack secondary pits, and commonly exhibit fusion with adjacent cells. The region of elongation is sharply delimited from the vegetative cortex which it overlies (Fig. 14) by marked differences in H/D ratios of cells in the two tissues. The cells of the vegetative cortex, elongation region, conceptacular meristem and epithallium are joined sequentially by primary pit connections and form readily discernible filaments.

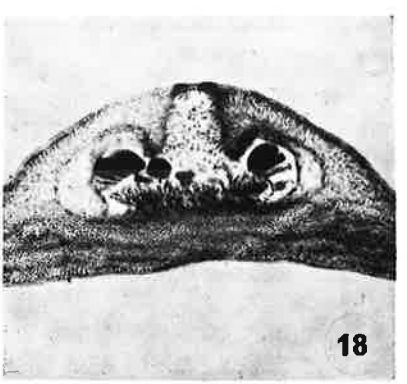
The fourth component of the roof is the pores which prior to spore release appear to be filled with a firm, densely staining, mucilaginous material (Figs 15, 16). The pore formation process is uncertain, and several explanations have been offered (see Lee, 1970). Since, however, far more pores develop than do tetrasporangia and since tetrasporangia are in direct contact with the plugs (Fig. 17), pore ontogeny may be similar to that described by Lee (1970) for *Melobesia mediocris* (Foslie) Setchell & Mason. Pores are generally 7–9 μm in diameter and 28–40 μm long, extending from the surface to the tetrasporangial chamber.

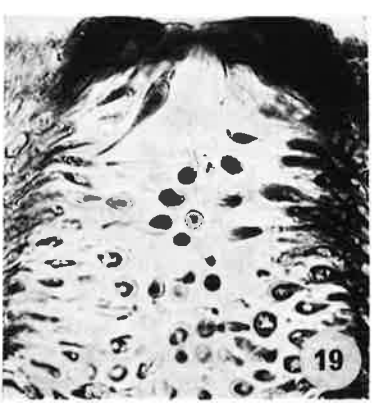
The tetrasporangial chamber is formed as a result of disintegration of cells in the elongation region which were originally derived from the conceptacular meristem. These cells become extremely elongate and devoid of contents prior to disintegration; the extent to which cellular decomposition occurs varies considerably from conceptacle to conceptacle (compare Fig. 15 and Fig. 16). The more or less ellipsoidal chamber is bound on top by cells from the conceptacular meristem, on the bottom by cells from the vegetative dorsal cortical meristem, and around the periphery by cells of the conceptacular elongation region. Details











FIGS 14–19. Conceptacle Anatomy. Fig. 14. Margin (t.s.) of tetrasporic conceptacle showing vegetative dorsal epithallium (DE), division of epithallial cells to form conceptacle roof tissue (CR) and subtending dorsal vegetative cortex (DC). ×420. Figs. 15, 16. Tetrasporic conceptacle chambers without (Fig. 15) and with (Fig. 16) vegetative tissue between sporangia. Fig. 15. ×175. Fig. 16. ×125. Fig. 17. Sporangium in direct contact with plug which blocks overlying pore. ×300. Fig. 18. Mature female conceptacle (t.s.). ×70. Fig. 19. Pore of female conceptacle filled with paraphyses and capped by a mucilaginous cover. ×425.

of tetrasporangial ontogeny remain uncertain and it is unknown whether tetrasporangial initials originate from the conceptacular meristem during early stages of development or from the dorsal cortical meristem which lines the floor of the chamber. Because of the markedly exerted nature of the conceptacle, it seems unlikely that sporangia develop adventitiously in the cortex as in *Phymatolithon* and *Leptophytum* (see Adey, 1966). Mature tetrasporangia have zonately divided contents, are up to 128 μm long and 63 μm in diameter, and are scattered over the entire floor of the chamber. Prior to release, the anterior end is directly connected to a mucilaginous plug which fills a pore in the roof (Fig. 17). Wall remnants of cells which disintegrated during chamber formation commonly are interspersed among the sporangia, but no paraphyses or central columella occur.

TABLE IV. Summary of numeric data on tetrasporic (T.C.) and female (F.C.) conceptacles

Character		Range (μm)* T.C.	F.C.
External basal diameter		600–900	600–1000
Height (above thallus surface)		130–195	200–450
Roof meristem cells:	L	5–8 (–12)	4–8 (–12)
	D	4–12	5–8
	L/D	0·5–1·5	0·6–1·2 (–2)
Roof elongation cells:	L	12–40 (–45)	12–30
	D	5–12	5–8
	L/D	1·5–5 (–5·5)	1·5–4
Roof pores:	L	28–40	125–180
Surface	D	7–9	50–100
Basal	D	7–9	140–175
Chamber: Diameter		318–607	380–550
Height (excluding pore)		95–118	120–180
Sporangia	L	74–128	57–82
	D	40–63	30–61

* Extreme values given in parentheses; L/D ratios expressed in units.

Mature female conceptacles (Fig. 18) were the only other type of reproductive structure available for study; male conceptacles remain unknown. The roof of mature female conceptacles is similar to that of tetrasporic conceptacles in being composed of a unistratose epithallium, a sub-epithallial meristematic region, and an elongation region. The cells comprising these tissues are similar in size, shape and content to those of the tetrasporangial conceptacles (Table IV), and the region of elongation also is sharply delimited from the subtending vegetative cortex.

The roof of female conceptacles differs from that of tetrasporangial conceptacles in possessing a single, central pore, probably formed as a result of cellular decomposition of both epithallial and meristemic cells. The pore opening is covered until maturity by a firm, thin mucilaginous film constituting the remains of the epithallial cells (Fig. 19). Pore diameter increases from epithallium to the chamber. The pore channel is partially filled by a number of unicellular, pigmented, uninucleate, clavate to pyriform paraphyses which represent modified cells from the elongation region (Fig. 19). The pore channel walls are composed primarily of cells from the elongation region and these cells

sometimes become enlarged and more irregular in shape than the columnar elongation cells elsewhere in the roof. Cell fusions occur in both the region of elongation and the conceptacular meristem, but not in the epithallium or between paraphyses.

The chamber of female conceptacles differs in shape (Fig. 18) and size (Table IV) from the tetrasporangial chamber and is bordered by elongation cells across the roof as well as around the peripheral walls. The floor, however, is composed of cells from the dorsal cortical meristem, which appears to give rise to carpogonial branches. Mature carposporophytes fill the chamber; carposporangia mainly occupy the periphery and sterile carposporophyte tissue occurs centrally. Sporangia terminate short (2–4 celled) branches whose cells are much enlarged and stain densely. Procarpic and immediate post-fertilization stages could not be found.

DISCUSSION

Since 1950 a number of classification schemes for the non-geniculate (and geniculate) Corallinaceae have been put forth (e.g. Hamel & Lemoine, 1953; Mason, 1953; Kylin, 1956; Johansen, 1969, 1976; Cabioch, 1971b, 1972; Adey & Macintyre, 1973), but the paucity of detailed data for many taxa has precluded conclusive assessments of these proposals (see also Johansen, 1976), and the choice of which one to follow is still fraught with subjectivity. In this discussion, the system outlined by Johansen 1976 (see also Adey & Johansen, 1972)—a system which considers the occurrence of genicula, secondary pit connections and tetrasporangial plugs to be of primary taxonomic importance—will be used as a framework for considering the position of *Mastophoropsis* within the Corallinaceae.

Johansen (1976) recognizes three subfamilies of non-geniculate Corallinaceae: (1) the Lithophylloideae, containing those genera possessing secondary pit connections but lacking tetrasporangial plugs; (2) the Mastophoroideae, containing those genera possessing cell fusions rather than secondary pit connections, but lacking tetrasporangial plugs, and (3) the Melobesioideae, containing those genera possessing both cell fusions (no secondary pit connections) and tetrasporangial plugs. The genus *Mastophoropsis* clearly belongs to the Melobesioideae, and except for *Sporolithon* all genera in this subfamily possess multiporate tetrasporic conceptacles.

Adey & Johansen (1972) delineated two tribes within the Melobesioideae: (1) the Melobesieae including those genera with "long" meristematic cells, cellular elongation confined largely to the meristem, and conceptacle primordia originating from the meristem; and (2) the Phymatolitheae including those genera with "short" meristematic cells, cellular elongation progressive behind the meristem and conceptacle primordia originating adventitiously in the perithallial (cortical) tissue. The use of conceptacle primordia in delineating tribes appears to be somewhat dubious since *Kvaleya*, placed by Adey & Johansen (1972) in the Phymatolitheae, is stated (Adey & Sperapani, 1971) to have primordia formed from the meristem. Moreover, sexual conceptacles of some species [e.g., Adey & Johansen, 1972, p. 160 under *Neopolyporolithon reclinatum* (Foslie) Adey et Johansen] form both in the meristem and adventitiously. Based on vegetative meristem characteristics, *Mastophoropsis* is assignable to the Phymatolitheae.

In addition to *Mastophoropsis*, the Phymatolitheae contains three other genera: *Kvaleya* Adey et Sperapani, *Leptophytum* Adey and *Phymatolithon* Foslie. *Mastophoropsis* differs from all three genera in possessing an erect, tenacular, non-encrusting, branched thallus rather than a crustose, adhering, non-branched thallus. *Mastophoropsis* also is distinct in the formation of both an upper and a lower epithallium consisting of cells which are angular in section rather than possessing a single epithallium whose cells are rounded in section. In addition *Mastophoropsis* differs from *Kvaleya* in the absence of haustoria, the presence of definite pigmentation, and the occurrence of a definite lower cortex and epithallium (in contrast to a unistratose hypothallium). It also differs from *Leptophytum* in the absence of densely staining cells (so called "pore cells"—see Adey, 1966) adjacent to tetrasporangial pores. *Mastophoropsis* like *Kvaleya* probably also differs from both *Leptophytum* and *Phymatolithon* in having conceptacle primordia formed in the cortical meristem rather than adventitiously.

Mastophoropsis is unique among genera of the sub-family Melobesioideae in its erect, branching taeniform habit, a characteristic shared with only two other genera of non-geniculate Corallinaceae—*Mastophora* Decaisne and *Metamastophora* Setchell. The latter two taxa, however, differ (unpublished personal observations; also see Setchell, 1943; Suneson, 1945) from *Mastophoropsis* in lacking tetrasporangial plugs and in having uniporate tetrasporic conceptacles each with several to many sporangia—characteristics which place them in the sub-family Mastophoroideae. The presence of angular epithallial cells (in section) in *Mastophoropsis* is a feature found in two other genera of the Melobesioideae—*Lithothamnium* Philippi and *Sporolithon* Heydrich. *Mastophoropsis*, however, differs from both in the nature of the meristem as well as in its erect taeniform habit. *Mastophoropsis* also differs from *Sporolithon* in having several to many tetrasporangia within each sporangial conceptacle rather than only one.

Thus, *Mastophoropsis* appears to be a distinctive taxon within the Corallinaceae and merits generic status. To date only one species, *M. canaliculata*, has been described.

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19

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STUDIES ON AUSTRALIAN MANGROVE ALGAE
I. Victorian Communities: Composition and Geographic Distribution

By
ALLAN DAVEY AND Wm. J. WOELKERLING

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5

STUDIES ON AUSTRALIAN MANGROVE ALGAE

I. Victorian Communities: Composition and Geographic Distribution

By ALLAN DAVEY* and WM. J. WOELKERLING*

ABSTRACT: This study of the algal communities associated with the temperate mangrove ecosystems of Victoria, Australia, documents the occurrence of 23 species including 6 Chlorophyta, 1 Chrysophyta, 3 Phaeophyta, and 13 Rhodophyta. Pertinent morphosystematic and distribution data are presented for each species. Although the Victorian mangrove algal flora is far more diverse than previously thought, it is exceedingly depauperate and pedestrian when compared with the southern Australian marine algal flora as a whole. Most species found are widely distributed on a global basis. Frequency data indicate that *Caloglossa leprieurii* occurs most commonly but that most species found occur only rarely or sporadically.

INTRODUCTION

Numerous accounts of mangrove vegetation have appeared since 1950 (see references listed in Chapman 1976, Lugo & Snedaker 1974, and Macnae 1968) and include various Australian based studies (e.g. Ashton 1972, Bird 1971, 1972, Clarke & Hannon 1967, 1969, 1970, 1971, Hutchings & Recher 1974, Macnae 1966, Ministry for Conservation, Victoria 1975, Saenger *et al* 1977). These reports, however, contain comparatively little data on the mangrove algal communities present. Indeed, most studies of mangrove algae have been confined to the tropics (e.g. Almodovar & Pagan 1971, Biebl 1962, Boergesen 1911, Burkholder & Almodovar 1974, Feldmann & Lami 1936, Kuenzler 1974, Post 1936 *et seq*, Taylor 1959, Tseng 1942, 1943).

In temperate regions (i.e. poleward of 30° lat.), mangroves occur only in southern Australia (Table 1) and northern New Zealand in the southern hemisphere, and only in southern Japan and in Bermuda in the northern hemisphere, but again, few algal data are available. Thus Hosokawa *et al* (1977) omit mention of algae in their review of Japanese mangrove ecosystems, while Collins and Hervey (1917) and Taylor and Bernatowicz (1969) present only cursory observations on Bermuda's mangrove algae. Similarly, only limited information is available for New Zealand (Chapman 1977, p 14, Chapman & Ronaldson 1958) and for southern Australia (Butler *et al* 1977a, 1977b, Post 1963, 1964a, Saenger *et al* 1977, Womersley & Edmonds 1958). No detailed floristic surveys of southern Australian mangrove algae have been undertaken, and virtually no ecological data have been collected.

This account presents results of studies on the algal communities associated with mangrove ecosystems in Victoria, Australia, in terms of composition, frequency of species occurrence and geographic distribution, and includes comparisons of these communities with one another, with the marine algal flora of southern Australia in general, and with mangrove algal communities elsewhere.

STUDY SITES

In Victoria, mangrove ecosystems are dominated entirely by *Avicennia marina* (Forster) Vierhapper and occur in five distinct regions (Fig. 1; Table 1). The mangroves generally form more or less open canopy scrub communities in which trees rarely exceed 4 m in height (Pl. 7, 1). This contrasts with tropical Australian mangrove ecosystems which generally develop multispecies closed forests with trees up to 30 m tall (Saenger *et al* 1977). The distribution of *Avicennia* in Victoria and southern Australia (Table 1) is probably controlled by winter air temperatures (Chapman 1976); in Melbourne the mean daily minimum temperature for July is 4°C (Macnae 1966). The stands of *Avicennia* (Pl. 7, 2) along the southern shore of Corner Inlet (38°55′ S) are the most poleward occurrences of mangroves known (Bird 1972).

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TABLE 1
LOCATIONS OF THE COOL TEMPERATE AUSTRALIAN MANGROVE ECOSYSTEMS

State	*Locality*	*References*
SOUTH AUSTRALIA	1. Ceduna - Streaky Bay Region	2, 4
	2. Gulf of St. Vincent (from Price to Port Adelaide)	2, 3
	3. Spencer Gulf (from Tumby Bay to Wallaroo)	2, 3
VICTORIA	1. Andersons Inlet	1
	2. Barwon Heads	1, 4
	3. Corner Inlet (from Millers Landing to east of Port Welshpool)	1, 4
	4. Port Phillip Bay (Hovells Creek and the Kororoit Creek Estuary)	1, 4
	5. Westernport Bay (from Sandy Pt. to Rhyll, Phillip Island)	1, 3, 4
WESTERN AUSTRALIA	1. Bunbury	3, 4

References: 1. Ashton (1972); 2. Butler *et al.* (1977a); 3. Macnae (1966); 4. Saenger *et al.* (1977).

Westernport Bay affords the most sheltered Victorian mangrove environment and much of the shoreline is fringed intertidally with *Avicennia* stands averaging 40-200 m in width. The trees are mostly 2-3 m tall, extend landward to the high tide mark, and produce numerous pneumatophores which serve as the main substrate for macroscopic algae (Pl. 7, 3). The next most extensive mangrove stands occur in Corner Inlet where most trees are 1-2 m tall and form stands which rarely exceed 40 m in width. In Andersons Inlet a more or less continuous fringe up to 20 m wide occurs with most trees less than 2.5 m tall. Comparatively poor developments of *Avicennia* occur at Barwon Heads and in Port Phillip Bay. At Kororoit Creek (Port Phillip Bay), the mangrove stand includes only one 2.0 m tall tree and 6 smaller trees.

MATERIALS AND METHODS

Entire *Avicennia* pneumatophores were collected randomly from throughout the mangrove fringe at 16 different localities between March and September 1977. Eight of the 16 study sites were in Westernport Bay, four in Corner Inlet, two in Port Phillip Bay and one each in Andersons Inlet and at Barwon Heads. The pneumatophores were field preserved in 1:10::formalin:seawater and returned to the laboratory for subsequent analyses. Species composition and frequency values were determined for each locality, noting reproductive status and other morphological features of interest for each algal taxon present. Microscopic Cyanophyta and Bacillariophyta have been excluded from this study.

Frequency data are based on observations of 10-40 pneumatophores collected in a random manner from near the seaward margin of each locality; a given frequency value is the ratio of the number of pneumatophores on which a particular alga occurred to the total number of pneumatophores sampled for frequency analyses at that locality. The relative profusion of taxa has been determined by assigning species to one of the following five categories based on frequency (F) values: *Rare* ($F < .05$); *Sporadic* ($F = .05$-$.24$); *Occasional* ($F = .25$-$.49$); *Common* ($F = .50$-$.75$); *Abundant* ($F > .75$). In the text the word 'prevalent' is used to include both the common and abundant frequency classes. This terminology represents a modification of that suggested by Kershaw (1973, pp. 9-12).

Herbarium vouchers, permanent slides and/or liquid preserved specimens of all species from each locality are deposited in LTB (Index Herbariorum abbreviation; see Holmgren & Keuken 1977, p. 485).

OBSERVATIONS

COMMUNITY COMPOSITION AND SPECIES DISTRIBUTION

Twenty-three species of coenocytic or multicellular eucaryotic algae (discussed below alphabetically within each division) occurred in the mangrove stands studied, including six Chlorophyta, one Chrysophyta, three Phaeophyta, and thirteen Rhodophyta. At each given locality from 2—13 species were detected (Table 2), and, with the exceptions of Hovells Creek and Kororoit Creek, red algae predominated in the community composition. Green algae occurred at all localities and red algae were collected from 15 of the 16 sample areas, while brown algae were found only at three study sites, and the Chrysophycean alga *Vaucheria* was encountered only once.

In the following list, data provided for each taxon include selected references of taxonomic or geographic significance, type locality, recorded geographic distribution, and brief notes relating to occurrence in Victorian mangrove ecosystems as well as data of taxonomic and/or morphologic interest.

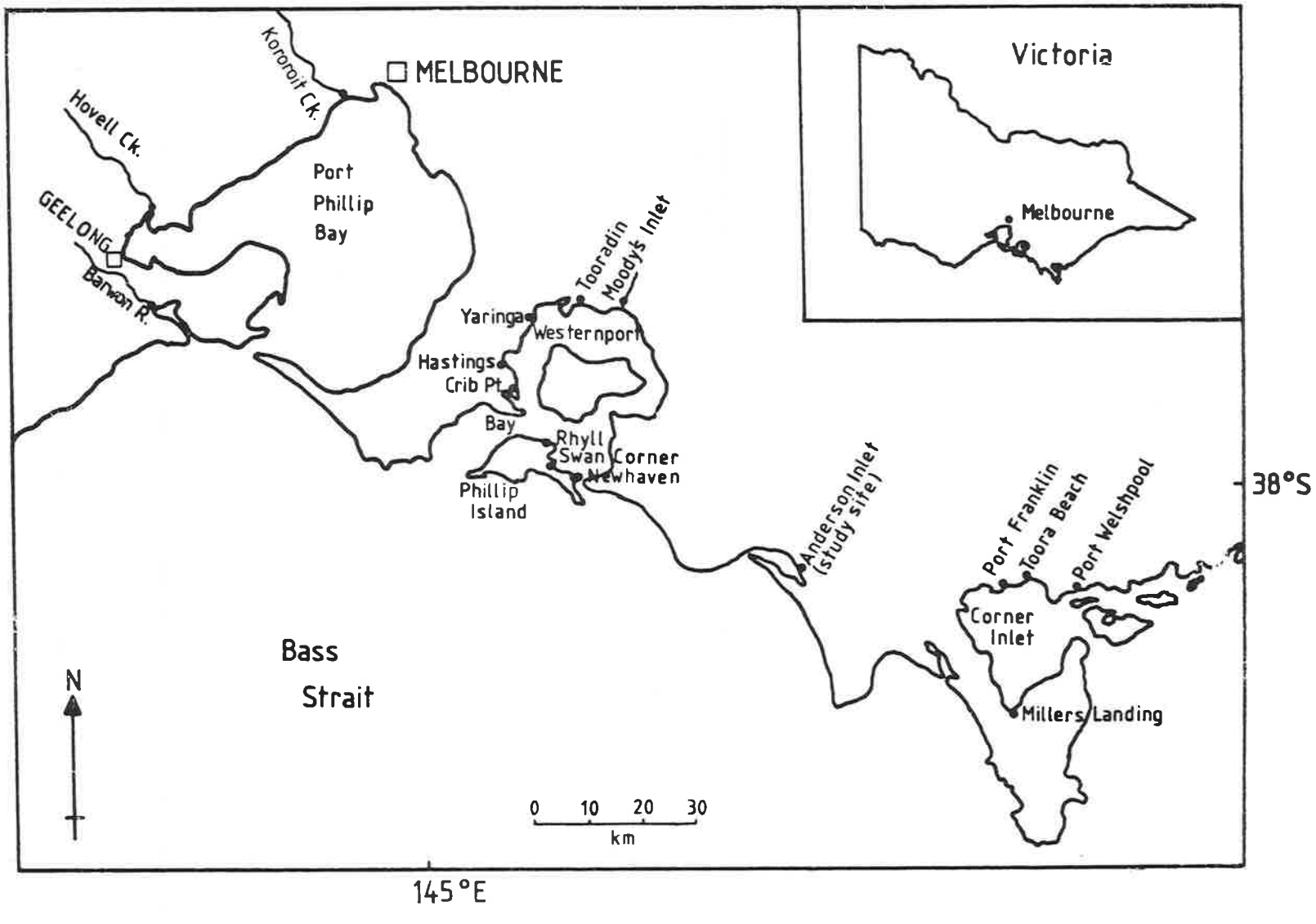

Fig. 1.—The 16 Victorian localities in which sampling was undertaken.

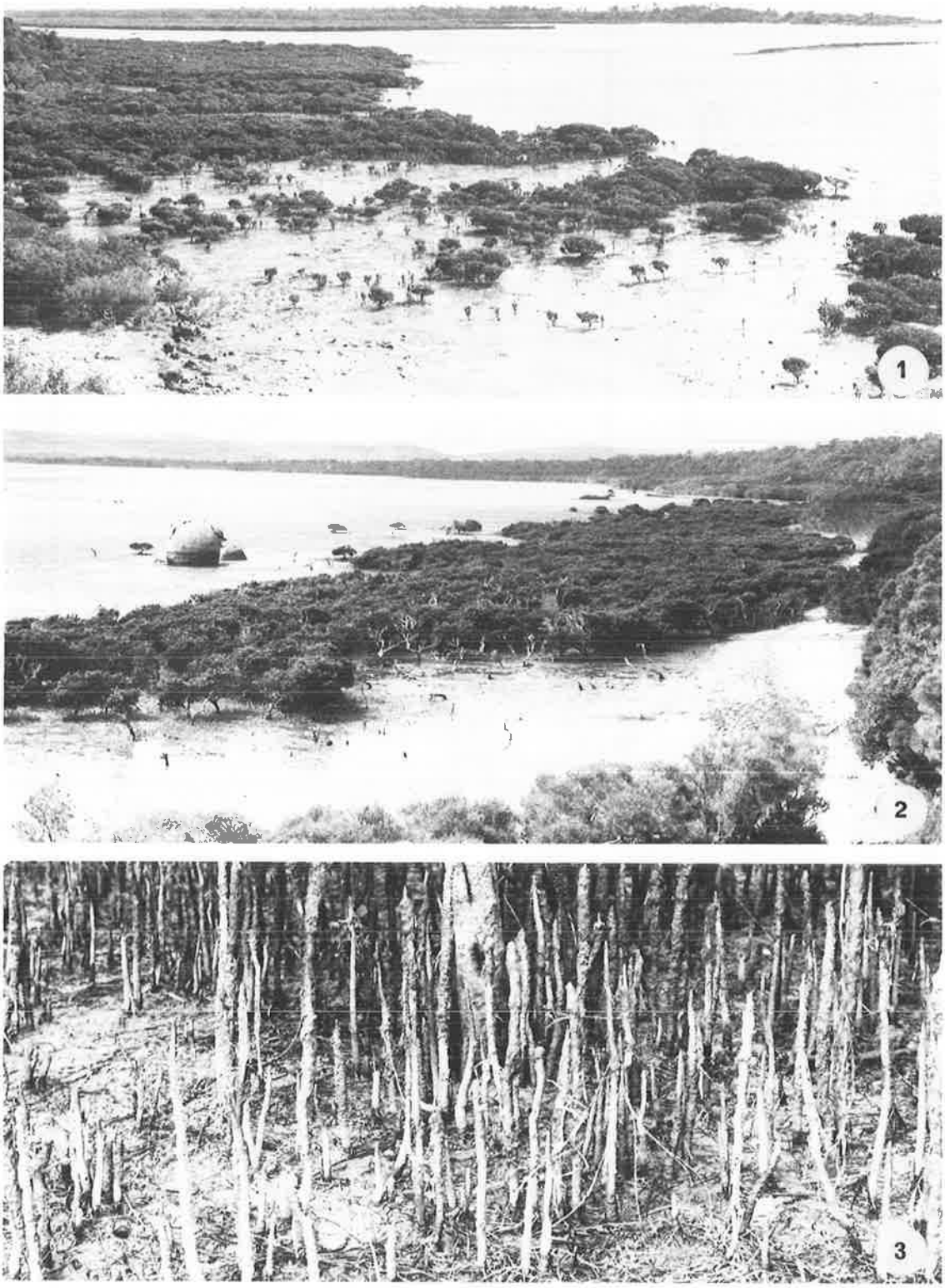

PLATE 7

TABLE 2
SUMMARY OF ALGAL COMMUNITY COMPOSITION DATA FOR VICTORIAN MANGROVE ECOSYSTEMS

Locality	*No. of Taxa from Each Division*				*Total*
	Chlorophyta	Chrysophyta	Phaeophyta	Rhodophyta	
Andersons Inlet	3	—	—	5	8
Barwon Heads	1	—	—	3	4
Crib Point	4	1	1	7	13
Hastings	3	—	—	5	8
Hovells Creek	2	—	—	1	3
Kororoit Creek	2	—	—	—	2
Millers Landing	2	—	—	4	6
Moodys Inlet	1	—	—	4	5
Newhaven	1	—	—	6	7
Port Franklin	2	—	—	4	6
Port Welshpool	2	—	2	5	9
Rhyll	2	—	—	6	8
Swan Corner	1	—	—	5	6
Toora Beach	3	—	—	5	8
Tooradin	2	—	—	6	8
Yaringa	2	—	2	9	13

Division CHLOROPHYTA

Genus **Chaetomorpha** Kuetzing, 1845

C. capillaris (Kuetzing) Boergesen 1925:45, Fig. 13. Womersley 1956:356.

TYPE LOCALITY — Nice, south of France.

DISTRIBUTION — Mediterranean and nearby Atlantic Ocean. In Australia, from American River Inlet, Kangaroo Island, and Westernport Bay, Victoria.

SPECIMENS EXAMINED — LTB 10336, 10347, 10358, 10374, 10380, 10387, 10393.

C. capillaris occurred at all Westernport localities studied except for Moodys Inlet and usually was encountered sparingly in association with *Bostrychia* and *Caloglossa*.

Genus **Cladophora** Kuetzing, 1843

Cladophora sp.

SPECIMENS EXAMINED — LTB 10326, 10350, 10359.

Young plants up to 4 mm tall were found attached to *Avicennia* pneumatophores at Hastings, Millers Landing, and Yaringa. Cells ranged in size from 30-40 μm broad and from 130-170 μm long, but reliable species identification of these diminutive plants was not possible.

Genus **Enteromorpha** Link, 1820

E. clathrata (Roth) Greville 1830: 181. Bliding 1963: 107, Fig. 64-68. Kylin 1949: 28, Fig. 27-29. Womersley 1950: 142; 1956: 352.

TYPE LOCALITY — Europe (see Womersley 1956, p. 352).

DISTRIBUTION — Widespread.

SPECIMENS EXAMINED — LTB 10187, 10193, 10203, 10211, 10219, 10224, 10318, 10327, 10337, 10351, 10374, 10394.

E. clathrata was encountered more often than any other green alga and grew at all stations except Hovells Creek, Newhaven, Swan Corner and Yaringa. It predominated the algal flora of pneumatophores at Kororoit Creek, but occurred only as scattered plants elsewhere.

Genus **Percursaria** Bory, 1828

P. percursa (C. Agardh) Rosenvinge 1893: 963. Abbott and Hollenberg 1976: 70, Fig. 23. Bliding 1963: 20, Fig. 5-6. Papenfuss 1960: 311, 314. Taylor 1960: 54.

TYPE LOCALITY — Denmark.

DISTRIBUTION — Widespread.

SPECIMEN EXAMINED — LTB 10205.

A population of plants was encountered at Hovells Creek but at none of the other study sites. This species apparently has not been recorded previously from southern Australia (see Womersley 1956, 1971).

Genus **Rhizoclonium** Kuetzing, 1843

R. riparium (Roth) Harvey 1851: pl. 239. Cribb 1954: 17, pl. 1, Fig. 9. Taylor 1957: 81, pl. 1, Fig. 3. Womersley 1956: 361.

TYPE LOCALITY — Northern Europe

DISTRIBUTION — Cosmopolitan

SPECIMENS EXAMINED — LTB 10206, 10220, 10319, 10338.

R. riparium plants occurred on *Avicennia* at Andersons Inlet and infrequently among *Caloglossa* and/or *Percur-*

EXPLANATION OF PLATE 7

1. The mangrove community at Rhyll showing the open canopy common in Victorian mangrove ecosystems. 2. The most poleward known mangrove community at Millers Landing, Corner Inlet, Victoria. Trees average 2 m in height. 3. *Avicennia* pneumatophores near the seaward fringe at low tide with associated algal communities

saria at Hovells Creek. Single specimens also were recorded from Crib Point and Toora Beach pneumatophores.

Genus **Ulva** Linnaeus, 1753

U. lactuca Linnaeus 1753: 1163. Bliding 1968: 540, Figs. 3-5. Womersley 1956: 353.
TYPE LOCALITY — Sweden.
DISTRIBUTION — Widespread.
SPECIMENS EXAMINED — LTB 10188, 10194, 10212, 10218, 10320, 10339.

Plants of *U. lactuca* occurred profusely on pneumatophores at Kororoit Creek and also grew conspicuously at stations along the North shore of Corner Inlet and in Andersons Inlet. One plant was found in Westernport Bay (Crib Point).

Division CHRYSOPHYTA

Genus **Vaucheria** deCandolle, 1801

Vaucheria sp.
SPECIMEN EXAMINED — LTB 10340.

Plants with several immature oogonia and antheridia and siphons up to 50 μm broad were entangled with *Chaetomorpha capillaris* on pneumatophores at Crib Point. Reliable species determination was not possible.

Division PHAEOPHYTA

Genus **Ectocarpus** Lyngbye, 1819

E. siliculosus (Dillwyn) Lyngbye 1819:131. Russell 1966:275, Figs. 3-4. Womersley 1967:190.
TYPE LOCALITY — Europe.
DISTRIBUTION — Widespread in temperate and boreal seas.
SPECIMENS EXAMINED — LTB 10341, 10360.

Plants up to 4 mm tall bearing plurilocular sporangia were encountered at the base of pneumatophores at Crib Point and Yaringa.

Ectocarpus sp.
SPECIMEN EXAMINED — LTB 10195.

Large sterile tufts of this taxon colonized a pneumatophore at Port Welshpool. Branching was mostly alternate and the main axes were ecorticate. Cells contained several more or less ribbon like chromoplasts and were up to 25μm broad and 40 μm long in the main axes. The absence of sporangia precluded accurate species identification.

Genus **Sphacelaria** Lyngbye, 1819

S. fusca (Hudson) C. Agardh 1828:34. Sauvageau 1902:206, Fig. 43. Taylor 1960:210. Womersley 1967: 199.
TYPE LOCALITY — Britain.
DISTRIBUTION — Reported from Bermuda, England, Northern France and southern Australia.
SPECIMENS EXAMINED — LTB 10198, 10361.

Several plants were found on pneumatophores at Port Welshpool and Yaringa. The specimens were mostly 3-4 mm tall and bore triradiate non-constricted, linear-armed propagula without central hairs.

Division RHODOPHYTA

Genus **Audouinella** Bory, 1823

A. microscopia (Naegeli) Woelkerling 1971:33, Figs. 10, 23A. Woelkerling 1972:85 *et seq*, Figs. 1-14, 1973a:86; 1973b:557, Figs. 46-51.
TYPE LOCALITY — Bay of Naples, Italy.
DISTRIBUTION — Widespread
SPECIMEN EXAMINED — LTB 10362.

One immature 6-celled plant grew epiphytically on a *Cladophora* plant attached to a pneumatophore at Yaringa.

Genus **Bostrychia** Montagne, 1842

B. intricata (Bory) Montagne 1852:317, Kuetzing 1865:9, pl. 23, figs, d-f. Tseng 1943:174, pl. 1, figs. 4-5.
TYPE LOCALITY — Falkland Islands.
DISTRIBUTION —Widespread in subantarctic regions and in warmer waters on littoral zone rocks, muds and mangroves.
SPECIMENS EXAMINED — LTB 10215, 10221B, 10357, 10371, 10379, 10386, 10392.

Plants of *B. intricata* were commonplace on *Avicennia* pneumatophores at Toora Beach and also all Westernport Bay localities except Crib Point and Hastings. All specimens examined were sterile and grew intermixed with other species of *Bostrychia*. Use of the name *B. intricata* rather than *B. mixta* Hooker and Harvey follows Tseng (1943), who regards the latter as a synonym of *B. intricata*. Post (1963, 1964a) records this taxon (as *B. mixta*) from littoral zone mud surfaces on Kangaroo Island, S.A., and at Tidal River, Victoria. Both localities are devoid of mangroves. Saenger *et al* (1977 p. 317) also record this taxon (as *B. mixta*) from mud and *Avicennia* pneumatophores in Queensland.

B. moritziana (Sonder in Kuetzing) J. Agardh 1863:862. Post 1936:10; 1963:57; 1964a:244. Taylor 1960:596.
TYPE LOCALITY — French Guiana.
DISTRIBUTION — Widespread in tropical and temperate seas.
SPECIMENS EXAMINED — LTB 10191, 10201, 10207, 10213, 10221A, 10321, 10328, 10334, 10348, 10355, 10369, 10377, 10384, 10390.

B. moritziana was encountered at more localities than any other species of *Bostrychia* and occurred everywhere except at the two Port Phillip Bay study sites. Plants often clothed *Avicennia* pneumatophores and in some cases bore cystocarps or tetrasporangia. Male plants were not observed. Specimens from southern Australia examined by Post (1963, 1964a) grew on littoral zone mud flats and rocks as well as on *Avicennia*.

B. radicans (Montagne) Montagne 1850:286. Post 1936:13; 1963:53; Taylor 1960:595. Tseng 1943:168, pl. 1, Figs. 1-3.
TYPE LOCALITY — Sinnamary, French Guiana.
DISTRIBUTION — Widely distributed in tropical and temperate waters.
SPECIMENS EXAMINED — LTB 10192, 10202, 10208, 10214, 10322, 10329, 10335, 10349, 10356, 10370, 10378, 10385, 10391.

The Victorian distribution of *B. radicans* and *B. moritziana* appear to be identical except for the absence of *B. radicans* at Moodys Inlet, and the two taxa almost always grew intermixed on pneumatophores. *B. radicans* plants also occurred epiphytically on *Caloglossa* and *Catenella*. Tetrasporic and cystocarpic plants of *B. radicans* were encountered on occasion, but male plants were not observed. Apparently, this taxon has not been reported from southern Australia before, but Saenger *et al* (1977) record it from Queensland.

B. scorpioides (Gmelin) Montagne 1842:39. De Toni 1905:1164. Falkenberg 1901:519, pl. 12, figs. 1-2. Kuetzing

1865:7, pl. 18, figs. a-d. Post 1936:34; 1963:78; 1964a:242. Taylor 1960:597.
B. harveyi Montagne 1852:317. De Berg 1949:499. De Toni 1905:1163. Garnet 1971:95. Harvey 1860:299; 1863:pl. 292.
TYPE LOCALITY — Great Britain.
DISTRIBUTION — Widely distributed in tropical and temperate waters.
SPECIMEN EXAMINED—LTB 10323.

Sterile plants of *B. scorpioides* grew on *Avicennia* pneumatophores at Andersons Inlet, but were not found elsewhere. Post (1964a) also recorded this species on mud from Tidal River, Leonard Bay and Sealers Cove at Wilsons Promontory. Application of the names *B. scorpioides* and *B. harveyi* to Australian plants requires further clarification including examination of relevant type collections. Post (1936, p. 34) considered *B. harveyi* to be a later synonym of *B. scorpioides*; however, de Berg (1949) argued that the two taxa are distinct, based on studies of New Zealand plants. Nevertheless Post (1963, 1964a) subsequently maintained that *B. harveyi* is identical to *B. scorpioides*, and until the matter can be clarified further from studies of additional Australian collections and comparisons with the types, it seems logical to follow Post, who has examined both Australian and European material. Saenger *et al* (1977, p. 317) also use the name *B. scorpioides*.

Genus **Caloglossa** J. Agardh, 1876

C. leprieurii (Montagne) J. Agardh 1876: 499. Dawson 1956: 57, Fig. 59. Feldmann & Lami 1936: 883. Papenfuss 1961: 8, Figs. 1-4. Post 1936: 46; 1963: 99; 1964a: 242. Womersley & Bailey 1970: 327.
TYPE LOCALITY — Cayenne, French Guiana.
DISTRIBUTION — Widespread in tropical and temperate waters.
SPECIMENS EXAMINED — LTB 10190, 10200, 10204, 10209, 10216, 10222, 10324, 10330, 10333, 10346, 10354, 10368, 10376, 10383, 10389.

C. leprieurii occurred at all localities except Kororoit Creek, thus making it the most widely distributed alga in Victorian mangrove ecosystems. In some cases it was the sole alga present on a given pneumatophore. Tetrasporangial and cystocarpic plants were observed on occasion, but most plants were sterile. King *et al* (1971), Post (1963, 1964a), Saenger *et al* (1977), and Sonder (1855, as *Delesseria*) previously recorded *C. leprieurii* from Victoria.

Genus **Catenella** Greville, 1830

C. nipae Zanardini 1872: 143, pl. 6A, Figs. 1-7. Min-Thein & Womersley 1976: 50, Figs. 17, 56. Post 1936: 68; 1963: 116, Fig. 8; 1964a: 251. Tseng 1942: 143.
TYPE LOCALITY — Sarawak, Borneo.
DISTRIBUTION — India, Indonesia, eastern and southeastern Australia, New Zealand (see Post 1936, 1963).
SPECIMENS EXAMINED — LTB 10189, 10210, 10217, 10223, 10325, 10331, 10332, 10345, 10353, 10367, 10375, 10382, 10388.

C. nipae occurred conspicuously on pneumatophores at all localities in Westernport Bay, Andersons Inlet, and Corner Inlet, but was not found in Port Phillip Bay or at Barwon Heads. Tetrasporic plants were commonplace and cystocarpic plants infrequent. Often *C. nipae* occurred as the sole alga on a particular pneumatophore.

Genus **Centroceras** Kuetzing, 1841

Centroceras sp.
SPECIMEN EXAMINED — LTB 10342.

A solitary sterile plant 6 mm tall occurred at the base of a pneumatophore at Crib Point. The filaments were up to 100 μm broad and successive nodes were separated by 11-12 cells, but reliable species identification was not possible.

Genus **Ceramium** Roth 1797

Ceramium macilentum J. Agardh 1894: 15. Womersley 1978: 232.
TYPE LOCALITY — Port Phillip Bay, Victoria.
TYPE — LD.
DISTRIBUTION — see Womersley 1978.
SPECIMEN EXAMINED — LTB 10343.

A single sterile tuft of filaments was encountered on one Crib Point pneumatophore.

Genus **Chondria** C. Agardh, 1817

Chondria sp.
SPECIMEN EXAMINED — LTB 10352.

Several tetrasporangial plants 4-5 cm tall colonized the lower half of a pneumatophore at Hastings. The tetrasporangial branches were markedly flattened and the sporangia averaged 40 μm in diameter.

Genus **Colaconema** Batters, 1896

C. humilis (Rosenvinge) Woelkerling 1971: 44, Figs. 15 J-O; 1937b: 529, Figs. 66-73.
TYPE LOCALITY — Spodobjerg, Langeland, Denmark.
DISTRIBUTION — Atlantic and Mediterranean shores of Europe, northeastern United States, southeastern Australia.
SPECIMEN EXAMINED — LTB 10363.

Plants occurred on an unidentified red alga epiphytic on a pneumatophore at Yaringa.

Genus **Diplocladia** Kylin, 1956

D. patersonis (Sonder) Kylin 1956: 504.
TYPE LOCALITY — Cape Paterson, Victoria.
DISTRIBUTION — S. Australia, Tasmania, Victoria.
SPECIMENS EXAMINED — LTB 10196, 10364.

Sterile plants up to 1.5 cm tall, colonized pneumatophores at Yaringa and Port Welshpool.

Genus **Polysiphonia** Greville, 1824

Polysiphonia sp.
SPECIMENS EXAMINED — LTB 10344, 10365, 10374, 10381, 10395.

Single tetrasporangial plants grew on pneumatophores at Crib Point, Newhaven, Rhyll, Tooradin and Yaringa. In all cases the plants were ecorticate with four pericentral cells, but reliable specific identification could not be made.

FREQUENCY DATA

Based on frequency data (Table 3), seven taxa (*Audouinella microscopica*, *Centroceras* sp., *Ceramium macilentum*, *Chondria* sp., *Colaconema humilis*, *Sphacelaria fusca*, *Vaucheria* sp.) of the total

TABLE 3
FREQUENCY OF SPECIES OCCURRENCE FROM THE 16 LOCALITIES STUDIED IN VICTORIA

Locality	Andersons Inlet	Barwon Heads	Crib Pt.	Hastings	Hovells Creek	Kororoit Creek	Millers Landing	Moodys Inlet	Newhaven
No. of pneumatophores sampled	40	39	25	26	39	16	30	10	22
Taxon									
CHLOROPHYTA									
Chaetomorpha capillaris			.32	.23					.23
Cladophora sp.				.03			.07		
Entermorpha clathrata	.03	.26	.04	.03		1.0	.07	.50	
Percursaria percursa					.23				
Rhizoclonium riparium	.55		.04		.23				
Ulva lactuca	.05		.04			1.0			
CHRYSOPHYTA									
Vaucheria sp.			.04						
PHAEOPHYTA									
Ectocarpus siliculosus			.04						
Ectocarpus sp.									
Sphacelaria fusca									
RHODOPHYTA									
Audouinella microscopica									
Bostrychia intricata								.90	.27
B. moritziana	.05	.26	.68	.73			.80	.40	.50
B. radicans	.40	.46	.60	.73			.54		.77
B. scorpioides	.25								
Caloglossa leprieurii	.43	1.0	.96	.96	1.0		.80	.30	.55
Catenella nipae	.68		.64	.53			.30	.30	.64
Centroceras sp.			.04						
Ceramium sp.			.04						
Chondria sp.				.03					
Colaconema humilis									
Diplocladia patersonis									
Polysiphonia sp.			.04						.05

TABLE 3 (*Continued*)

Locality	Port Franklin	Port Welshpool	Rhyll	Swan Corner	Toora Beach	Tooradin	Yaringa	
No. of pneumatophores sampled								
Taxon	24	40	21	23	40	24	25	$\bar{F}$
CHLOROPHYTA								
Chaetomorpha capillaris			.19	.17		.29	.36	.26
Cladophora sp.							.04	.05
Enteromorpha clathrata	.29	.38	.09		.18	.04		.24
Percursaria percursa								.23
Rhizoclonium riparium					.03			.21
Ulva lactuca	.08	.10			.10			.23
CHRYSOPHYTA								
Vaucheria sp.								.04
PHAEOPHYTA								
Ectocarpus siliculosus							.08	.06
Ectocarpus sp.		.05						.05
Sphacelaria fusca		.03					.04	.04
RHODOPHYTA								
Audouinella microscopica							.04	.04
Bostrychia intricata			.19	.69	.15	.17	.08	.35
B. moritziana	.38	.40	.72	.50	.50	.75	.68	.53
B. radicans	.29	.33	.67	.53	.53	.75	.68	.56
B. scorpioides								.25
Caloglossa leprieurii	.54	.75	.48	.60	.60	.83	.56	.69
Catenella nipae	.67	.48	.38	.53	.53	.79	.64	.55
Centroceras sp.								.04
Ceramium macilentum								.04
Chondria sp.								.03
Colaconema humilis							.04	.04
Diplocladia patersonis		.08					.04	.06
Polysiphonia sp.			.05			.04	.04	.04

of 23 recorded must be considered rare ($F < .05$ for all localities) and an additional six (*Cladophora* sp., *Diplocladia patersonis*, *Ectocarpus siliculosus*, *Ectocarpus* sp., *Percursaria percursa*, *Polysiphonia* sp.) classed as rare ($F < .05$) or sporadic ($F = .05$-$.24$) depending on the locality. This includes two of the six species of Chlorophyta, all of the Chrysophyta and Phaeophyta and seven of the 13 Rhodophyta. All of these species appear to be relatively inconsequential in Victorian mangrove ecosystems.

Of the remaining 10 taxa, four (*Bostrychia moritziana*, *B. radicans*, *Caloglossa leprieurii*, and *Catenella nipae)* were common ($F = .50$-$.75$) or abundant ($F > .75$) at most localities of occurrence, and six (*Bostrychia intricata*, *B. scorpioides*, *Chaetomorpha capillaris*, *Enteromorpha clathrata*, *Rhizoclonium riparium*, *Ulva lactuca*) showed marked variations in frequency values and could be considered rare to abundant depending upon locality. Based on mean frequency values [i.e. $\sum F/N$, where $\sum$'F' is the sum of all recorded frequencies > 0 and 'N' is the total number of localities at which the alga occurred; (see Table 3)], *Caloglossa leprieurii* is the most conspicuous alga in the Victorian mangrove ecosystems.

At any given locality (Table 3) from 1-5 species of algae were common ($F = .50$-$.75$) or abundant ($F > .75$). In two instances (Andersons Inlet, Moodys Inlet) one of the prevalent species ($F = .50$-1.0) was a green alga, and in one other instance (Kororoit Creek), both prevalent species were green algae. For the remaining 13 localities, common or abundant frequency values occurred only among red algae.

At half the study sites, only one or two species had frequency values of .50 or greater; at the other study sites, from three to five species occurred with frequency values of .50 or more. No clear relationship, however, seems to exist between the number of prevalent species and the total number of species present at a locality (Table 4).

TABLE 4
RELATIONSHIPS BETWEEN THE NUMBER OF PREVALENT ALGAL SPECIES ($F = .50 — 1.0$) AND THE TOTAL NUMBER OF ALGAL SPECIES IN VICTORIAN MANGROVE ECOSYSTEMS

Locality	*# Prevalent Species*	P_s/T_s[1]
Barwon Heads	1	.25
Hovells Creek	1	.33
Port Welshpool	1	.11
Andersons Inlet	2	.25
Kororoit Creek	2	1.00
Moodys Inlet	2	.40
Port Franklin	2	.33
Rhyll	2	.25
Millers Landing	3	.50
Crib Point	4	.31
Hastings	4	.50
Newhaven	4	.57
Toora Beach	4	.50
Tooradin	4	.50
Yaringa	4	.31
Swan Corner	5	.83

[1] P_s = Number of prevalent species; T_s = Total number of species.

DISCUSSION

The algal flora of Victoria's mangrove ecosystems is exceedingly depauperate and pedestrian when compared with the southern Australian marine algal flora as a whole. Based on published species estimates (Womersley 1959), only six of the 98 Chlorophyta, three of the 191 Phaeophyta, and thirteen of the 725 Rhodophyta species known to occur in southern Australian seas were encountered in Victorian mangrove ecosystems. (Data on the Chrysophyta are too meagre to make meaningful comparisons). This represents percentage occurrences of 6.1, 1.6, and 1.8 respectively. Furthermore, only two (*Ceramium macilentum*; *Diplocladia patersonis*) of the 23 taxa found are endemic to southern Australia; the remaining taxa all have been recorded outside Australian waters, and most are widespread. Two species (*Bostrychia radicans*, *Percursaria percursa*), however, apparently have not been reported from southern Australia previously. All 23 species are known to occur outside of mangrove environments, but six species encountered in this study (*Audouinella microscopica*, *Colaconema humilis*, *Diplocladia patersonis*, *Ectocarpus siliculosus*, *Percursaria percursa*, *Sphacelaria fusca*) apparently have not been reported previously from mangrove ecosystems.

Of the 16 localities examined, four (Barwon Heads, Hovells Creek, Kororoit Creek, Moodys Inlet) were estuarine in nature, while 12 were not subject to the influence of fresh or brackish water. The total flora at these four localities was less diverse (2-5 taxa) than that of the more marine sites (6-13 taxa), and only one species (*Percursaria percursa*) appeared to be confined to these estuarine environments. In contrast, 14 species occurred only in the marine environments (Table 3). The four ecologically most significant algae (based on frequency values, see Table 3) all occurred at every marine locality sampled; however, none occurred at Kororoit Creek. In addition, *Bostrychia radicans* did not occur at Moodys Inlet, and *Catenella nipae* was not found at Barwon Heads. Thus, estuarine influence appears to affect adversely algal diversity within the mangrove ecosystems investigated.

Results from this study also suggest that the Victorian mangrove algal flora (i.e. Chlorophyta,

TABLE 5
COMPARISONS OF ALGAL FLORAS RECORDED FROM VARIOUS AUSTRALIAN MANGROVE ECOSYSTEMS BASED ON DATA FROM SAENGER *et al.* 1977 AND THIS STUDY

Taxon	*Victoria (Present Study)*	*Victoria (Saenger et al.)*	*N.S.W.*	*Qld.*	*Australia (Saenger et al. and This Study)*
Chlorophyta	6	—	—	5	7
Chrysophyta	1	—	—	—	1
Phaeophyta	3	—	—	1	4
Rhodophyta	13	3	4	17	24
Total	23	3	4	23	36
Bostrychia	4	2	3	7	7
Caloglossa	1	1	—	3	3
Catenella	1	—	1	1	1
Total	6	3	4	11	11

Phaeophyta, Rhodophyta) is far more diverse than previously realized and that its species richness may be comparable to that of Queensland mangrove ecosystems (Table 5). Thus 20 (87%) of the 23 species found during this study were not recorded previously from Victorian mangroves, and the species total for Victoria is now identical with that reported (Saenger *et al* 1977) for tropical Queensland. Species composition in the two areas differs substantially, however, and none of the Chrysophyta or Phaeophyta are common to both regions. Four of the seven Chlorophyta and six of the 24 Rhodophyta occur in both regions, and in the total floras, less than one-third (28%) of the algal species are reported from both tropical Queensland and temperate Victorian mangrove environments. Comparisons of species distribution of *Bostrychia*, *Caloglossa* and *Catenella* indicate that all species of these genera found on Victorian mangroves are also recorded from Queensland mangroves, and reveal also that 2 additional species of *Caloglossa* and 3 of *Bostrychia* occur (based on published records) only on Queensland mangroves. Such comparisons must be viewed with caution, however, since the Queensland data are based solely upon investigations of *Avicennia* pneumatophores, and studies of the algal flora associated with other Queensland mangrove species may produce data which will markedly alter statements made here. The absence of data precludes comparisons of the Victorian and Queensland mangrove algal floras with those of the Northern Territory, South Australia and Western Australia. Likewise data from New South Wales are too meagre (Table 5) to permit meaningful comparative discussions.

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STUDIES ON *METAMASTOPHORA* (CORALLINACEAE, RHODOPHYTA). I. *M. FLABELLATA* (SONDER) SETCHELL: MORPHOLOGY AND ANATOMY

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A morphological–anatomical study of Australian populations of *Metamastophora flabellata* (Sonder) Setchell, the type species of *Metamastophora* (Corallinaceae, Rhodophyta), has revealed that the primarily erect or ascending non-geniculate thallus possesses a dorsi-ventral organization of tissues. All conceptacles are uniporate and arise dorsally. Two distinct vegetative meristems occur: an apical primary meristem from which hypothallial cells are produced basipetally and a sub-epithallial secondary meristem which generates perithallial cells basipetally and secondary epithallial cells acropetally. Primary epithallial cells arise from divisions of subapical hypothallial cells. In younger parts, tissues are produced only dorsal to the hypothallium; in veins and stipes, tissue production occurs both dorsal and ventral to the hypothallium. Mature tetrasporic conceptacles contain peripheral tetrasporangia with zonately divided contents and a central sterile columella. Gametic conceptacles produce fertile tissue across the entire conceptacle chamber floor. After fertilization, the zygotic nucleus or a derivative is transferred (presumably) to an auxiliary cell through cells of the carpogonial branch; no tubular transfer siphon develops. Mature fusion cells are composed of the amalgamated supporting cells of carpogonial branches and are initiated from a single supporting cell which functions as an auxiliary cell. Unbranched 3–4 celled gonimoblast filaments arise from the fusion cell, do not become connected to other cells, and produce terminal carposporangia. Results from this study have led to a redefinition of hypothallium and perithallium in relation to meristems rather than substrate. In addition, carposporophyte ontogeny in the Corallinaceae is considered in terms of the presumed mode of transfer of the zygotic nucleus to the fusion cell, the extent of fusion cell development, and gonimoblast filament production in relation to auxiliary cells and fusion cells.

Published information on the genus *Metamastophora* Setchell (Corallinaceae, Rhodophyta) has been restricted primarily to records of geographic occurrence and to limited anatomical observations. Most earlier references containing relevant data are given by Setchell (1943). Lemoine (1911, p. 182) and Cabioch (1972, p. 197) have reported briefly on the vegetative anatomy of several specimens referrable to *Metamastophora*, and Suneson (1945) has presented some anatomical information on male and tetrasporangial plants in three South African collections of *M. lamourouxii* (Decaisne ex Harvey) Setchell (as *Mastophora*). However, data on female plants and on carposporophytes are lacking, and no detailed morphological-anatomical accounts based on southern Australian populations have appeared. Moreover, the taxonomic status of *Metamastophora* has remained uncertain, and Johansen (1976, p. 232) placed it among a group of poorly known or unclearly understood Corallinaceae.

This paper presents results of detailed morphological-anatomical studies on southern Australian populations of *Metamastophora flabellata* (Sonder) Setchell, the designated (Setchell, 1943, p. 130) type species of the genus. Male, female and tetrasporangial individuals have been examined, and some details of female

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conceptacle and carposporophyte development have been elucidated, thus providing an opportunity to comment on the carposporophyte-ontogeny hypothesis proposed by Lebednik (1977). Although results are based primarily on studies involving plants from Rottnest Island, Western Australia, they also incorporate data from numerous other individuals collected throughout southern Australia, including syntype specimens. Distributional, nomenclatural and taxonomic data are considered elsewhere (Woelkerling, 1980).

MATERIALS AND METHODS

The principal population utilized in this investigation was gathered at depths of 1–4 m off limestone reefs at Cape Vlaming, Rottnest Island, W. Australia in February 1978. This population includes 29 dried plants (male, female, tetrasporangial) and associated liquid preserved specimens currently deposited at **LTB** (numbers 10457A–10457CC). Numerous other southern Australian collections from **ADU, LTB, MEL, MELU, TCD** and **UWA** also have been examined and annotated; photographs of all specimens and prepared microscopic slides have been retained at **LTB.**

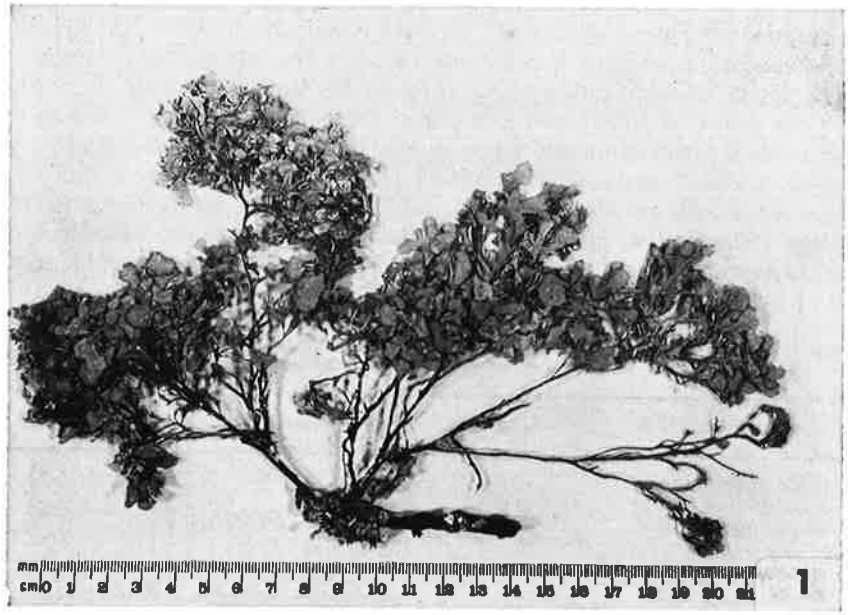
Microtechnique and scanning electron microscopy procedures follow Woelkerling (1978) except that material for optical microscopy was stained prior to dehydration rather than after sectioning; in addition the three resin infiltration steps were carried out for 1 h each under vacuum rather than for periods of 8–12 h or more without vacuum. These changes allowed for more rapid (<48 h vs >72 h) and more efficient processing of material. Because $KMnO_4$ can affect cell contents adversely, some material used in the ontogenic studies was left unstained and photographed under dark field optical microscopy or interference contrast microscopy. In addition, some details were elucidated from squash preparations or freehand sections of decalcified tissue stained with 5% aqueous aniline blue, post-stain fixed in 0·6 HNO_3 and mounted in 20% aqueous "Karo" dextrose with 2% phenol added to prevent fungal growth.

OBSERVATIONS

EXTERNAL MORPHOLOGY

One to several non-geniculate, compressed to flattened upright axes arise from an irregularly discoid to applanate pseudoparenchymatous holdfast and produce moderately to profusely branched plants up to 20 cm tall (Fig. 1). Setchell (1943, p. 130) indicated in the generic protologue that plant bases were attached by rhizoids; no evidence for such an attachment mechanism was observed in this study. The basal, stipe-like portions of upright axes are of relatively uniform width, appear more or less transversely elliptical in cross-sectional outline, rarely exceed 2 mm in diameter, and branch irregularly. At varying distances above the holdfast, stipes abruptly or gradually become distally flattened and expanded, ultimately bearing irregularly, pseudodichotomously or polychotomously branched lamina-like portions. In some specimens, the laminae remain nearly linear or only slightly expanded and are generally less than 2 mm broad, whereas in other specimens, laminae become moderately to markedly flabelliform near the apices and are up to 11 mm broad. All intermediate conditions occur, and this results in considerable variation in general appearance (Fig. 2). Where transition from stipe to lamina is gradual, the stipe commonly assumes a vein-like aspect before becoming indistinguishable (Fig. 3). Numeric data relating to the vegetative system appears in Table 1.

Both dorsal and ventral surfaces of younger axes, commonly but not invariably, are traversed by a series of minute, concentric, anteriorly convex channel-like markings (Fig. 4) which, as Suneson (1945, p. 254) has noted, delineate the



FIGS 1–3. Vegetative morphology. Fig. 1. Habit of plant attached to *Amphibolis* rhizome. Fig. 2. Variation in lamina appearance and branch tip flabellation in a series of specimens. Fig. 3. Transition from stipe to vein in a branch. ×1·9.

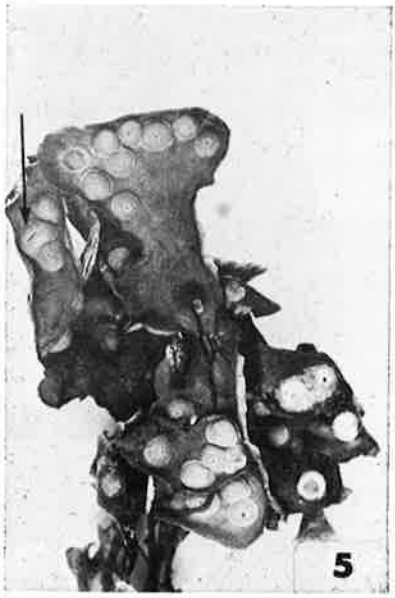
position of various cell types (see below). In living and liquid preserved plants the laminae are almost always flat. In dried specimens, however, the apical and lateral margins commonly become interruptedly involute and/or revolute.

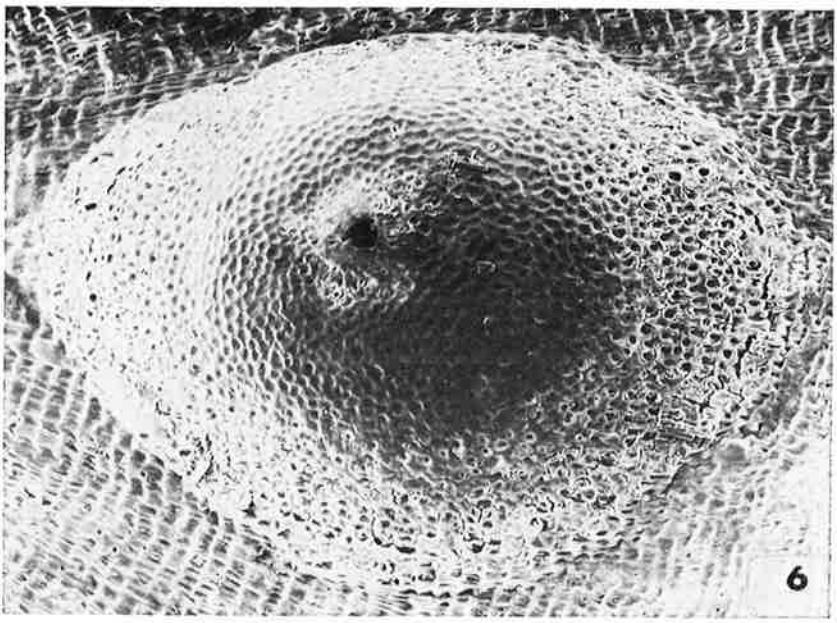
The degree of calcification varies considerably both from plant to plant and from one part of a given plant to another. Generally, the ventral surfaces show more evident calcification and hence appear more pruinose than dorsal surfaces (Fig. 4). Calcium carbonate deposition seems to occur largely at the branch apices but usually no distinct $CaCO_3$ ridges form as in *Mastophoropsis* (Woelkerling, 1978, p. 214, fig. 4). Like in *Mastophoropsis* plants, variable loss of $CaCO_3$ deposits apparently takes place, and older tissues may bedome mottled and/or irregularly foveate.

TABLE I. Summary of morphological and anatomical measurements in vegetative structures. Extreme values are given in parentheses

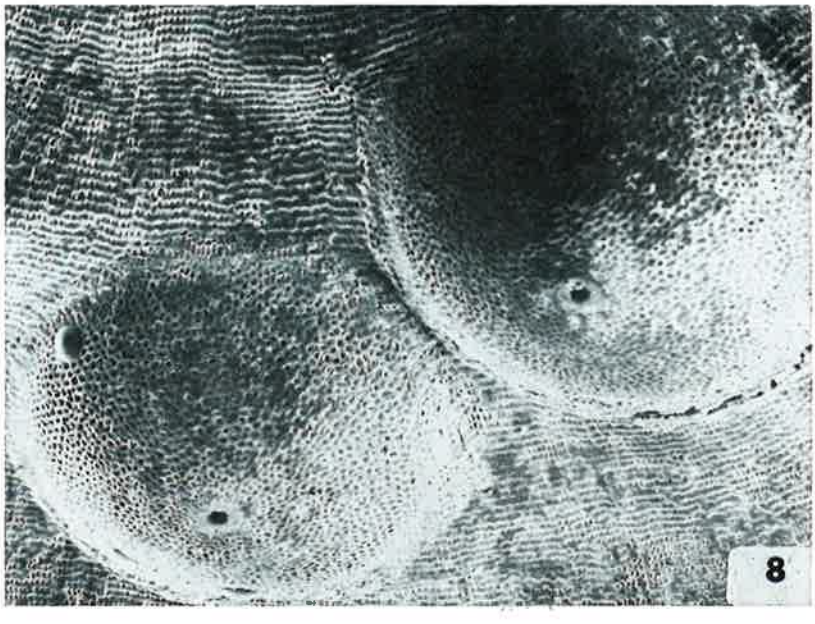
Character	Unit	Range	
Thallus height	cm	5–21	
Stipe width	mm	0·4–2·5 (–3·8)	
Median branch width	mm	(0·75) 1–9 (–11)	
Branch tip width	mm	(0·6–) 1–9 (–11)	
		L.S.	*T.S*
Young hypothallium:			
Cell length (height)	μm	(35–) 41–85	35–74
Cell diameter	μm	11–30 (–41)	(8–) 11–19 (–27)
L/D	ratio	(1·8–) 2·2–5·0 (–5·5)	(2·0–) 2·7–5·5 (–6·5)
Mature hypothallium:			
Cell length (height)	μm	(30–) 35–76	22–56
Cell diameter	μm	(11–) 16–38 (–46)	8–25
L/D	ratio	(1·0–) 1·6–3·5 (–5·0)	(1·4–) 2–4·5 (–6·5)
Young epithallium:			
Cell length (height)	μm	(8–) 11–22	(8–) 11–22 (–27)
Cell diameter	μm	(11–) 14–35 (–41)	8–19 (–25)
L/D	ratio	0·4–1·0	0·7–2·0 (–2·4)
Mature epithallium:			
Cell length (height)	μm	14–25	10–25
Cell diameter	μm	(14–) 22–49	8–19
L/D	ratio	0·4–1·3 (–1·4)	0·7–2·0 (–2·8)
Secondary meristem:			
Cell length (height)	μm	11–33	(11–) 14–33
Cell diameter	μm	(14–) 22–43	(6–) 8–19 (–27)
L/D	ratio	(0·3–) 0·5–1·0	(0·6–) 1–2 (–3)
Perithallium:			
Cell length (height)	μm	19–82 (–109)	8–40 (–52)
Cell diameter	μm	6–19	5–16 (–19)
L/D	ratio	(1–) 2–9 (–11·5)	(0·5–) 1–4·5 (–5·8)

Conceptacles occur singly or in small irregularly disposed groups near branch tips and along laminae (Fig. 5). Development and orientation are strictly dorsiventral with the uniporate conceptacle roofs always projecting above the dorsal thallus surface. Conceptacle floors usually are clearly delimited on the ventral





FIGS 4–6. Vegetative and reproductive morphology. Fig. 4. Branch tips showing concentric channel-like markings and varying degrees of calcification. Note greater $CaCO_3$ deposition near tips on ventral surface (arrow). ×2·5. Fig. 5. Branch with numerous tetrasporic conceptacles. Note double conceptacle (arrow). ×4·5. Fig. 6. Uniporate tetrasporic conceptacle. ×82.



FIGS 7–8. Gametic conceptacles in surface view. Fig. 7. Male conceptacle with porate rostrum. ×57. Fig. 8. Female conceptacles. ×47.

side of the thallus and commonly possess slightly convex external surfaces. Tetrasporic and female conceptacles (Figs 6, 8) are hemispheroidal to conoidal, are up to 1600 μm broad at the base, protrude up to 860 μm above the surrounding dorsal thallus surface, and possess single apical pores which are circular to angustate-elliptical in outline. Male conceptacles, in contrast, possess a distinctive conoidal-rostriform shape (Fig. 7) with basal diameters up to 1300 μm. They protrude up to 2000 μm above the surrounding dorsal thallus surface and have single more or less circular apical pores. No externally visible evidence of pore blockage or protection during early conceptacle development was found in the material examined, and details of pore formation remain unknown. Table II summarizes numeric data relating to the reproductive structures of *M. flabellata*. With one exception, all gametic plants examined were dioecious; the monoecious specimen (**ADU** A11076a) bears several male conceptacles amongst a predominance of female ones.

INTERNAL ANATOMY

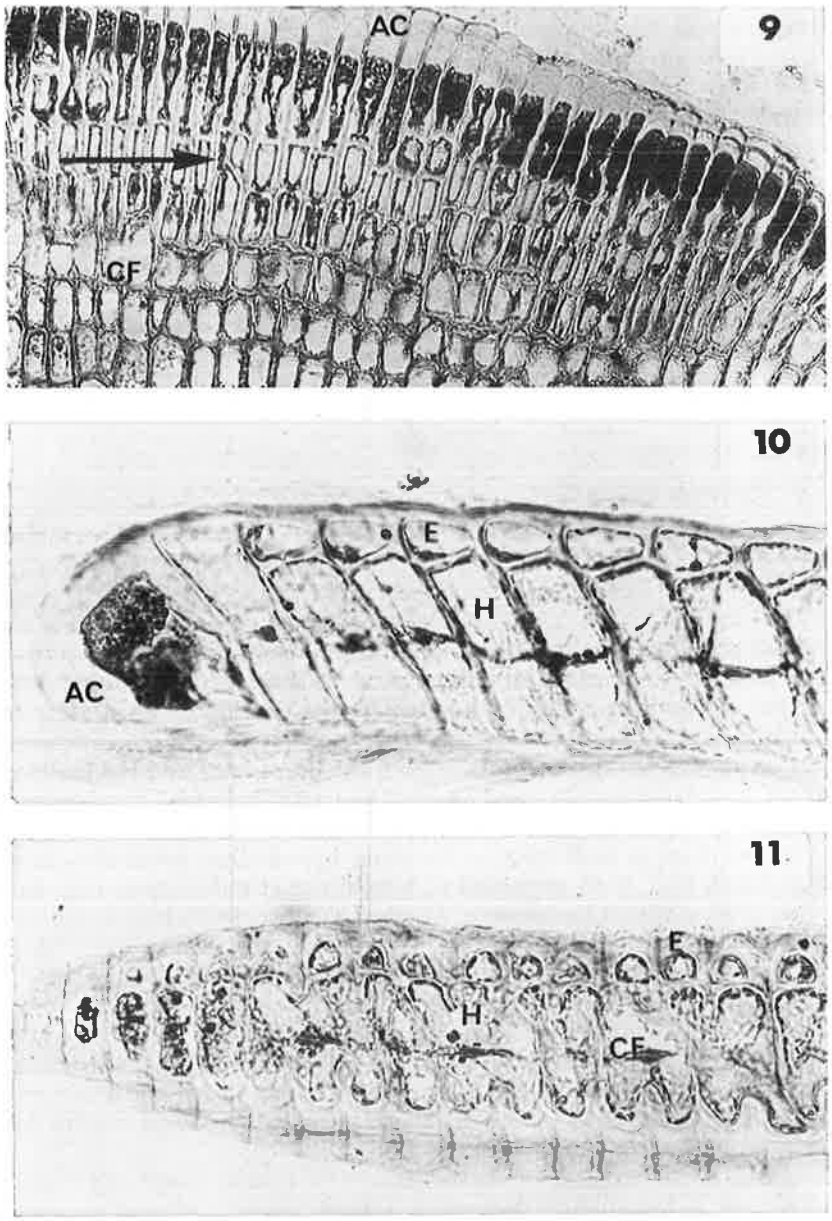
1. *The vegetative system*

The ascending branches possess a multiaxial, dorsi-ventral organization (Figs 9–11). The flattened branch apices consist of numerous laterally contiguous filaments (Fig. 9), each composed of a series of rhombohedroidal cells (Fig. 10), and each terminating in a conspicuous meristematic apical cell with a convex distal cell wall. Increase in filament (and branch) length results from transaxial-longitudinal divisions of apical cells to produce basipetally additional rhombohedroidal cells which collectively constitute the developing unistratose hypothallium.

[To emphasize the distinctness between the tissue level and the thallus level of plant body organization and to maintain terminological consistency with most pre-1978 literature, the terms hypothallium, perithallium, and epithallium are retained here in preference to the terms hypothallus, perithallus, and epithallus which have been employed in several recent publications (e.g. Bold & Wynne, 1978, p. 509; Chamberlain, 1978b; Lebednik, 1978).]

Except for apical and occasionally subapical cells, nearly every rhombohedroidal hypothallial cell, in turn, divides asymmetrically in the transverse plane to produce a smaller dorsal cell; collectively these smaller dorsal cells constitute the developing primary epithallium (Fig. 10). The flabellate appearance of many branch tips (Fig. 2) occurs as a consequence of lateral hypothallial filament production (Fig. 9, arrow). Prolific lateral filament formation produces very broad apices; scant development of lateral filaments produces narrow branch apices.

As noted by Suneson (1945), hypothallial cells appear rhomboidal in outline when viewed in longitudinal sections of branch tips (Fig. 10) but appear more or less rounded-rectangular in outline when branch tips are sectioned transversely (Fig. 11). Similarly, epithallial cells appear rectanguloid-trianguloid (l.s.) or domoid (t.s.). Extensive fusion of hypothallial cells of adjacent filaments occurs (Fig. 11), but no fusion of hypothallial cells within the same filament was observed (Figs 9, 10). Epithallial cells apparently never undergo fusion, and once formed, they do not divide again.



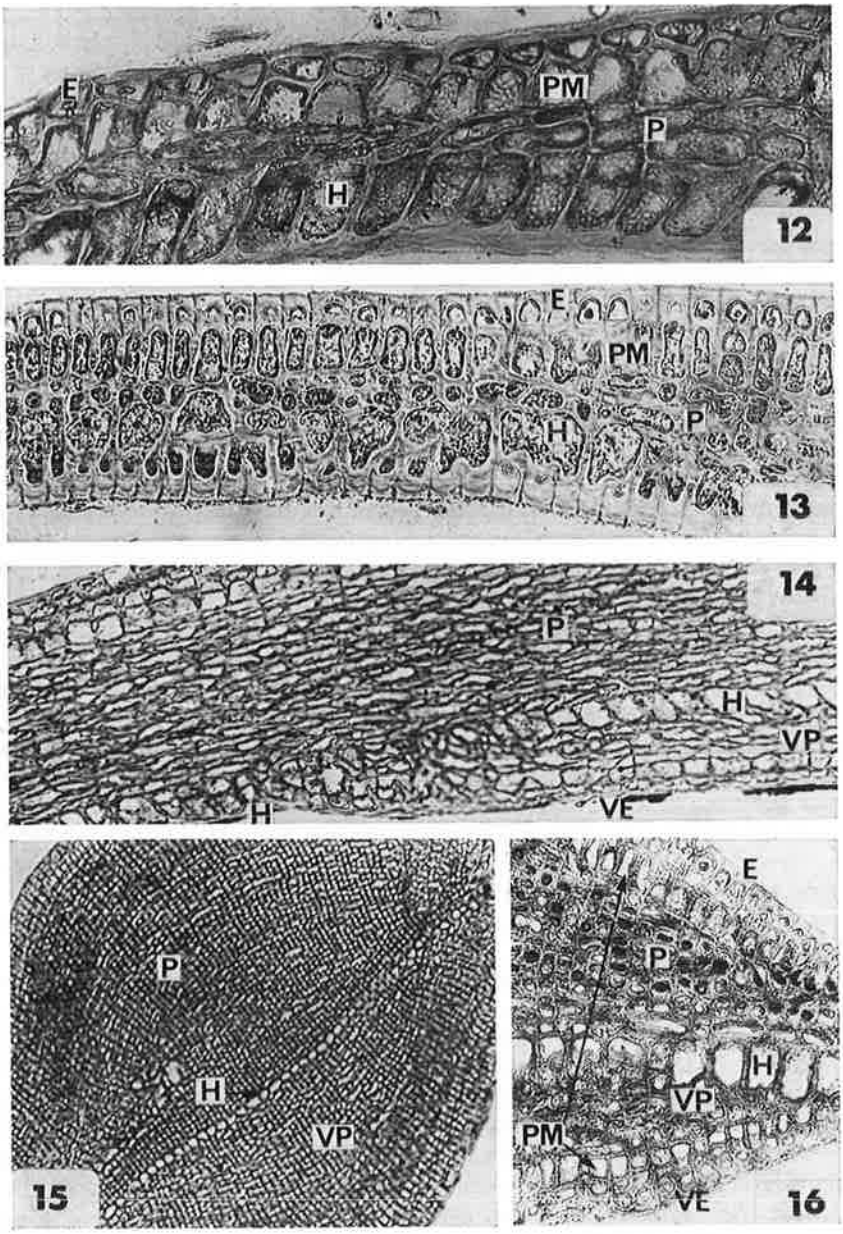
FIGS 9–11. Branch tip anatomy. Fig. 9. Peridermal section of a part of a branch tip showing multiaxial nature and origin of lateral hypothallial filaments (arrow). ×260. Fig. 10. Longitudinal section through branch tip showing apical cell, cells of a hypothallial filament and the developing epithallium. ×390. Fig. 11. Transverse section just behind apex showing fusions of cells of adjacent hypothallial filaments and one lateral margin of a branch. ×390. AC, apical cell; CF, cell fusions; E, epithallium; H, hypothallium.

Development of a perithallium usually begins within 2 mm of branch apices, and except in older veins and stipes, tissue formation takes place only in a dorsal direction (Figs 12–13). Initially, hypothallial cells divide to produce a unistratose layer of sub-epithallial cells which Suneson (1945) terms a cortex. In longitudinal sections of branches (Fig. 12), these sub-epithallial cells appear trapezoidal, rhomboidal, rectangular, or somewhat irregular in outline, and may undergo partial fusions with one another. In transverse sections of branches (Fig. 13), sub-epithallial cells appear more or less rectanguloid in outline, are dorsiventrally elongate and only occasionally show fusions with one another. This sub-epithallial layer remains meristematic.

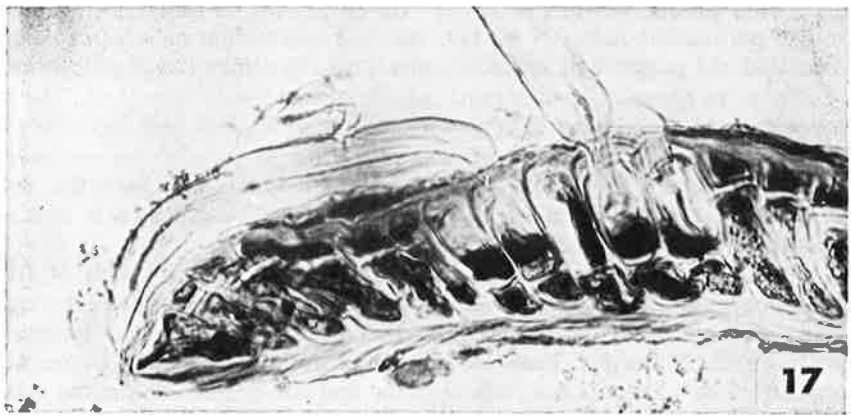
Almost concurrently, a variable number of additional cell layers, collectively described as a medulla by Suneson (1945), arise as a result of meristematic activity of sub-epithallial cells. Transverse divisions of sub-epithallial cells occur occasionally (Fig. 13), but more commonly, new cells are formed from lateral protrusions arising from the ventral portions of sub-epithallial cells (Fig. 12). In longitudinal sections of branches, sub-epithallial derivatives appear irregularly tubular in outline and axially elongate (Fig. 12). In transverse sections of branches, sub-epithallial derivatives vary considerably in outline (Fig. 13). Further cell divisions of sub-epithallial derivatives apparently also may contribute to perithallial development, but the extent to which this occurs remains uncertain.

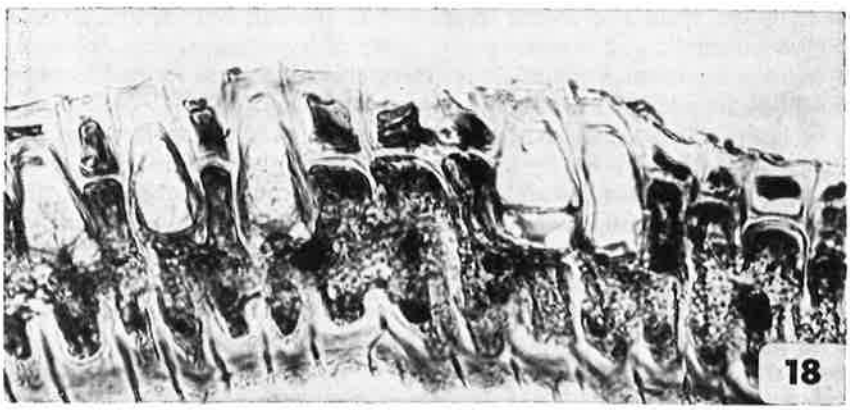
In veins and stipes of older branches (Figs 14–16), perithallial and epithallial tissues occur both dorsal and ventral to the hypothallium and over 75 layers of cells may be present (Fig. 15). At first, a ventral epithallium is produced; then a ventral perithallium forms. These ventral tissues are similar anatomically to their dorsal counterparts although the ventral perithallium usually is not as extensively developed (Fig. 15). Another distinctive feature of veins and stipes is the presence of a multilayered epithallium, derived from transverse divisions of sub-epithallial cells. These acropetally derived epithallial cells form more or less distinct rows beneath each original epithallial cell, apparently never undergo fusion, are linearly interconnected by primary pits, and are similar in size and shape to surface epithallial cells. Up to 6 epithallial cell layers have been observed in stipes.

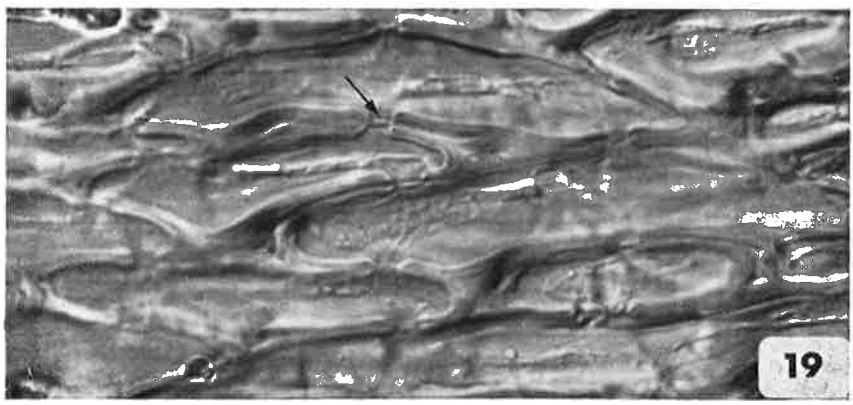
Trichocyte production apparently is uncommon (detected in $<10\%$ of all specimens examined), occurs sporadically within particular plants, and shows no obvious relationship to depth, season, or reproductive status. Trichocytes arise dorsally from transverse divisions of hypothallial cells near thallus apices and margins prior to development of perithallial tissue (Figs 17–18). They may occur singly, in pairs, or in longitudinal rows, and are conspicuously larger (up to 41 μm broad) than epithallial cells which they almost always replace. Trichocytes may or may not be densely protoplasmic and may or may not bear evident, coenocytic hair-like extensions (Fig. 17). In the material examined, trichocytes did not divide further, fuse with other cells, or form secondary pit-connections. Their function is unknown; their taxonomic significance is considered elsewhere (Woelkerling, 1980). The reported absence of trichocytes in *Metamastophora* by other investigators (Cabioch, 1972, p. 197; Segawa, 1959) no doubt reflects the infrequency of trichocyte occurrence in this taxon.



FIGS 12–16. Vegetative anatomy of older branches and veins and stipes. Fig. 12. Longitudinal section of branch. ×257. Fig. 13. Transverse section of branch. ×257. Fig. 14. Longitudinal section of vein showing development of tissues ventral to the hypothallium. ×102. Fig. 15. Transverse section of stipe. ×75. Fig. 16. Transverse section of large vein showing a several layered epithallium. ×147. E, epithallium; VE, ventral epithallium; P, perithallium; PM, secondary meristem; VP, ventral perithallium; H, hypothallium.







FIGS 17–19. Trichocytes and secondary pit-connections. Fig. 17. Longitudinal section of branch tip showing 5 consecutive trichocytes (3 with hair-extensions) in a single filament. Note small size of subtending hypothallial cells. ×450. Fig. 18. Transverse section near branch tip showing 5 trichocytes. ×450. Fig. 19. Longitudinal section through older perithallium showing secondary pit-connections between contiguous cells. Note pit plug (arrow) ×850.

Secondary pit-connections have been observed only in longitudinal sections of older perithallial tissue (Fig. 19). Because perithallial cells often become compressed, the presence of secondary pits is usually difficult to detect; however, they appear to occur as a consistent feature in the plants examined. The only other genera of Corallinaceae for which both cell fusions and secondary pit-connections are reported are *Sporolithon* [syn. *Archaeolithothamnium* (see Cabioch, 1970; 1972, p. 218) and *Synarthrophyton* (see Townsend, 1979). The taxonomic significance of this combination of characters is discussed elsewhere (Woelkerling, 1980).

In summary, two distinct vegetative meristems occur in plants of *Metamastophora flabellata*. One, designated here as the primary meristem, is situated apically and gives rise to hypothallial tissue and contributes to increase in branch length. The other, designated here as the secondary meristem, arises secondarily and produces perithallial tissue and sub-surface epithallial cells in veins and stipes. Internal organization is dorsi-ventral, and except at extreme branch apices, from 2 to 75 cell layers may be present. Branch tips, in contrast are monostromatic and are composed solely of hypothallial cells belonging to the primary meristem. Cells of the primary epithallium are formed from hypothallial cells immediately behind the primary meristem.

The term 'primary meristem' is used in preference to the term 'peripheral apical meristem' employed by Chamberlain (1978a) because the former can be applied throughout the Corallinaceae and also because it emphasizes the primordial type of growth involved. The term 'peripheral apical meristem' can be used only for encrusting, non-geniculate corallines; moreover this latter term appears potentially confusing because two different levels of anatomical organization are referred to simultaneously. Thus apical is correctly applied when discussing growth sites within individual filaments producing hypothallial cells whereas peripheral refers to the position of the entire meristem in the plant. Similarly, the term 'secondary meristem' is used here in preference to the term 'sub-apical meristem' (Chamberlain, 1978a) because the former better describes the origin of the entire meristem within the plant. Although the term sub-apical is correctly applied with reference to the growth sites within individual filaments producing perithallial cells basipetally, it is potentially confusing when applied to the meristem as a whole because in *Metamastophora* and in most other non-geniculate corallines this type of meristem is not confined to 'subapical regions' of the plant but rather occurs over much of the thallus, including regions relatively remote from apices or margins, Other authors (e.g. Adey, 1964, p. 379; Johansen, 1976, p. 226) have used the term 'intercalary meristem'.

2. *Tetrasporangial conceptacles*

The ontogeny of tetrasporangial conceptacles in Australian plants of *M. flabellata* and in South African specimens which Suneson (1945) referred to *Mastophora lamourouxii* appears to be identical (see Suneson, 1945 for details). All conceptacles consist of a roof, a floor, and a chamber (Fig. 20). The unistratose epithallium and a secondary meristem constitute the two dorsal-most tissues of the roof. The unistratose hypothallium constitutes the ventral-most layer of the floor. As noted by Suneson (1945), the conceptacular epithallium arises during conceptacle development and a localized portion of the original

vegetative epithallium ruptures and is sloughed off. The rupture point between epithallia usually is evident around the conceptacle margin (Fig. 20). Cell fusions never involve cells of the epithallium or hypothallium, but sometimes fusions do occur between adjacent cells of the secondary meristem.

The entire conceptacle chamber is bordered by a multistratose perithallium composed of cells of various shapes and sizes, which may undergo differing degrees of fusion. Three modifications of perithallial tissues are evident. Firstly, disintegration of certain perithallial cells results in enlargement of the conceptacle chamber. Remains of these cells commonly line the periphery of the chamber (Fig. 20). Secondly, certain other perithallial cells adjacent to the conceptacle pore become greatly expanded and swollen and form a distinctive pore lining (Fig. 20). The function of these cells is unknown, but they do not appear to

TABLE II. Summary of numeric data relating to male (M.C.), female (F.C.) and tetrasporic (T.C.) conceptacles

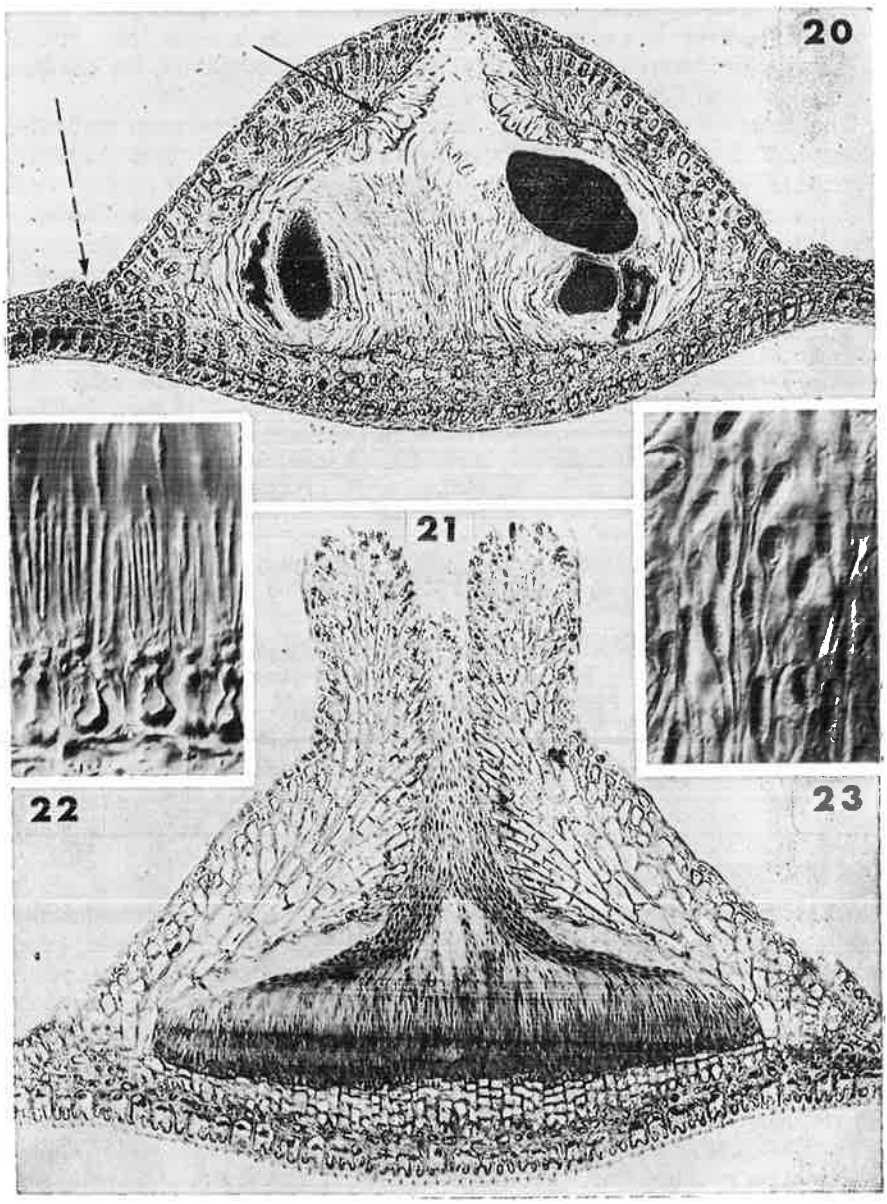
Character	Range (μm)*		
	M.C.	F.C.	T.C.
External basal diameter	1050–1300	750–1600	(750–) 850–1600
Height (above thallus surface)	900–1500 (–2000)	350–860	340–700
Roof pores:			
Length			
Surface diameter	550–900	100–203 (–309)	90–220 (–273)
Basal diameter	37–91	31–88	(16–) 30–100 (–328)
Chamber:			
Height (excluding pore)	200–364	145–435	230–510
Diameter	850–950	760–1075	625–900 (–1000)
Sporangia:			
Length	—	220–300	175–340
Diameter	—	110–190	90–240

* Extreme values given in parentheses.

block the pore during conceptacle development. Masaki (1968) reported similarly enlarged cells in tetrasporic and/or female conceptacles of various taxa he assigned to the genera *Dermatolithon*, *Lithophyllum* and *Porolithon* and referred to them as 'papillary cells' or 'papillae'. Thirdly, perithallial cells on the floor of the conceptacle chamber become modified to produce either sporangial initials and sporangia around the periphery of the chamber floor or elongate sterile filaments which collectively form a central columella of tissue (Fig. 20). At maturity many cells of the columella appear senescent or partially disintegrated. Mature sporangia are up to 340 μm long and 240 μm wide (Table II) and contain zonately divided contents. Bisporangia were not observed.

3. *Gametic conceptacles*

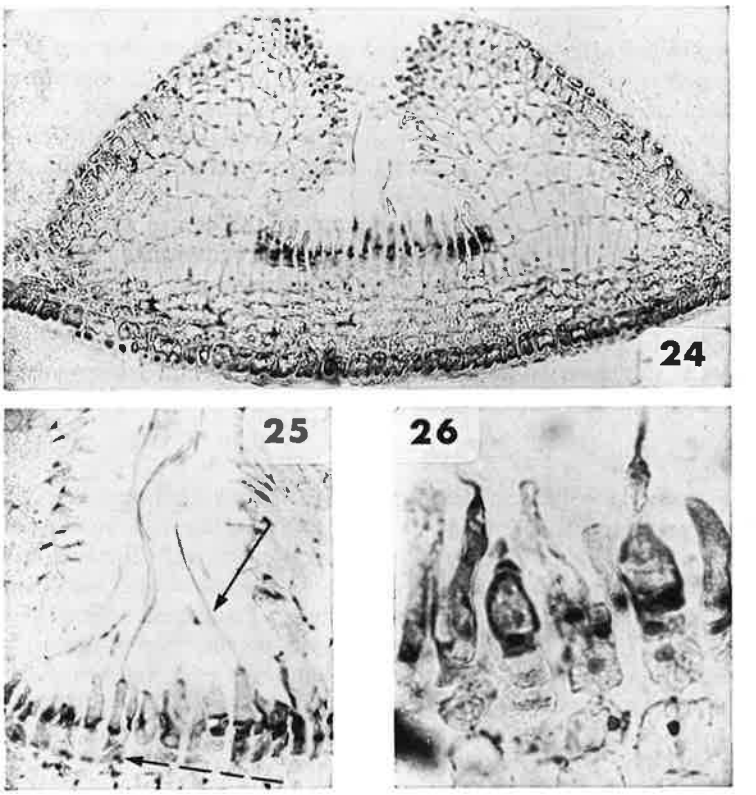
Mature male conceptacles (Fig. 21) possess a number of distinctive structural features. The conceptacle roof, for example, is commonly 10 or more cells thick; in other conceptacle types it is rarely more than 5–6 cells thick. In male conceptacles it is not possible to distinguish readily between the secondary meristem and its derivatives in the roof. Instead, the tissue beneath the epi-



FIGS 20–23. Tetrasporic and male conceptacles. Fig. 20. Mature tetrasporic conceptacle with central columella. Note point of rupture (dashed arrow) of vegetative epithallium and swollen perithallial cells lining the pore channel (arrow). ×73. Fig. 21. Mature male conceptacle. ×94. Fig. 22. Developing spermatangia attached to cells lining the conceptacle chamber floor. ×400. Fig. 23. Mature spermatangia in pore channel. ×325.

thallium appears more or less uniform and is composed of rectanguloid (in outline) cells organized into laterally contiguous filaments. Cell fusions are infrequent, and perithallial cells lining the elongate pore channel are not enlarged, swollen or otherwise markedly modified. Similarly, perithallial cell disintegration and cell remnants were not found around the periphery of the chamber in the specimens examined.

As in other conceptacle types, perithallial cells beneath the chamber floor commonly fuse with one another but not with cells of the subtending unistratose hypothallium, which constitutes the ventral-most layer of the conceptacle. However, virtually all perithallial cells lining the chamber floor (which do not fuse with other cells) give rise to functional spermatangial tissue, a situation in sharp contrast to tetrasporangial conceptacles where both fertile and sterile tissues arise from the floor. At maturity, the entire chamber is filled with more or less ovoid spermatangia, each bearing a long, hyaline, basal attachment stalk



FIGS 24–26. Female conceptacles. Fig. 24. Conceptacle with carpogonial branches in various states of maturity. ×62. Fig. 25. Carpogonia with trichogynes. Note trichogyne (arrow) on one of the more peripherally situated carpogonia, and supporting cell (dashed arrow) with 2 carpogonial branches. ×240. Fig. 26. Peripheral carpogonia with arrested trichogyne development. ×420.

presumably of cell wall material (Figs 22–23). Spermatangial ontogeny in *M. flabellata* is the same as that described by Suneson (1945) for specimens he referred to *Mastophora lamourouxii* and involves development of several spermatangia from each of the spermatangial initials lining the conceptacle floor (Fig. 22).

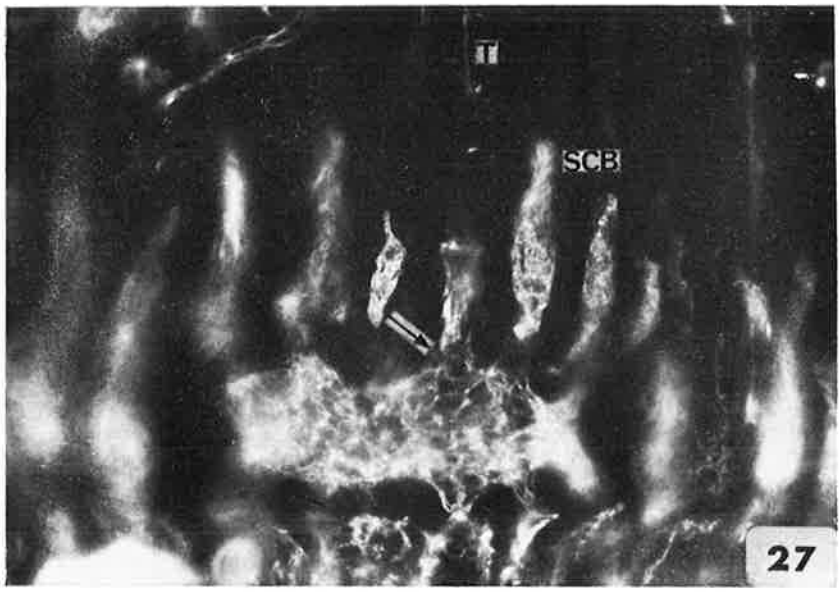
Female conceptacles (Figs 24, 31) structurally are similar to tetrasporangial conceptacles; the same vegetative tissues are present and the same organization of the vegetative tissues surrounding the conceptacle chamber is evident. Likewise, a new conceptacular epithallium arises, replacing a localized portion of the original vegetative epithallium which ruptures and is lost during conceptacle formation. However, major differences occur in development of reproductive and associated structures. Carpogonial branches arise over the entire floor of the female conceptacle and a sterile columella does not develop (Fig. 24). Instead, more or less vertically elongate perithallial cells (termed basal cells by Ganesan, 1962; Kylin, 1956; Lebednik, 1977; Suneson, 1943; and disc cells by Fritsch, 1945, p. 646) lining the chamber floor give rise to fertile axes, each composed of a supporting cell and a single (or occasionally a pair) two-celled carpogonial branch (Figs 25–26). When only a single carpogonial branch is produced, the supporting cell appears as the ventral-most cell of a 3-celled filament borne on a vertically elongate perithallial cell. All cells of the fertile axis appear much more densely cytoplasmic than the progenitor perithallial cells. Cell fusions involving these progenitor perithallial cells have not been observed.

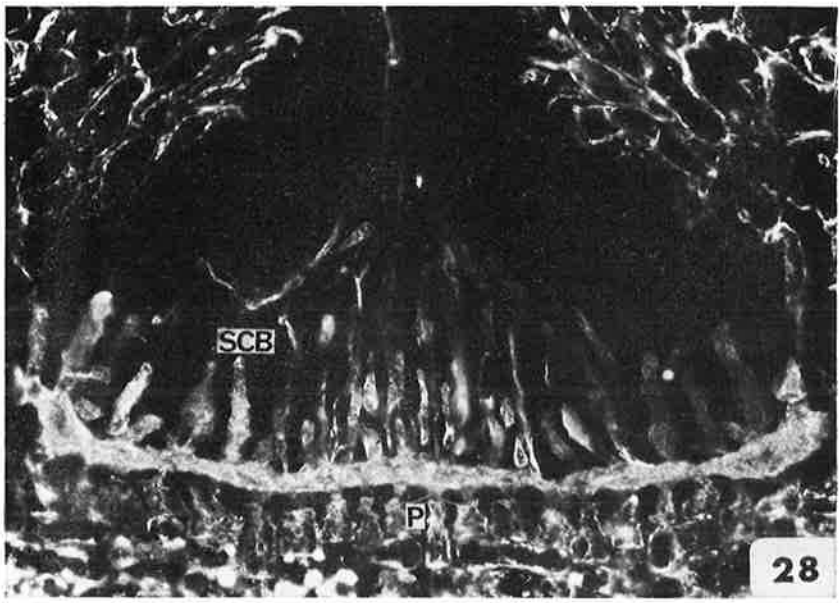
Normally only a few carpogonia situated in the centre of the conceptacle chamber floor reach full reproductive maturity but occasionally more peripheral carpogonia also develop completely (Fig. 25). Trichogynes of these carpogonia become extremely elongate and ultimately may protrude through the conceptacle pore. Growth of trichogynes in most or all of the more peripherally situated carpogonia (Fig. 26) is usually arrested. Karyogamy and trichogynes bearing attached spermatia have not been observed.

4. *Carposporophytes*

Mature carposporophytes develop within female conceptacles following presumed karyogamy; each consists of a large fusion cell and gonimoblast filaments bearing terminal carposporangia. Fusion cell formation initially involves the fertilized carpogonium and its hypogynous and supporting cells but quickly extends to include supporting cells of adjacent unfertilized carpogonial branches (Fig. 27). The zygotic nucleus presumably migrates from the transformed carpogonial branch into the developing fusion cell below. Examination of numerous conceptacles containing very young fusion cells has failed to uncover any evidence for formation of a tubular siphon (Ganesan, 1962, p. 110; Lebednik, 1977, p. 391; Suneson, 1937, p. 10) or a carpogonial or auxiliary cell outgrowth (Minder, 1910; Suneson, 1937, p. 55; see also Dixon, 1973, p. 159 and Rosenvinge, 1917, p. 245) through which a zygotic nucleus or a derivative thereof could migrate from the carpogonium to another cell.

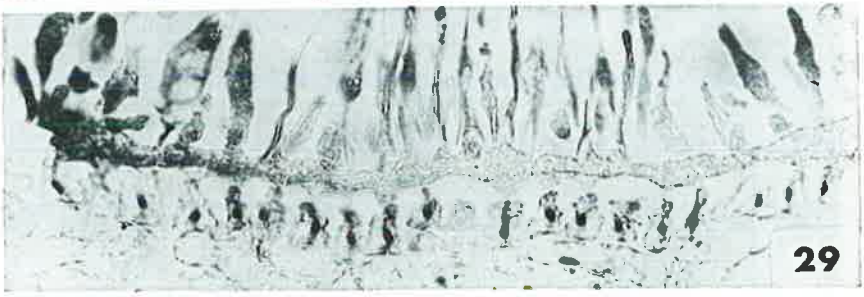
The developing fusion cell grows progressively larger as additional supporting cells become incorporated; ultimately it extends across much of the conceptacle floor and includes the supporting cells of all or nearly all of the original

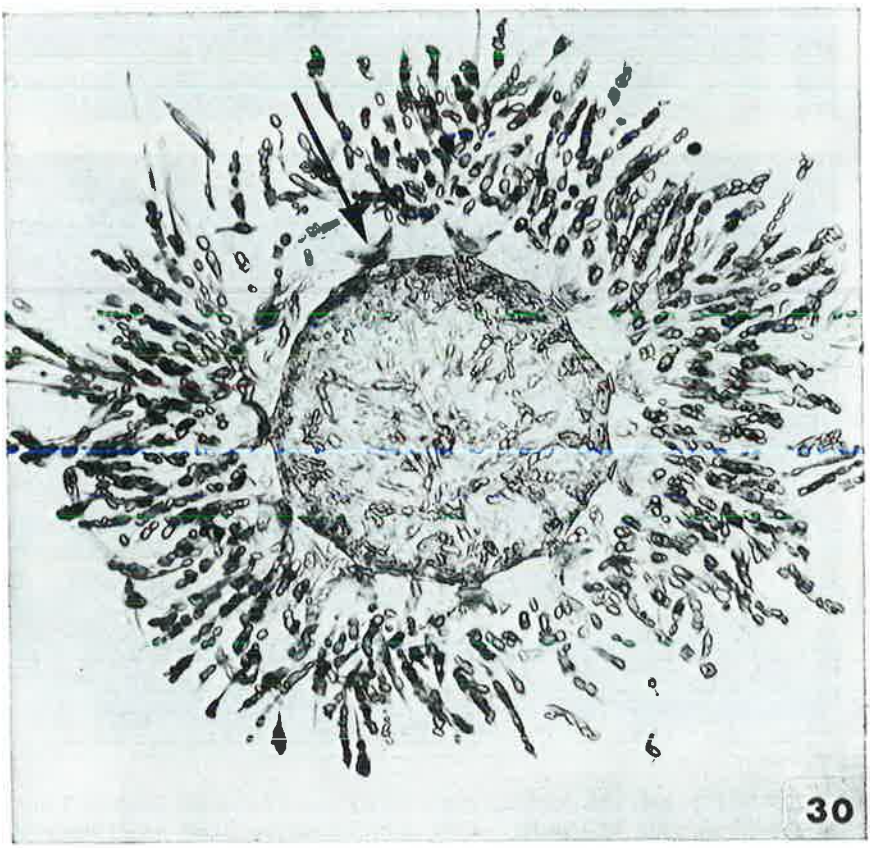




FIGS 27–28. Fusion cell development. Fig. 27. Very young fusion cell involving 7 supporting cells showing open channel (arrow) into carpogonial branch which produced the zygotic nucleus. Note trichogyne remains (T) and adjacent senescing carpogonial branches (SCB) without trichogynes. ×500. Fig. 28. Fusion cell just prior to gonimoblast filament production. Note how all supporting cells have become incorporated into the fusion cell, senescing carpogonial branches (SCB) on dorsal surface and ventral attachment of fusion cell to elongate perithallial cells (P) on conceptacle floor. × 300.

carpogonial branches (Fig. 28). Unfertilized carpogonial branches do not become incorporated into the fusion cell but instead senesce on the dorsal surface of the maturing fusion cell, from which they usually remain separated by cell wall material (Fig. 27). Commonly, these carpogonial branches become clavate or otherwise enlarged and elongate, appear to contain globules of senescent

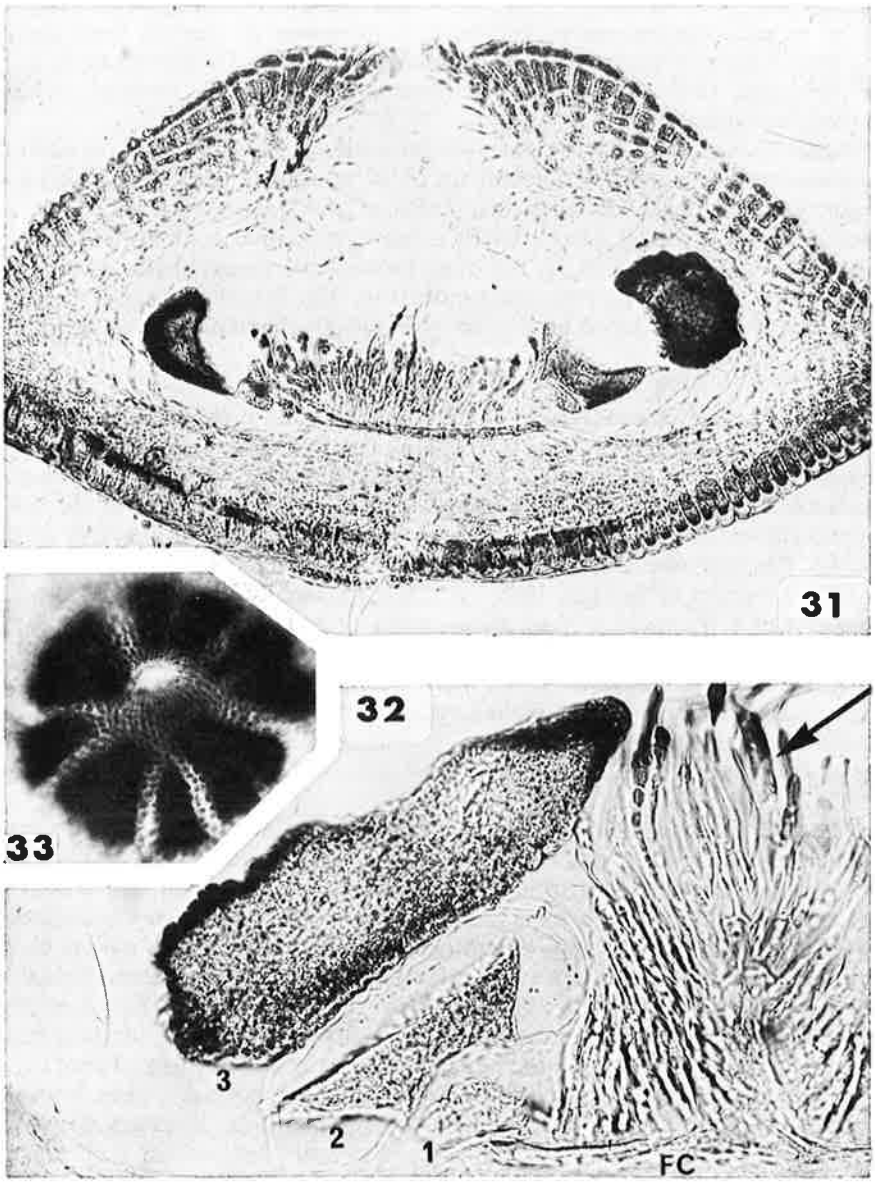




FIGS 29–30. Fusion cells. Fig. 29. Fusion cell attachment to conceptacle floor by means of intact perithallial cells containing haploid nuclei. ×290. Fig. 30. Mature fusion cell with remains of carpogonial branches and a marginal ring of 11 basal cells of gonimoblast filaments (arrow). ×170.

cytoplasm (?), and become unicellular (Fig. 32). Any carpogonial branches and supporting cells not involved in fusion cell formation apparently degenerate.

The fusion cell permanently remains attached to the conceptacle floor by means of the vertically elongate perithallial cells which originally produced the



FIGS 31–33. Carpospore production. Fig. 31. Sectional view of conceptacle with mature carposporphyte. ×80. Fig. 32. Three celled gonimoblast filament (1–3) with terminal carposporangium (3). Note fusion cell (FC) and senescing carpogonial branches (arrow). ×260. Fig. 33. Surface view of conceptacle with mature carposporangia. ×60.

fertile axes (Figs 28–29). Although these cells commonly become distorted and peg-like, they never merge with the fusion cell and hence retain their presumably haploid nuclei (Fig. 29). Whether or not the haploid nuclei in the supporting cells involved in fusion cell ontogeny degenerate remains unanswered, and consequently it is not known if the fusion cell contains both diploid and haploid nuclei or only diploid nuclei. Fusion cells presumed to contain both diploid and intact haploid nuclei have been recorded in other Corallinaceae (e.g. by Balakrishnan, 1947; Ganesan, 1962; Suneson, 1937), but the function and fate of these nuclei are uncertain.

Mature fusion cells (Fig. 30) resemble flattened spheroids and bear (in addition to senescing carpogonial branches) up to 12 marginal, unbranched, 2–3 (–4) large celled gonimoblast filaments. Cells of the gonimoblast filaments are interconnected by large pits, contain dense cytoplasmic contents and do not fuse with other cells (Figs 31, 32). The terminal carposporangia form a ring around the periphery of the conceptacle (Fig. 33). Whether successive carposporangia can be produced on a given gonimoblast filament remains uncertain.

DISCUSSION

The thallus of *Metamastophora flabellata* is noteworthy among the non-geniculate Corallinaceae in that a primarily erect or ascending habit occurs in conjunction with a dorsiventral organization of tissues. This combination of characters creates problems with reference to the traditional use of the terms 'hypothallium' and 'perithallium' for describing the vegetative anatomy of this species. Presently the term 'hypothallium' (first suggested by Areschoug, 1852, p. 520) is defined (Johansen, 1976, pp. 226–7) generally as the ". . . lowermost filaments of a crust which have grown more or less parallel to the substrate", and the term 'perithallium' (first suggested by Rothpletz, 1891, p. 307) is applied generally to those filaments arising from the hypothallium such that ". . . they are oriented more or less at right angles to the substrate". In *M. flabellata*, however, the reverse situation occurs: 'hypothallial' filaments grow more or less perpendicular to the substrate and 'perithallial' filaments grow more or less parallel to the substrate.

To avoid potential confusion, three different solutions seem possible. One is to use the terms medulla and cortex, the respective homologues (Johansen, 1976) of hypothallium and perithallium. These terms have been applied widely to describe the vegetative anatomy in protuberances of non-geniculate Corallinaceae and in erect thalli of geniculate Corallinaceae, both of which show a more or less radial or bilateral organization of tissues. They also have been applied to *Mastophoropsis* (Woelkerling, 1978), a dorsiventrally organized, non-geniculate member of the Corallinaceae with an erect or ascending habit. In all these cases, the axial filaments constituting the medulla form a multidimensional core which is surrounded by cortex, and both medullary and cortical tissues originate from a single meristem. In *Metamastophora flabellata*, however, the axial filaments lie in a single plane, and, except in veins and stipes, they are not surrounded completely by other tissues. More importantly the axial filaments of *M. flabellata* are produced by one meristem while the remaining vegetative tissues are produced by a second meristem. Thus the use of the terms 'medulla' and 'cortex' seems inappropriate.

The second solution is to adopt the terminology used by Suneson (1945) for South African plants of *Metamastophora* which he referred to *Mastophora lamourouxii*. Suneson recognized four tissues: a ventral hypothallium, a dorsal layer of cover-cells (= epithallium), a cortex, and a medulla. This terminology, however, is inconsistent with general usage for coralline algae and also is potentially misleading. Firstly, the presumed homology between hypothallium and medulla within the Corallinaceae breaks down since Suneson used both terms to describe different tissues within the same organism. The tissue termed a medulla by Suneson is not hypothallial but rather perithallial in nature. Secondly, Suneson's terms cortex and medulla really apply to the same tissue (the perithallium): his cortex actually is the meristematic layer of his medulla. This results in artificially separating one tissue into two. Thus it seems best not to perpetuate the usage of Suneson's terminology.

The third solution, which has been adopted here, is to define hypothallium and perithallium in relation to thallus meristems (see Cabioch, 1972, p. 171) rather than substrate (which has no direct genetic control over anatomical organization). Thus hypothallium, as used here, refers to the tissue derived basipetally from a primary meristem. This meristem may be located apically as in *Metamastophora* or peripherally as in *Heteroderma*, *Melobesia*, and a number of other encrusting Corallinaceae. The term perithallium, as used here, refers to the vegetative tissue derived basipetally from a secondary meristem. Cells constituting the secondary meristem arise by division from hypothallial cells; they are not derived from and never formed a part of the primary meristem as occurs in geniculate Corallinaceae (see Johansen, 1969, p. 17).

In most non-geniculate Corallinaceae, this secondary meristem lies just beneath the surface tissue or epithallium. The epithallium is composed of anatomically and functionally distinctive cells (Bailey & Bisalputra, 1970; Johansen, 1976). The surface layer of epithallial cells in *Metamastophora flabellata* arises from lateral divisions of hypothallial cells situated immediately behind the primary meristem. Any subsurface layers of epithallial cells, in contrast, arise acropetally from the secondary meristem.

The definitional changes proposed here do not affect past usage of the terms hypothallium and perithallium in relation to most non-geniculate Corallinaceae, which appear to possess both primary and secondary meristems. However, certain taxa [e.g. *Mesophyllum lichenoides* (Ellis) Lemoine—see Hamel & Lemoine, 1953, p. 77], characterized by a so-called co-axial hypothallium (Johansen, 1976, p. 233), require re-examination to determine whether or not both primary and secondary meristems do occur. As noted by Dixon (1973, pp. 58, 83) such taxa possess a vegetative anatomy similar to intergenicular portions of certain geniculate Corallinaceae; in these plants primary growth results from a single apically situated meristem, most cells of which become laterally displaced and may subsequently contribute to increase in thallus girth (Johansen, 1969, p. 17). If, indeed, only one vegetative meristem is present, it would seem best to apply the terms cortex and medulla because these tissues are derived from the same meristem (Dixon, 1973, p. 72; Johansen, 1969, p. 17) and thus are fundamentally the same.

One consequence of these definitional changes is that perithallium and cortex become analogous rather than homologous since they arise from two different

meristems. Hypothallium and medulla, however, technically remain homologous since both are derived from a primary meristem. This relational alteration does not affect the practical usage of the terms.

Results from this study indicate that *Metamastophora flabellata* is procarpic; the supporting cell of the fertilized carpogonial branch functions as the auxiliary cell. Prior to initiation of gonimoblast filaments, however, this auxiliary cell develops into a large fusion cell which incorporates most or all of the supporting cells present in the conceptacle.

The details of post-fertilization development elucidated here for *M. flabellata* provide a basis for comparative discussion and comment on certain aspects of carposporophyte ontogeny within the Corallinaceae. One aspect concerns the manner in which the zygotic nucleus or its derivative(s) presumably gets from the fertilized carpogonium to the auxiliary cell or developing fusion cell. Actual transfer or migration apparently never has been documented convincingly for any member of the Corallinaceae. However, at least three different pathways of transfer have been reported. One involves formation of a direct channel within cells of the carpogonial branch presumably as a result of partial or complete breakdown of contiguous cell walls. This pathway has been reported or inferred in *Amphiroa ephedraea* (Lamarck) Decaisne by Johansen (1968), *Bossiella californica* subsp. *schmittii* (Manza) Johansen by Johansen (1973), *Calliarthron tuberculosum* (Postels et Ruprecht) Dawson by Johansen (1969), *Corallina mediterranea* Areschoug in J. Agardh by Yamanouchi (1921, as *C. officinalis* var. *mediterranea*), *Phymatolithon rugulosum* Adey by Adey (1964) *Lithothamnion glaciale* Kjellman by Adey & Adey (1973) and *Metamastophora flabellata* (this paper). A second pathway involves reported production of a tubular siphon [variously referred to as a transfer tube (Lebednik, 1977), a connecting filament (e.g. Fritsch, 1945; Suneson, 1937), an ooblast (e.g. Smith, 1955), or an ooblastema (e.g. Balakrishnan, 1947; Ganesan, 1962)] from the fertilized carpogonium directly to the supporting cell without involvement of other cells. This pathway has been reported in *Fosliella lejolisii* (Rosanoff) Howe by Suneson (1937), p. 10 (as *Melobesia*), *Mesophyllum conchatum* (Setchell et Foslie in Foslie) Adey by Lebednik (1977) and *Tenarea ascripticia* (Foslie) Adey by Ganesan (1962) (as *Dermatolithon*), and apparently is presumed by Lebednik (1977, p. 394, Fig. 19) to occur throughout the Corallinaceae. A third pathway involves development of an "upward directed process" from the auxiliary cell which fuses with the fertilized carpogonium. This has been reported only in *Choreonema thuretii* (Bornet in Thuret et Bornet) Schmitz by Minder (1910) and by Suneson (1937, p. 57) and noted by Dixon (1973, p. 159) and Rosenvinge (1917, p. 214).

Photographic documentation supporting the existence of any one of these pathways is available only for *Metamastophora flabellata* (see Fig. 27); in all other cases only verbal statements and/or drawings (which often appear stylized to varying degrees) have been provided. Moreover, Johansen (1968, p. 322) strongly questions the existence of a pathway involving production of a tubular siphon. It is noteworthy also that Lebednik's presumption that such tubular siphons occur throughout the Corallinaceae (Lebednik, 1977, p. 394, Fig. 19) is based on a single observation (Lebednik, 1977, p. 391) in which the supposed siphon was not intact. Thus until further detailed studies are undertaken and

supported by photographic documentation and until existing reports are substantiated by additional work, the events immediately following fertilization in the Corallinaceae will remain largely shrouded by uncertainty.

A second aspect of carposporophyte ontogeny requiring comment concerns the relationship between the mature fusion cell and the subtending layer of perithallial cells. In *Metamastophora flabellata*, the fusion cell is formed only from supporting cells of carpogonial branches, while the subtending layer of elongate perithallial cells functions only as an anchoring mechanism. This situation also occurs in a number of other non-geniculate Corallinaceae [e.g. *Fosliella farinosa* (Lamouroux) Howe—see Balakrishnan, 1947 (as *Melobesia*); *Lithophyllum expansum* Philippi—see Suneson, 1937; *Tenarea ascriptica* (Foslie) Adey—see Ganesan, 1962 (as *Dermatolithon*)]. However, in other non-geniculate Corallinaceae [e.g. several (?) species of *Clathromorphum* and *Mesophyllum*—see Lebednik, 1977; *Melobesia pacifica* Masaki—see Masaki, 1968, p. 8, pls. 39-40; *Mesophyllum lichenoides* (Ellis) Lemoine—see Suneson, 1937, p. 66; 1943, p. 55 (both as *Lithothamnion*); *Mesophyllum philippi* (Foslie) Adey—see Pilger, 1908 (as *Lithothamnion*)] the fusion cell is formed both from supporting cells and at least some subtending perithallial cells. Moreover, Suneson (1943, p. 54) notes that in several taxa the subtending perithallial cells appear densely cytoplasmic, even before karyogamy. The significance of this variation in subtending perithallial cell appearance and involvement in fusion cell formation remains uncertain. However, cell fusions apparently do not occur between these subtending perithallial cells (at least prior to karyogamy), and argument could be made that these cells constitute a part of the fertile axis whether or not they appear densely cytoplasmic.

A final aspect requiring comment concerns development of gonimoblast filaments. In *Metamastophora flabellata*, gonimoblast filaments do not fuse with any other cells, are unbranched and bear terminal carposporangia. Similar development apparently occurs in a number of other non-geniculate Corallinaceae including *Fosliella farinosa* (Lamouroux) Howe (see Balakrishnan 1947, as *Melobesia*), *Melobesia pacifica* Masaki (see Masaki, 1968), and *Tenarea dispar* (Foslie) Adey (see Masaki & Tokida, 1960, pl. 4, as *Dermatolithon*).

A more complex type of gonimoblast development, in contrast, occurs in at least some species of *Clathromorphum*, *Melobesia* and *Mesophyllum* (see Lebednik, 1977 for details). In these taxa only the more centrally situated supporting cells become incorporated into the fusion cell. More peripherally located supporting cells and their arrested carpogonial branches remain intact. When the fusion cell produces gonimoblast filaments, open contact or partial fusion occurs between certain cells of the gonimoblast filaments and the supporting cells of the peripheral carpogonial branches prior to carpospore formation. Although connections are established between cells of gonimoblast filaments and other cells, the gonimoblast filaments remain readily recognizable as distinct structures bearing terminal carposporangia (Lebednik, 1977, figs 10, 12, 13, 16, 18). Growth of gonimoblast filaments does not stop when open contact between cells occurs and no new filaments bearing sporangia develop from the partially fused cells.

The fusion of gonimoblast filament cells with other cells prior to carpospore formation is not unique to *Clathromorphum*, *Melobesia* and *Mesophyllum* but

occurs in a diversity of other Rhodophyta, including members of the Acrotylaceae (Kraft, 1977a), the Dicranemaceae (Kraft, 1977b), the Mychodeaceae and Mychodeophyllaceae (Kraft, 1978), the Nizymeniaceae (Searles, 1968; Womersley, 1971), the Rhodophyllidaceae (Min-Thein & Womersley, 1976) and the Solieriaceae (Kraft, 1975; Min-Thein & Womersley, 1976). Because of this and because the carpospore bearing filaments emanate from the fusion cell, it is difficult to accept Lebednik's (1977, p. 391 et seq.) interpretation of carposporophyte ontogeny and his associated terminology. It appears, rather, that development of carposporophytes in *Clathromorphum*, *Mesophyllum* and *Melobesia* is similar to other non-geniculate Corallinaceae for which data are available in that one of the supporting cells involved in fusion cell formation functions as the auxiliary cell. The more peripheral supporting cells not involved in fusion cell formation may become connected secondarily to developing gonimoblast filaments in some taxa but they do not function as auxiliary cells. In addition, filaments producing carpospores originate from the fusion cell and not from other cells with which gonimoblast filament cells have established open contact. It follows, then, that the taxa studied by Lebednik (1977) are procarpic with supporting cells functioning as auxiliary cells in a manner similar to that in *Metamastophora flabellata*.

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STUDIES ON *METAMASTOPHORA* (CORALLINACEAE, RHODOPHYTA). II. SYSTEMATICS AND DISTRIBUTION

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A monographic revision of the *Metamastophora* (Corallinaceae, Rhodophyta) based on inductive and taxometric analyses of data obtained from all relevant type collections and over 500 other specimens has led to the conclusion that the genus is monotypic. Critical assessments of over 60 morphological/anatomical characters including those used previously for diagnostic purposes has failed to reveal any basis upon which taxa can be delineated reliably within the genus. Several taxa hitherto recognized as distinct species represent monstrosities in which the deformities are induced by the presence of particular invertebrates. The generic description is emended to take account of newly obtained data; lectotype specimens are designated; and all pertinent taxonomic and nomenclatural information is summarized. *Metamastophora* occurs definitely only in southern Australia and southern Africa; other records are doubtful and almost certainly are based on misidentifications. The genus is assigned to the subfamily Lithophylloideae and its relationships to other Corallinaceae are considered.

Setchell (1943) established the genus *Metamastophora* for nongeniculate Corallinaceae (Rhodophyta) possessing (1) a tenaculate, branched, taeniform habit; (2) partly or entirely polystromatic vegetative thalli with little internal differentiation of tissues; and (3) uniporate tetrasporangial conceptacles. Setchell recognized five species including three [*M. canaliculata* (Harvey in Hooker) Setchell, *M. flabellata* (Sonder) Setchell—the designated type species (Setchell, 1943, p. 130) and *M. plana* (Sonder) Setchell] which are based on southern Australian type collections. The two other species [*M. lamourouxii* (Decaisne ex Harvey) Setchell and *M. stelligera* (Endlicher et Diesing) Setchell, the latter including *Mastophora hypoleuca* Harvey] are based on South African type collections.

Because specimens of only one (*Metamastophora flabellata*) of the five taxa were available to him, Setchell (1943, p. 130) considered his "outline" as tentative and recognized the need for further detailed studies. Consequently taxon concepts within *Metamastophora* were rather vague, and species were delineated primarily on apparent (but not demonstrated) differences in branching, thallus thickness, branch margin morphology and pruinosity.

Suneson (1945), using the old generic name *Mastophora*, provided some additional data on three South African collections as well as several specimens in the J. Agardh herbarium (**LD**) and concluded independently of Setchell that *Mastophora hypoleuca* and *Metamastophora stelligera* were conspecific. Later, May (1965), apparently utilizing data from Setchell (1943), published a key to species of *Metamastophora* recorded from Australia. No detailed comparisons of type collections have been made and no critical assessments of the relative

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variability in and the consequent taxonomic value of characters used in species delineations have been published. As a result, uncertainty has continued to surround *Metamastophora* and its included species, and Johansen (1976, p. 232) relegated the genus to a group of poorly known or unclearly understood Corallinaceae.

Subsequently, two papers containing data on southern Australian taxa assigned by Setchell (1943) to *Metamastophora* have appeared. One (Woelkerling, 1978) reported the occurrence of multiporate tetrasporangial conceptacles in the lectotype and other specimens of *M. canaliculata*, thus necessitating removal of this species from *Metamastophora* and resulting in the establishment of a new genus (*Mastophoropsis*) to accommodate it. The other paper (Woelkerling, 1980) presented a morphological/anatomical account of *Metamastophora flabellata*, the type species, and contained data which suggested that at least some characters used by Setchell (1943) may be too variable or otherwise unacceptable to serve as reliable criteria for delineating species.

The present study provides a monographic revision of *Metamastophora* based on inductive and taxometric analyses of data obtained from syntype or lectotype and isotype specimens of all taxa assigned by Setchell (1943) to the genus and from numerous other specimens and populations collected primarily along southern Australian coasts. Specific objectives have been to re-evaluate criteria previously used to delineate species within the genus, to determine whether any other morphological or anatomical characters could function as reliable criteria for species separation, and to reassess species concepts based on results from the first two objectives. Nomenclatural, taxonomic, and distributional information also are provided and relationships of *Metamastophora* to other genera of the Corallinaceae are considered.

MATERIALS AND METHODS

Data for inductive and taxometric analyses have been obtained on over 60 morphological and anatomical characters; more than 500 individuals have been examined including syntype or lectotype material of all species referable to *Metamastophora*. The collections studied include both single plants and populations of 2–37 individuals gathered concurrently from a particular locality. Specimens borrowed from **ADU, MEL, MELU, NSW, TCD** and **UWA** have been annotated; photographs of these and prepared microscope slides have been retained at **LTB** along with the author's personal collections. Microtechnique, microscopy procedures and terminology follow Woelkerling (1980).

Inductive analyses involved assessment of all data utilizing the principles of orthodox taxonomy (Davis & Heywood, 1963, p. 78). Taxometric analyses involved both classification and ordination procedures employing data matrices generated with the use of Gower's general similarity coefficient (Sneath & Sokal, 1973, p. 135) modified to include negative matches. Classification was hierarchical, agglomerative, non-overlapping, and based on a "UPGMA" strategy (Sneath & Sokal, 1973, p. 230). Ordination involved the Bray–Curtis analysis outlined by Cox (1972). The 59 characters (Table I) examined taxometrically include all those (except pruinosity) used previously (e.g. Harvey, 1849; May, 1965; Setchell, 1943; Sonder, 1848) to delineate species as well as a number of others found to exhibit variability in the present study. Two types of data matrices were analysed: one involving only vegetative characters and one involving both vegetative and reproductive characters. The latter included only tetrasporangial plants because too few male and female plants were available for meaningful taxometric work and because the type collections of all species do not include both male and female as well as tetrasporangial individuals. However, both sexual and tetrasporangial plants were included in the analyses involving only vegetative features. The 43 plants selected for taxometric analyses collectively satisfied all criteria listed in Table II. Mean values for numeric characters nearly always represent 5–10 measurements per individual. Wherever possible, cell measurements of more mature tissues were obtained from regions other than veins and stipes where the peri-

thallium encompassed 4–8 layers of cells. Cell measurements of young tissues were obtained from regions devoid of a perithallium but not immediately behind the primary meristem.

TABLE I. Characters utilized in taxometric analyses of *Metamastophora*

I. *Binary characters* (each scored as present or absent)	
1–4	Branching: divaricate, fastigiate, irregular, subdichotomous
5–8	Branch apices: flabellate, obtuse, involute, flat
9–10	Branch margins: involute, flat
11	Transverse concentric striae
12	Veins
II. *Numeric characters* (scored as a single or a mean value for each individual)	
13	Thallus height
14–16	Stipe width, median branch width, branch tip width
17–22	Young hypothallial tissue (ls & xs); cell length (height), cell diameter, L/D ratio
23–28	Young epithallial tissue (ls & xs); cell length (height), cell diameter, L/D ratio
29–34	Older hypothallial tissue (ls & xs); cell length (height), cell diameter, L/D ratio
35–40	Older epithallial tissue (ls & xs); cell length (height), cell diameter, L/D ratio
41–46	Perithallial tissue (ls & xs); cell length (height), cell diameter, L/D ratio
47–52	Perithallial meristem (ls & xs); cell length (height), cell diameter, L/D ratio
53–57	Tetrasporangial conceptacles: external basal diameter, roof pore diameter, roof pore length, chamber diameter, chamber height (excluding pore)
58–59	Mature tetrasporangia: length, diameter

TABLE II. Criteria satisfied in selecting plants for taxometric analyses

I. Type collection material to include:	
A.	Lectotype specimens of *Metamastophora flabellata*, *M. lamourouxii*, *M. plana* and *Mastophora hypoleuca*
B.	A syntype specimen of *Metamastophora stelligera* (a lectotype has yet to be chosen from specimens presumably at **W**; see also Suneson 1945, p. 252 regarding material at **LD**)
C.	Additional isotypes of *M. lamourouxii*, *M. plana* and *Mastophora hypoleuca* to increase representation of these taxa
II. Additional Australian material to represent:	
A.	All months of the year
B.	The known depth range
C.	The known geographic range
D.	Both collections comprising single specimens and populations
E.	The observed range of morphological and anatomical variation
F.	Specimens referred by Harvey (1855, 1863) to *Mastophora lamourouxii and M. plana*
G.	Male, female and tetrasporangial individuals (*only* for matrix involving just vegetative features)

ASSESSMENT OF CHARACTERS AND DELINEATION OF TAXA

TAXOMETRIC ANALYSES

Results from all ordinations and cluster analyses are similar (Table III) and indicate that a high degree of uniformity occurs among all individuals involved. This uniformity also is evident among specimens from the various type collections (Table II) both when considered alone and when considered in conjunction with other specimens utilized in these analyses. Moreover, examination of the raw data (comprising over 13,000 observations) has failed to reveal any discontinuities in ranges of values for any of the continuous characters studied. Finally, all binary attributes are present in the vast majority of specimens

TABLE III. Values of similarity measures (for cluster analyses) and correlation coefficients (for ordinations) for *Metamastophora* data

Specimens involved	Characters examined	S.M. (for final fusion)	C.C.
All specimens	Vegetative only	1·0000	1·0
Tetrasporangial specimens	Vegetative and reproductive	0·[illegible]685	1·0
Only type specimens	Vegetative and reproductive	0·8852	0·9999

examined, and their occasional absence in individuals therefore appears to be fortuitous and of no taxonomic significance.

Several conclusions follow from these results. Firstly, none of the 59 characters examined (Table I) can be employed reliably either alone or in combination to delineate species within *Metamastophora*. These include all characters related to branching patterns, branch apices, and branch margin morphology utilized to separate species in the monograph of Setchell (1943), and used (for diagnostic purposes) in keys (May, 1965, p. 357) and in early floristic accounts and catalogues (e.g. Areschoug, 1852; Harvey, 1849; Sonder, 1848). Thus if the taxa presently assigned to *Metamastophora* are to be recognized as distinct species, some other bases for delineation must be found.

A second conclusion is that the individuals examined are vegetatively monomorphic. No discernible vegetative differences of taxonomic significance occur among the male, female and tetrasporangial plants involved in these analyses, including type specimens. This supports and extends the observations of Suneson (1945) relating to the uniform vegetative anatomy in taxa presently assigned to *Metamastophora*.

INDUCTIVE ANALYSES

In addition to the 59 characters examined taxometrically, several other characters which have been or potentially could be employed in species delineation also require assessment. Because of their nature or because of the comparative availability of material, these characters had to be excluded from the taxometric analyses.

Setchell (1943, p. 132) and May (1965) considered differences in the degree of pruinosity to be of diagnostic significance at the species level. In *Metamastophora*, the pruinose appearance of fronds results from the variable surface deposits of calcium carbonate. Because the degree of calcification can vary considerably both within and among *Metamastophora* plants (see Woelkerling, 1980), the degree of pruinosity also varies considerably within and among individuals. Hence, little reliance can be placed on use of pruinosity as a diagnostic character.

The occurrence of trichocytes in plants of *Metamastophora* (Woelkerling, 1980) appears to be sporadic and thus of little taxonomic consequence for purposes of species delineation. Segawa (1959) suggested that the genus *Metamastophora* could be distinguished from the genus *Mastophora* by the absence

of trichocytes. However, trichocytes can occur in both genera and thus are of no diagnostic importance. The taxonomic relationships of the two genera are discussed below. Secondary pit-connections and cell fusions both occur consistently in the same plants and thus this character combination is of no diagnostic importance at the species level. The supra-generic implications of this character combination are considered in the discussion section of this paper.

Setchell (1943, p. 132), apparently relying on the illustrations of Kuetzing (1858), used relative thallus thickness as the primary criterion distinguishing *M. flabellata* (Sonder) Setchell from *M. lamourouxii* (Decaisne ex Harvey) Setchell. Thus in *M. flabellata*, branches were thought to be chiefly di-oligostromatic whereas in *M. lamourouxii*, branches were thought to be monostromatic. Comparisons of the designated lectotypes, however, show that both possess the same internal vegetative anatomy. Except at extreme apices neither is monostromatic. Young portions are distromatic (a unistratose hypothallium overlain by a unistratose epithallium); older portions contain additional layers of perithallial tissue. Detailed anatomical accounts are presented by Suneson (1945) and Woelkerling (1980). Kuetzing's illustration (1858, pl. 98, fig. 1) no doubt represents a young branch in longitudinal view, but he does not show the comparatively small-celled epithallium. Examination of type collection material of other taxa presently assigned to *Metamastophora* reveals that they also possess the same vegetative anatomy. Thus differences in thallus thickness cannot be used reliably as a criterion of species separation within the genus.

Critical studies of the types and other collections of *M. flabellata* and *M. lamourouxii*, moreover, have failed to reveal any other criteria which can be used reliably to separate the two taxa. Consequently they are considered conspecific with the specific epithet "flabellata" (Sonder, 1845) having nomenclatural priority over the specific epithet "lamourouxii", first validly published (see Setchell, 1943, p. 131 for details) by Harvey (1849). Areschoug (1852, p. 526) also regarded the two taxa as conspecific (using the 1849 specific epithet "lamourouxii" rather than the 1845 specific epithet "flabellata"), a judgement accepted by most subsequent writers (except Kuetzing, 1858; see Table IV for references) until Setchell (1943) again recognized two distinct species. Since 1943 Setchell's proposals have been followed by most authors. Results from the present study, however, support Areschoug's conclusions rather than Setchell's.

TABLE IV. Pertinent systematic data on *Metamastophora flabellata*

Synonomy and References:

Metamastophora flabellata (Sonder) Setchell, 1943: 131. Cabioch, 1972: 197, Fig. 22B. Guiler, 1952: 87. Hodgkin, Marsh & Smith, 1959: 88. May 1965: 357. Shepherd & Womersley, 1970: 133, Fig. 16; 1971: 165. Woelkerling, 1980: et. seq., Figs 1–36. Womersley, 1950: 167, 1953: 38.

Mastophora flabellata (Sonder) Harvey, 1849: 108: Kuetzing, 1849: 697; 1858: 47, pl. 97, Fig. 1a-g.

Melobesia flabellata Sonder, 1845: 55. Sonder, 1848: 188.

Mastophora hypoleuca Harvey, 1849: 108, pl. 41, Figs 1–3. Areschoug, 1852: 527. Barton, 1893: 202. Delf & Michell, 1923: 119. De Toni, 1905: 1775. Heydrich, 1897: 46. Lemoine, 1911b: LXV. Mazza, 1916–1922: 1167. Printz, 1929: 47, pl. 75, Fig. 1. Papenfuss, 1968b: 275. Setchell, 1943: 132. Suneson, 1945: 252, 253.

Mastophora lamourouxii Decaisne ex Harvey, 1849: 108, pl. 41, Figs 1–5. Areschoug, 1852: 526 (pp.). Bastow, 1899: pl. 1; pl. 2, Fig. 110. Barton, 1893: 202. De Toni, 1905: 1774; 1924: 695. De Toni & Forti, 1922: 60. De Toni & Levi, 1888: 67. Harvey, 1855: 547; 1857: 4 (No. 441); 1863: XXX, pl. 263 (discussion). Heydrich, 1897: 46. Kuetzing, 1858: 47, pl. 98, Figs. 2h–1. Lemoine, 1911b: LXV. Lucas, 1909: 56; 1913: 163; 1929a: 27; 1929b: 53. Lucas & Perrin, 1947: 391, Fig. 197. Mazza, 1916: 1163 (pro-parte). Reinbold, 1897: 63; 1899: 51. Sonder, 1880: 20. Suneson, 1945: 251 et. seq. Figs 1–3, pl. 1. Tate, 1882: 19. Tisdall, 1898: 507. Wilson, 1892: 177.

Mastophora lamourouxii Decaisne var. *latior* Sonder, 1880: 20.

Mastophora lamourouxii Decaisne ex Harvey f. *plana* (Sonder) Foslie, 1908: 18. Printz, 1929: 47, pl. 75, Figs 4–5.

Mastophora lamourouxii Decaisne f. *typica* Foslie in Printz, 1929: 47, pl. 75, Figs 1–3.

Melobesia lamourouxii Decaisne ex Schramm & Mazé, 1865: 16 (only as to binomial).

Metamastophora lamourouxii (Decaisne ex Harvey) Setchell, 1943: 131. May, 1965: 357. Segawa, 1959: 221.

Mastophora plana (Sonder) Harvey, 1849: 108. Areschoug, 1852: 527. De Toni, 1905: 1775; 1924: 695. De Toni & Forti, 1922: 61. De Toni & Levi, 1888: 67. Harvey, 1855: 547; 1857: 4 (No. 442); 1863: XXX, pl. 263 (discussion). Heydrich, 1897: 46. Lemoine, 1911a: 182, Fig. 104; 1911b: LXV. Lucas, 1909: 56; 1913: 163. Kuetzing, 1849: 697; 1858: 47, pl. 98, Figs 1a–f. Rosanoff, 1866: 13. Schmitz & Hauptfleisch, 1897: 542, Fig. 286c. Sonder, 1880: 20. Suneson, 1945: 251, 256, 257.

Melobesia plana Sonder, 1845: 55. Sonder, 1848: 188.

Metamastophora plana (Sonder) Setchell, 1943: 133. May, 1965: 357. Rayss, 1959: 20.

Mastophora rostrata J. Agardh ex Suneson, 1945: 260 (nom. nud.).

Metamastophora stelligera (Endlicher & Diesing) Setchell, 1943: 132. Papenfuss, 1968b: 274.

Mastophora stelligera (Endlicher & Diesing) Kuetzing, 1849: 697. Areschoug, 1852: 528. Barton, 1893: 202. De Toni, 1905: 1777; 1924: 695. Suneson, 1945: 252.

Melobesia stelligera Endlicher & Diesing 1845: 290.

Peyssonelia caulescens Kuetzing, 1849: 694. Barton, 1893: 142. Papenfuss, 1968b: 275.

Lichenella brentii Gray. Hastings, 1960: 245.

Type Locality: Western Australia

Type: **MEL** 516739; see text and Fig. 1

Specimens Examined: See Materials and Methods section.

Sonder (1845, 1848) separated *Metamastophora plana* (Sonder) Setchell from *M. flabellata* (Sonder) Setchell on superficial differences in branching and branch shape which are more or less evident in the designated lectotype specimens (Figs 1, 2). These differences, however, almost certainly are caused by colonies of the bryozoan *Neoeuthyris woosteri* (MacGillivray) Bretnall which cover nearly the entire ventral surfaces of syntype specimens of *Metamastophora plana* but do not occur on syntype specimens of *M. flabellata*. Examination of another *Metamastophora* collection (**ADU**, A30794—see Fig. 3) extensively but not completely covered by *Neoeuthyris* and several reports on *Neoeuthyris* in the zoological literature [Hastings, 1960, 1964; Gray, 1858, 1859 (who presumably used the name *Lichenella brentii* for *Neoeuthyris*—but see Hastings, 1960, Opinion, 1961)] provide additional supporting evidence that *Neoeuthyris* is the causal agent.

Presence of the bryozoan always appears to result in marked reduction in the extent of branching of the alga, the occurrence of longitudinal furrows on the dorsal surface of the alga which more or less demarcate the position of individual zooecia on the ventral surface, and the broadening of lower portions of indivi-

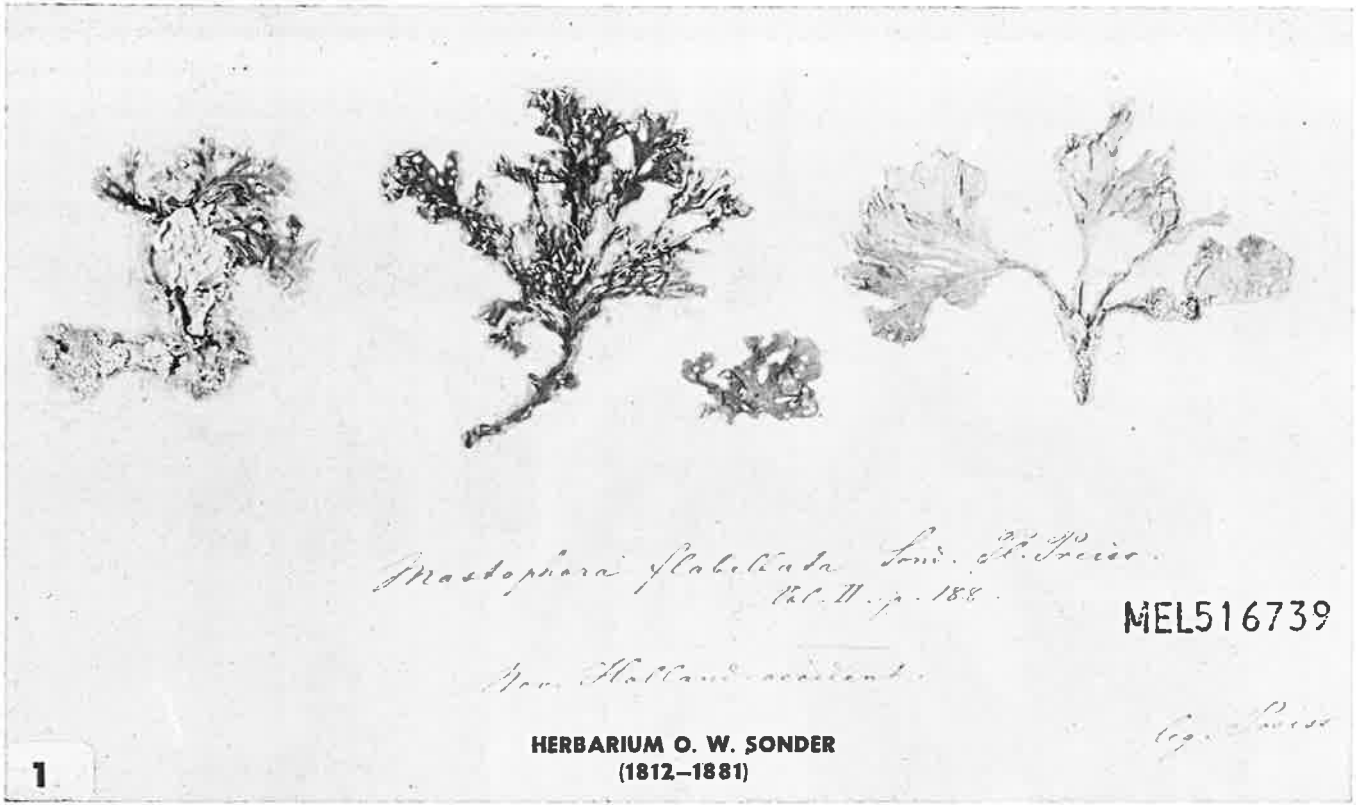
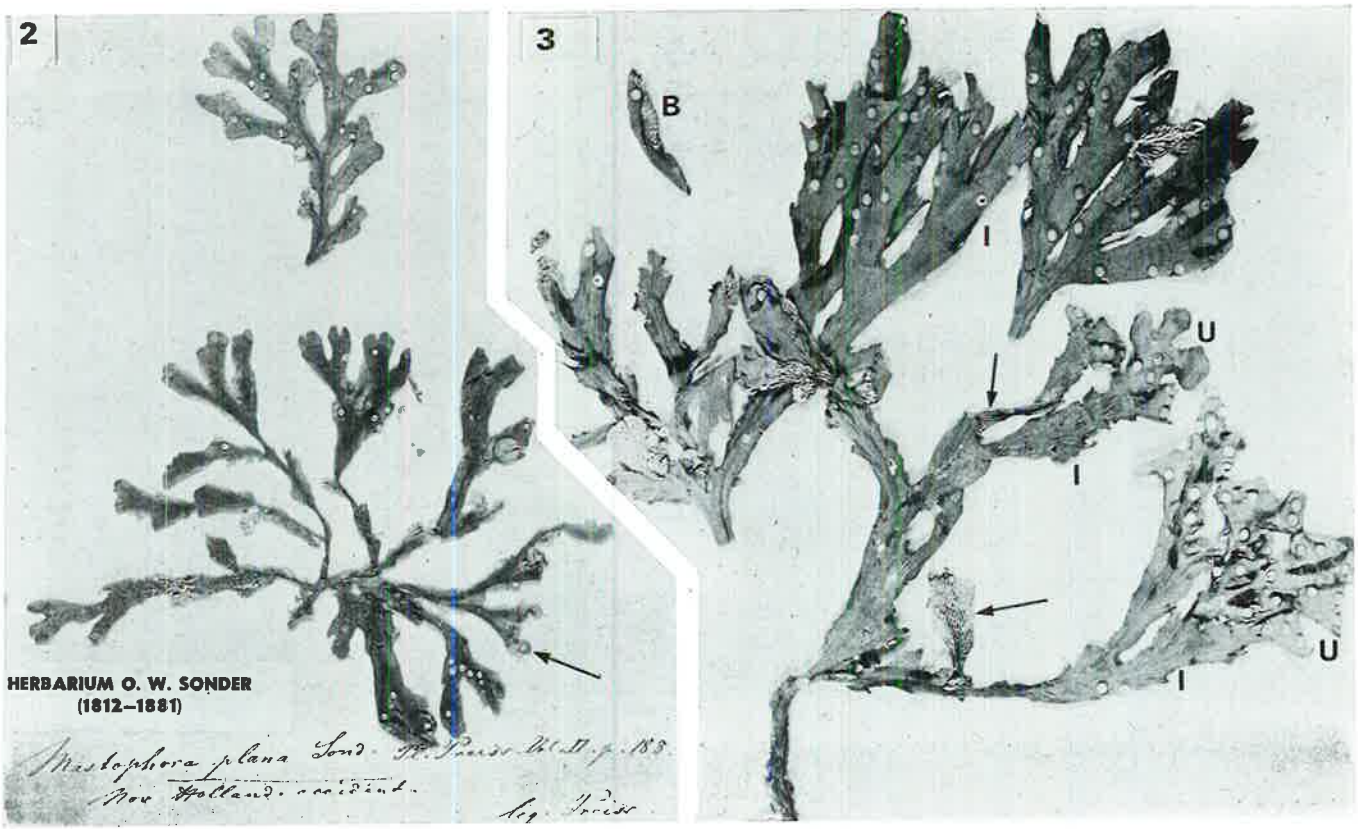


FIG. 1. Lectotype sheet of *Metamastophora flabellata* (Sonder) Setchell. Specimen housed at MEL, handwriting is Sonder's. ×0·83.



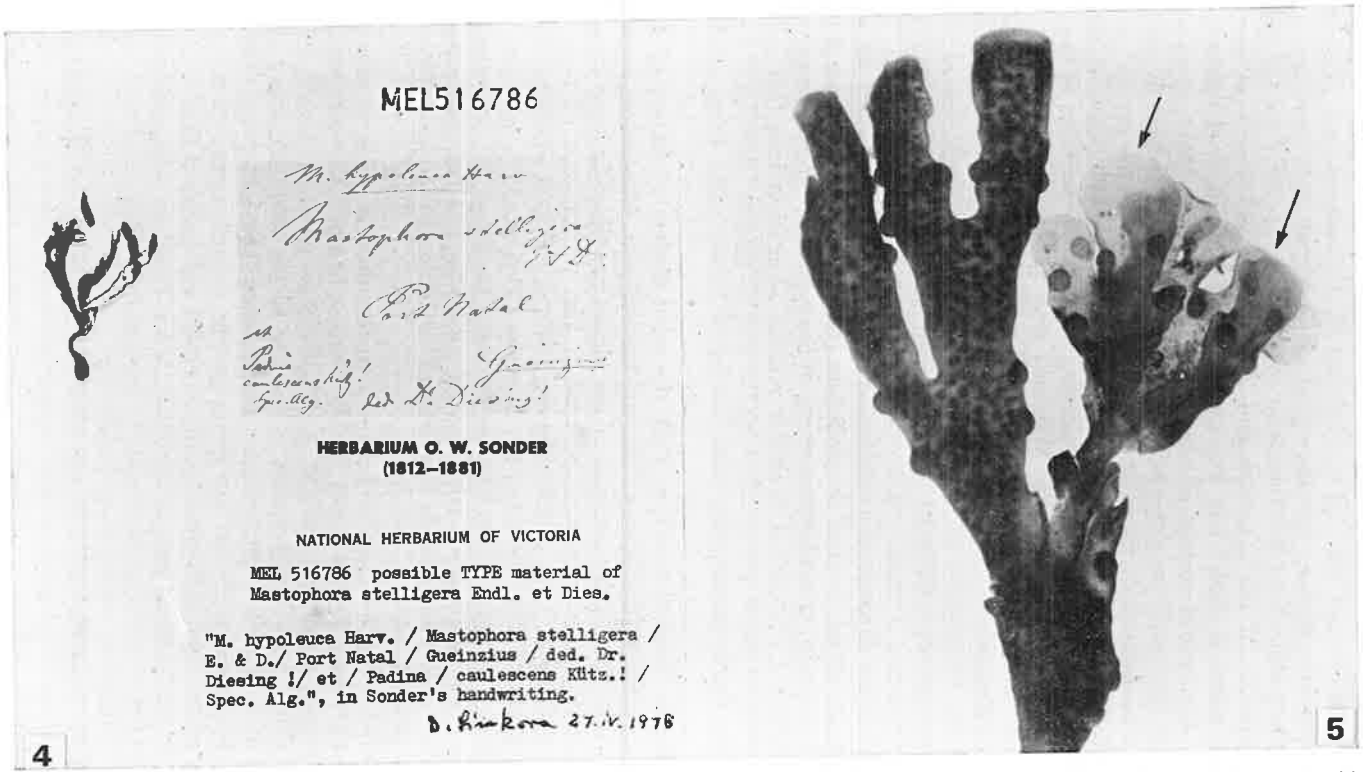
FIGS 2–3. *Metamastophora* plants deformed by the bryozoan *Neoeuthyris*. Fig. 2. Lectotype sheet of *Metamastophora plana* (Sonder) Setchell housed at **MEL**; handwriting is Sonder's. Note that one branch tip (arrow) is uninfected by the bryozoan. ×0·66. Fig. 3. Specimen from **ADU** (A 30794) showing remains of bryozoan (B), calcification pattern induced on ventral surface by bryozoan (arrows), and differences between infected (I) and uninfected (U) portions of branches. ×0·79.

dual algal branches which normally would assume a stipe-like appearance (Figs 2, 3). Portions of the alga not infected by *Neoeuthyris* look like normal plants of *Metamastophora flabellata* (Fig. 3); internal algal anatomy is not affected. These superficial deformities to the algal host result from the growth and development of the bryozoan and its weakly calcified vertical (but not horizontal) zooecial walls. The localized zooecial deposition of calcium carbonate on the ventral surface of the alga (Fig. 3) creates the appearance of longitudinal furrowing on the dorsal surface. Similarly, the actively growing bryozoan almost certainly provides a template which alters the normal growth of the alga, thus restricting algal branch development to coincide with that of the bryozoan and also causing a broadening of the lower portions of the algal branches. Patricia Cook (British Museum) who presently is studying *Neoeuthyris* and related taxa, concurs (personal communication) with this interpretation of *Neoeuthyris* induced effects; and Hastings (1964, p. 246) comments further on the *Neoeuthyris* related deformities to host *Metamastophora* plants. When proper culture techniques are developed, laboratory experiments involving *Neoeuthyris* and *Metamastophora* should confirm these observations. Thus, available evidence supports the conclusion that syntype specimens of *M. plana* represent a deformed state of *M. flabellata* induced by the presence of *Neoeuthyris*. In addition, critical comparisons of the type collections have provided no morphological/anatomical basis for reliable separation into two species; thus they are considered conspecific with the specific epithet "flabellata" chosen for retention (both protologues were published in the same paper—Sonder, 1845).

According to Setchell (1943, p. 133), the most distinctive feature of *Metamastophora stelligera* (Endlicher et Diesing) Setchell [syn. *Mastophora hypoleuca* Harvey] is that "the under surfaces of the blades are white-farinose or white-lanate, with depressed dark-colored spots". The protologues of both taxa (Endlicher et Diesing, 1845, p. 290; Harvey, 1849, p. 108, 109, pl. 41, fig. 2) also include mention of this characteristic. Suneson (1945, p. 253), however, concluded that this spotted, white stratum belonged to an animal. Examinations of syntype material of both taxa and of an additional formalin-preserved Mozambique collection during the present investigation confirm Suneson's conclusion (Figs 4, 5).

The animal is an ascidian and has been identified as *Didemnum stilense* Michaelson (Family Didemnidae) by Dr Patricia Mather of the Queensland Museum. According to Berrill (1950, p. 115), didemnid ascidians usually contain minute, stellate calcareous granules in the test which when abundant give a white opacity to the colonies. Endlicher and Diesing (1845), Harvey (1849) and Setchell (1943) apparently did not recognize the animal nature of this white opacity or of the dark spots (the ascidian zooids) and assumed that both were generated by and formed part of the plant. Since, however, this assumption is in error and these characteristics relate to the ascidian, they are of no relevance to species delineation within *Metamastophora*.

Portions of *Metamastophora* fronds covered ventrally by the ascidian possess several superficial deformities which include involute branch margins, thicker-appearing fronds and more or less lanceolate branches with obtuse tips (Fig. 5). Uninfected portions (Fig. 5, arrow) of the alga, in contrast, have branches



FIGS 4–5. Specimens from southern Africa. Fig. 4. Syntype specimen of *Metamastophora stelligera*, in MEL. ×0·65. Fig. 5. Portion of liquid preserved specimen showing an ascidian-infected branch (left) and an uninfected branch (right, arrows). ×2·43.

which look like those of normal plants of *Metamastophora flabellata*. Thus the above-mentioned superficial branch characteristics induced by the presence of the ascidian (some of which were noted by Setchell, 1943) also cannot be considered for purposes of taxon delineation within *Metamastophora*.

Internal anatomy apparently is not affected by the presence of the ascidian; comparisons of infected and non-infected plants (including syntype specimens of *M. flabellata*, *M. stelligera* and *Mastophora hypoleuca*) indicate that a uniform anatomy occurs in all cases. Indeed, critical taxometric and inductive analyses of the syntype collections of the three above taxa have failed to find any characteristics which can be used reliably to separate them. Consequently, they are considered conspecific here. The specific epithet "flabellata" (published 24 Jan. 1845) has priority over the specific epithets "stelligera" (published 25 April 1845) and "hypoleuca" (published in 1849).

SYSTEMATIC CONCLUSIONS

Results from this taxometric and inductive assessment of characters and from two previous papers (Woelkerling, 1978, 1980) support the contention that *Metamastophora* is monotypic and includes only *M. flabellata* (Sonder) Setchell. Two [*M. plana*, *M. stelligera* (including *Mastophora hypoleuca* Harvey)] of the four other taxa placed in *Metamastophora* by Setchell (1943) represent deformed states of *M. flabellata*. A third taxon [*M. canaliculata* (Harvey) Setchell] has been removed to the genus *Mastophoropsis* (Woelkerling, 1978). The fourth taxon (*Metamastophora lamourouxii*) cannot be distinguished specifically from *M. flabellata* on any consistently reliable basis. None of the characteristics used by previous authors and none of the additional characteristics studied here appear to have meaningful diagnostic value. Consequently no basis could be found on which to recognize more than one species of *Metamastophora* at present.

TAXONOMY AND DISTRIBUTION

GENERIC DIAGNOSIS

Metamastophora (Setchell) emend.

Thallus nongeniculate, anchored by a pseudoparenchymatous holdfast and producing ascending, branched, flattened, stipose to taeniform dorsiventral axes; structurally composed of a unistratose hypothallium and a unistratose primary epithallium which arise from a primary apical meristem and of a several to many-layered perithallium generated from a secondary intercalary subepithallial meristem. Cell fusions common in hypothallium and perithallium; secondary pit-connections occasional to common in perithallium. Trichocytes, when present, arising singly or in groups near thallus apices and margins. Reproductive structures borne on dorsal surface; tetrasporic conceptacles uniporate with a central sterile columella arising from the spore chamber floor. Tetrasporangia lacking apical plugs.

TYPE SPECIES: *Metamastophora flabellata* (Sonder) Setchell 1943: 131. Basionym: *Melobesia flabellata* Sonder 1845: 55.

The generic diagnosis has been emended to indicate that plant attachment is effected by a pseudoparenchymatous holdfast (Woelkerling, 1980) rather than by rhizoids (Setchell, 1943, p. 130); that considerable internal differentiation of tissues and two distinct vegetative meristems are present; that the cell fusions, secondary pit-connections and trichocytes all can develop; that a dorsiventral

organization of tissues occurs; and that each tetrasporic conceptacle contains a central, sterile columella. All these features are evident in the type species.

SPECIES DATA:

Description, Synonomy, Typification

Metamastophora is monotypic; a detailed account of the type species, *M. flabellata*, based on southern Australian collections has been presented elsewhere (Woelkerling, 1980). Specimens from southern Africa examined during the present study are similar in all respects to southern Australian material. Deformities caused by bryozoans and ascidians relate only to external morphology. Pertinent systematic data including references and synonomy are summarized in Table IV.

Sonder (1845) provided only a short protologue for *M. flabellata* and did not specify a holotype. Subsequently Sonder (1848) published some additional details and referred to a collection No. 2603 of Preiss. Neither of the two syntype sheets in the Sonder Herbarium (**MEL**) bears a Preiss number, but **MEL** 516739 contains a notation in Sonder's script referring to the 1848 paper, and the four individuals affixed to this sheet collectively (see Stafleu, 1978, Art. 9) have been selected as the nomenclatural lectotype (Fig. 1). All four are fragments and lack holdfasts. The second specimen from the left bears tetrasporic conceptacles; the other three possess carposporic conceptacles.

Lectotypes also have been chosen for *Mastophora lamourouxii* Harvey (an unnumbered tetrasporic plant in **TCD** and *Melobesia plana* Sonder (**MEL** 516775—see Fig. 2). Johansen (unpublished annotation) previously has proposed an unnumbered tetrasporic plant in **TCD** as lectotype of *Mastophora hypoleuca* Harvey; his annotated specimen is designated here officially as lectotype. Lectotypification of *Mastophora stelligera* Endlicher et Diesing awaits the study of syntype material in Europe; only a single small but reproductively mature syntype specimen (**MEL** 516786) has been available for examination during this investigation (Fig. 4).

The name *Mastophora lamourouxii* Decaisne ex Harvey var. *latior* Sonder (1880, p. 20) is a nomenclatural synonym of *Metamastophora flabellata* (Sonder) Setchell; the name *Mastophora rostrata* J. Agardh ex Suneson (1945, p. 260) is a nomen nudum based on male plants of *Metamastophora flabellata* in **LD**. The names *Melobesia lamourouxii* Decaisne (1842a, p. 126; see also Decaisne, 1842b, p. 114 and Endlicher, 1843, p. 50) and *Mastophora lamourouxii* Decaisne ex Krauss (1846a, p. 211; 1846b, p. 207) are nomina nuda based on specimens of *Padina rosea* Lamouroux (never validly published—see Setchell, 1943, p. 131) in the herbarium of Lamouroux (**CN**). Whether or not the Lamouroux material is referrable to *Metamastophora* remains uncertain; consequently the Decaisne and Krauss names have been omitted from the synonomy in Table IV.

Papenfuss (1968b, p. 275) has examined the type collection of *Peyssonnelia caulescens* Kuetzing (1849) and determined it to be the same as *Metamastophora stelligera*, regarded here as a synonym of *M. flabellata*. Hastings (1960, p. 245) transferred the binomial *Lichenella brentii* from the animal kingdom to the plant kingdom, selecting as lectotype, the algal portions of specimens used by Gray (1858, 1859) for the protologue of a bryozoan. Gray's algal material (housed at **BM**) is deformed *Metamastophora flabellata*. For further data on *Lichenella*,

see the report of the General Committee in *Taxon* (Vol. 15, Nov. 1980).

Distribution

Metamastophora flabellata grows in the sublittoral zone and in deeper littoral tide pools throughout southern Australia and occurs at least as far north as Kalbarri, W.A. on the west coast. Specimens have been collected in all months of the year and at depths of up to 48 m. On Rottnest Island, W. Australia, tetrasporangial, male and female plants together predominate the flora of many sublittoral vertical rock faces during summer. The genus has not been recorded from New South Wales.

The reported occurrence of *Metamastophora* in Queensland by May (1965, as *M. plana*) is based on specimens from Brampton Island (May, 1951) which have been examined and found to belong to *Mastophora rosea*. Similarly the Queensland records of Bailey (1913) and Lucas (1931, both as *M. plana*) are based on the De Toni (1905, p. 1775) opinion that the specimens from Cape York identified by Sonder (1871, p. 54) as *M. foliacea* really belong to *M. plana*. Examination of Sonder's collections in **MEL**, however, has revealed that the Cape York material is true *Mastophora* and definitely distinct from *Metamastophora plana*.

M. flabellata also grows in southern Africa (Cape of Good Hope, Durban, Umhlali and Xai-Xai—see Harvey, 1849; Suneson, 1945), but details relating to seasonal and vertical distribution of African populations remain unknown.

All other geographic records have not been verified and must be regarded as extremely doubtful. Thus the reported occurrence of *Metamastophora* in Guadeloupe [Schramm & Mazé, 1865, p. 16; 1866, p. 38 (both as *Melobesia lamourouxii*); Mazé & Schramm, 1870–77, p. 203 (as *Mastophora lamourouxii*) —later reiterated by Murray, 1888, p. 337; 1889b, p. 21; Barton, 1893, p. 202; Lemoine, 1917, p. 151] has not been confirmed and is considered an uncertain record by Taylor (1960, p. 402). Similarly the provisional record from the Red Sea [Rayss, 1959, p. 20 (as *M. lamourouxii*)—subsequently mentioned by Lemoine 1966, p. 3 and catalogued by Papenfuss, 1968a, p. 81] requires verification. Records of *Metamastophora* from various South Pacific islands [Dickie, 1876a, p. 239; 1876b, p. 448; 1877, p. 489 (all as *Mastophora lamourouxii*; Helmsley, 1885, p. 273 as *M. lamourouxii*); Safford, 1905, pp. 52, 178 (as *M. lamourouxii*); Schmidt, 1928, p. 82 (as *M. lamourouxii* and *M. plana*); Schumann & Lauterbach, 1901, p. 34 (as *M. lamourouxii*); Tsuda & Wray, 1977, p. 110 (as *M. lamourouxii* and *M. plana*)] are based either on almost certain misidentifications or on nomenclatural errors; all are regarded here with extreme doubt, and it is likely that the specimens involved all belong to *Mastophora rosea* (C. Ag.) Setchell rather than the genus *Metamastophora*.

RELATIONSHIPS TO OTHER CORALLINACEAE

In considering the probable affinities of *Metamastophora* to other Corallinaceae, the classification system of Johansen (1976; see also Lebednik, 1977, p. 381 and the 1978 addendum) has been selected to provide a framework for discussion, recognizing, of course, that the choice of any of the more recently proposed classification schemes (e.g. Adey & MacIntyre, 1973; Cabioch, 1971, 1972; Hamel & Lemoine, 1953; Johansen, 1969, 1976; Kylin, 1956; Mason,

1953) is subjective due to the paucity of detailed data for many taxa (Woelkerling, 1978, p. 223) and the resulting fluid state of our knowledge of coralline structure and relationships (Johansen, 1976, p. 224).

In the Johansen system, the occurrence and nature of the genicula, the occurrence of tetrasporangial plugs and the occurrence of secondary pit-connections are considered to be of primary taxonomic importance. Johansen recognizes three subfamilies of nongeniculate Corallinaceae: (1) the Lithophylloideae, containing those genera lacking tetrasporangial plugs but possessing secondary pit-connections; (2) the Mastophoroideae, containing those genera lacking both tetrasporangial plugs and secondary pit-connections; and (3) the Melobesioideae, containing those genera possessing tetrasporangial plugs but lacking (exception: *Sporolithon*—see below) secondary pit-connections. The occurrence of cell fusions is not considered directly, but Johansen (1976, p. 234—see also keys in Adey & MacIntyre, 1973, Gordon et al., 1976) implies that they develop in all nongeniculate genera which presumably lack secondary pit-connections. Using the Johansen classification, the genus *Metamastophora* clearly belongs to the Lithophylloideae.

Johansen (1976, p. 232) and Lebednik (1977, p. 381) assign three other genera to the Lithophylloideae: *Ezo*, *Lithophyllum* and *Tenarea*. [The inclusion or exclusion of *Pseudolithophyllum* Lemoine within the Lithophylloideae depends on proper resolution of a lectotypification problem (see Lemoine, 1978) which requires further study of both proposed lectotypes to determine the presence or absence of secondary pit-connections irrespective of the occurrence of cell fusions; until this situation is settled, meaningful discussions involving relationships between *Metamastophora* and *Pseudolithophyllum* are not possible.] Like *Metamastophora* the genera *Ezo*, *Lithophyllum* and *Tenarea* all possess tetrasporic conceptacles which house a central, sterile columella within the spore chamber. Both *Metamastophora* and *Tenarea* also possess unistratose hypothallia in which the cells are vertically elongate and usually over 1·5 diameters long (Adey, 1970, pp. 3, 6; Woelkerling, 1980); some authors (e.g. Adey, 1970, Adey & MacIntyre, 1973, Littler, 1971) refer to the tissue as a palisade hypothallium. *Metamastophora*, however, differs from all three genera in possessing both secondary pit-connections and cell fusions, and in having an ascending, branched, taeniform thallus rather than a primarily encrusting thallus. It also differs from *Ezo* in the absence of haustoria, the presence of abundant pigmentation, and the absence of a presumed parasitic relationship.

The ascending, branched, taeniform habit of *Metamastophora* also occurs in *Mastophoropsis* (subfamily Melobesioideae) and in *Mastophora* (subfamily Mastophoroideae). However, secondary pit-connections are unknown in either genus. In addition, plants of *Mastophoropsis* produce multiporate tetrasporic conceptacles rather than uniporate tetrasporic conceptacles (Woelkerling, 1978), and plants of *Mastophora* (unpublished personal observations on specimens sent from Guam by Professor Roy T. Tsuda) apparently differ from those of *Metamastophora* in lacking both a secondary vegetative meristem and a vegetative perithallium, and in producing rhizoidal extensions from hypothallial cells for anchorage rather than possessing a pseudoparenchymatous holdfast.

The presence of both secondary pit-connections and cell fusions in plants of *Metamastophora* is a character combination reported only in two other

genera presently assigned to the Corallinaceae—*Sporolithon* (syn. *Archaeolithothamnion*—see Cabioch, 1970, 1972, p. 218) and *Synarthrophyton* (see Townsend, 1979). Both genera, however, differ in almost all other respects including the possession of tetrasporangial plugs, a different tetrasporic conceptacle morphology, and an encrusting habit. Johansen (1976; see also Adey & Johansen, 1972, pp. 177–178) places *Sporolithon* in the subfamily Melobesioideae because of the presence of tetrasporangial plugs, thus implying that this character overrides in importance the occurrence of secondary pit-connections in so far as the delineation of subfamilies of nongeniculate Corallinaceae is concerned. Townsend (1979) also assigned *Synarthrophyton* to the Melobesioideae. It is possible that critical studies of other nongeniculate coralline genera will reveal that the occurrence of secondary pit-connections (together with cell fusions) is more common than is presently thought, and eventually it may become necessary to reassess the diagnostic importance of secondary pit-connection occurrence as a subfamilial characteristic in the nongeniculate Corallinaceae. At present however, available data appear to be too meagre to engage in further speculation on either the relative importance of tetrasporangial plug occurrence vs. secondary pit-connection occurrence or the use (Cabioch, 1972, pp. 264–267; see also Chamberlain, 1978, pp. 230–234) of secondary pit-connection/cell fusion occurrence in delineating subfamilies within the Corallinaceae.

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OBITUARY

Ellen Marion Delf-Smith, D.Sc., F.L.S. (1883–1980)

Dr E. Marion Delf-Smith, for many years an Honorary Member of the British Phycological Society, died on 23 February 1980 at the age of ninety-seven. Her scientific career encompassed the whole of the first half of this century. Educated at the James Alleyn Girls' School, Dulwich, and at Girton College, Cambridge, she studied under such historic figures as Marshall Ward and F. F. Blackman. Soon after graduating, when she had just embarked on research in plant physiology, she was appointed to start the teaching of Botany at Westfield College, University of London. She went to Westfield in 1906 and, with several short interludes, remained there until her retirement in 1948.

In the early years there were few facilities for science teaching at Westfield and she had no help. Equipment grants and technicians were unknown, and if she wanted a specimen she had to go out and collect it and prepare it herself. Despite these difficulties, she managed, by working at the Joddrell Laboratory, Kew, to take her London D.Sc. in 1912. Her main studies were in plant physiology, but in later years her interests widened to take in the marine algae and indeed a large number of other subjects. She was always alert for new developments in the botanical field and often had her students working on topics which did not really come to the fore until years later.

In 1914 she left Westfield to take up a research Fellowship at Girton, but the demands of the First World War made her feel that she should be more directly involved in war work and she went to the Lister Institute to undertake research in vitamins. After the war, she was induced to return to Westfield, as she was again in the early 1920s, when she had spent some time in South Africa pursuing the marine algae in Cape Town and vitamin research at the Medical Research Hospital in Johannesburg. From 1922 her connection with Westfield was unbroken and she directed the developing Botany Department through its removal to a new building and over its war years in evacuation in Oxford.

These are the years that generations of her old students will remember. Naturally reserved and always slightly detached, she had a quite remarkable gift for stimulating and training students. She was able to discern the faintest spark of interest in a student and to fan it into a flame. She had the highest of standards and, while infinitely patient with real difficulties, was always keenly critical and would accept nothing but the best. Her early struggles in the department had developed a degree of determination, initiative and perseverance, and these were not the least of her legacies to her students, so many of whom proceeded to posts in higher education and research. On the occasion of her ninetieth birthday in 1973, a large gathering of her old students was held at Westfield and tributes poured in from former students, many atrributing their scientific awakening to her stimulus and interest.

In 1928 she married Percy John Smith, well-known as an artist, etcher and letterer. She continued in her full-time post, not so common a practice in those years as now. It was the happiest of marriages, the artist and the scientist complementing each other in many ways and managing to share each other's interests. It was very sad that he pre-deceased her by many years and that she had a long period of declining health and loneliness. She leaves, however, a very large number of former students and colleagues who realize how much they owe to her not only as a teacher who trained them but as a personal friend.

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EFFECTS OF IN SITU NITROGEN AND PHOSPHORUS ENRICHMENT OF THE SEDIMENTS ON THE SEAGRASS *HETEROZOSTERA TASMANICA* (Martens ex Aschers.) den Hartog IN WESTERN PORT, VICTORIA, AUSTRALIA

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Abstract: The rhizosphere of *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog was enriched in situ with ammonium and/or phosphate at a rate of 100 g $N \cdot m^{-2}$ and 20 g $P \cdot m^{-2}$ each month from August (winter) through February (late summer) in a 2×2 factorial experiment. Ammonium enrichment resulted in increased levels of total nitrogen in the rhizomes (from 0.83 to 1.03% of dry wt) and leaves (from 1.63 to 1.82%) and caused a 20% increase in leaf growth rate. Phosphate enrichment resulted in increased levels of total phosphorus in the rhizomes (from 0.16 to 0.18%), but no increase in total phosphorus in the leaves nor any change in the leaf growth rate. Neither ammonium nor phosphate enrichment caused a change in above sediment standing crop or shoot density. It is suggested that nitrogen limits the growth rate of *H. tasmanica* plants in northern Western Port during spring and early summer, but that an increase of 5 to 100 times the control level of nitrogen and phosphorus in the rhizosphere of these plants appears to have little direct effect on their growth or on standing crop during the first year of enrichment.

INTRODUCTION

Nitrogen and phosphorus uptake by seagrasses and the movement of these nutrients to other components of the ecosystem have been the subject of a number of recent studies (McRoy & Barsdate, 1970; McRoy *et al.*, 1972; Patriquin, 1972; Patriquin & Knowles, 1972; Harlin, 1973; Barsdate *et al.*, 1974; McRoy & Goering, 1974; Capone *et al.*, 1979). However, the effects of various levels of these nutrients on seagrass growth has received little attention. Raymont (1947) reported an increase in biomass of the seagrass *Zostera* after adding sodium nitrate and superphosphate to a Scottish Loch. Buljan (1957) reported an increase in community oxygen production of *Posidonia oceanica* after enriching a bay in the Adriatic Sea with a phosphate fertilizer and earth extract, and Orth (1977) observed leaf length, biomass and density increases in *Zostera marina* in Chesapeake Bay, U.S.A. after a nitrogen/phosphorus/potassium fertilizer was spread on the mud surface at low tide. Although Orth demonstrated nutrient limitation of seagrass growth, none of these studies discriminated between the separate effects of nitrogen enrichment and

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phosphorus enrichment. The objective of the present study has been to determine the response of the seagrass, *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog, in Western Port, Victoria to in situ enrichment by nitrogen alone, phosphorus alone, and both nitrogen and phosphorus.

Methods

H. tasmanica is common in sheltered bays and estuaries along the southern Australian coast (Den Hartog, 1970; Cambridge, 1975) and dominates ≈ 140 km^2 or 20% of Western Port (Bulthuis, 1980). The experimental site was located in a uniform bed of *H. tasmanica* encompassing ≈ 2.5 km^2 in northern Western Port (Fig. 1). Irregular semidaily tides of up to 3 m leave the bed exposed from 1 to 5 h during spring tides. Average baywide concentrations of inorganic nitrogen and phosphorus in the water are low (1.0 μg-at. N $\cdot$ l^{-1} and 0.3 μg-at. P $\cdot$ l^{-1}; Ministry for Conservation, 1975). The prevailing water circulation is clockwise around French Island so nutrients from the Bunyip River are carried to the south-east, away from the experimental site (Fig. 1).

Five g of powdered NaH_2PO_4 and/or 30 g of $(NH_4)_2SO_4$ were wrapped in "Kleenex" tissues and 50 of these batches were placed by hand at 0.1 m depth in the sediment in each 3-m^2 sample plot using an evenly divided grid marking system (Patrick & Delaune, 1976). The roots and rhizomes of *H. tasmanica* were located from 0 to 0.2 m depth in the sediment with most in the upper 0.15 m. The holes made in this process were capped with sediment to retard diffusion of the nutrients into the overlying water. Nutrients were added as NH_4^+ and PO_4^{3-} because the sediments were anoxic and these forms of nitrogen and phosphate would be expected to predominate in the sediment and to be available for uptake by the seagrass (McRoy *et al.*, 1972; Montgomery *et al.*, 1979).

Rates of application of nitrogen and phosphorus were high (100 g N $\cdot$ m^{-2} and 20 g P $\cdot$ m^{-2}) compared to maximum computed uptake rates (3.0 g N $\cdot$ m^{-2} $\cdot$ month^{-1} and 0.4 g P $\cdot$ m^{-2} $\cdot$ month^{-1}) in order to ensure that neither nitrogen nor phosphorus would be growth limiting in plots enriched with these nutrients. Maximum uptake rate was estimated by:

$$U = G \times dw \times D \times \%N \times k,$$

where U = uptake, G = maximum leaf growth, dw = dry weight $\cdot$ mm^{-1} leaf, D = maximum density of plants, $\%N$ = maximum percentage of nitrogen or phosphorus in leaves, $k = 2$, to estimate uptake and storage in the roots and rhizomes. Each treatment (i.e. control, ammonium enrichment (+ N), phosphate enrichment (+ P) and ammonium plus phosphate (+ N + P)) was done in triplicate. All plots were enriched monthly from August 1977 to February 1978 and the response measured each month.

In a subsidiary experiment, the effect of sediment disturbance was tested. The sediments of three plots were disturbed by penetrating 0.1 m depth into the sediment, by hand, at 50 places on an evenly divided grid marking system except without addition of ammonium or phosphate. A second set of three plots was left undisturbed. Plots were disturbed in October 1976 and plant response measured bimonthly from November 1976 to June 1977. Plots were disturbed and plant response measured monthly from August 1977 to February 1978, concurrently with the enrichment experiment.

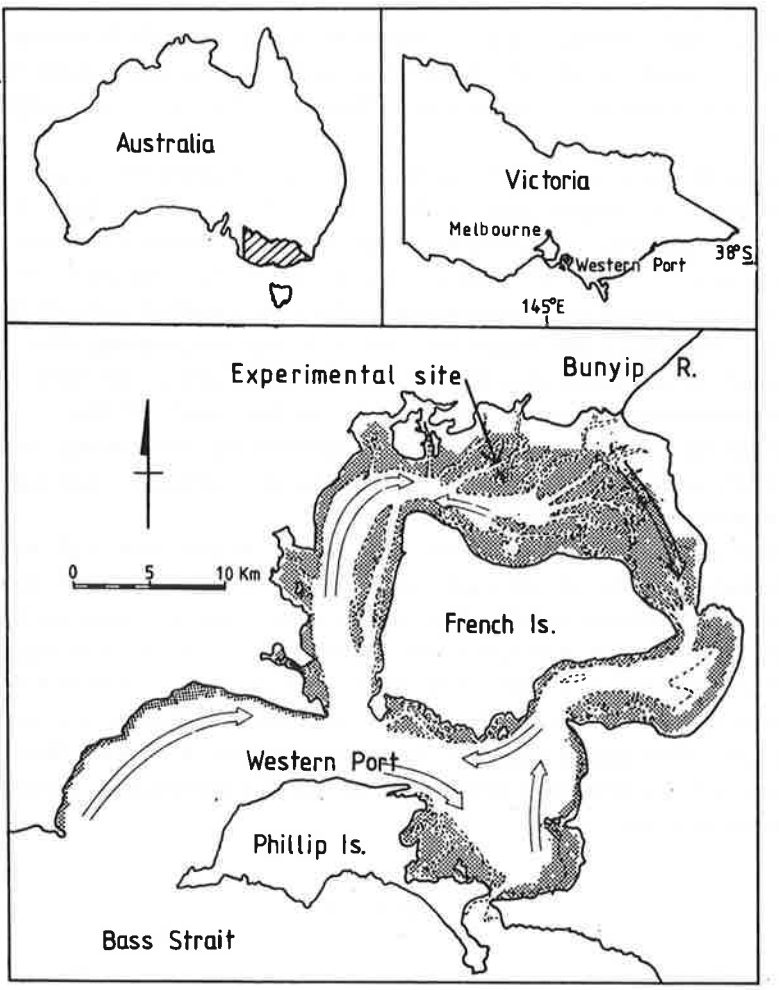

Fig. 1. Western Port, Victoria: dashed lines indicate the extent of the intertidal area; stippled areas indicate where seagrasses are the dominant benthic vegetation; open arrows indicate the general circulation pattern (general circulation redrawn from Harris *et al.*, 1979; seagrass distribution redrawn from Bulthuis, 1980).

The ammonium and reactive phosphorus concentration of sediment interstitial water was measured in all plots during the enrichment experiment to assess the effectiveness of the enrichment and during the sediment disturbance experiment to assess the effect of disturbance. Interstitial water was sampled by placing a dialysis bag (with a pore size having a molecular weight cutoff of 6000–8000) of distilled water in the sediment and allowing 8 days for equilibration (Mayer, 1976). Equilibration time had been determined in previous experiments which indicated that reactive phosphorus and ammonium equilibrated within 2 days in the laboratory and salinity equilibrated within 3 days in the field; after 16 days however, the dialysis bags had numerous small holes, possibly caused by bacterial decay. After equilibration the contents of dialysis bags were placed in sterile Whirlpak bags and immediately frozen on dry ice. Reactive phosphorus and ammonium were determined by the methods of Strickland & Parsons (1968) on a Perkin-Elmer autoanalyser.

All plant shoots in a 0.0625-m^2 quadrat (this size had the lowest variance : mean ratio of quadrats ranging from 0.00391 m^2 to 0.25 m^2; Kershaw, 1973) were harvested for standing crop estimates. Leaves were separated from stems, dried to constant mass at 75 °C and weighed. Shoot density was measured in 0.0151-m^2 quadrats. Leaf growth was measured by marking the lignified stems of 10 plants in each plot, measuring the length of each leaf and remeasuring after 6–8 days. The growth of all leaves originating from the same apical meristem was added together and expressed as mm of leaf growth per shoot apex per day.

Total nitrogen of the leaves and living rhizomes was determined on a Perkin-Elmer CHN autoanalyser. Total phosphorus was determined by acid digestion and the ammonium molybdate method.

Analysis of variance (ANOVA) was used to test the response of *H. tasmanica* to the treatments. In the disturbance experiment a two-way ANOVA was used to assess the effects of time and disturbance. In the enrichment experiment a three-way fixed model ANOVA was used, the factors being: A, N enrichment, $a = 2$; B, P enrichment, $b = 2$; C, time (Aug., Sept., ...Feb.), $c = 7$. ANOVA was carried out on nitrogen concentration, phosphorus concentration, leaf growth rate, standing crop (log-transformed), and density. The non-parametric Wilcoxon–Mann–Whitney test was used to assess the ammonium and reactive phosphorus concentration of the interstitial water.

Results

SEDIMENT DISTURBANCE

There were no significant differences between disturbed and undisturbed plots in interstitial ammonium or reactive phosphorus, leaf growth rate, standing crop or plant density at the 95% level of confidence as tested by one-way ANOVA each

month during 16 months of periodic disturbances. Similarly, for all months, neither the means of all these parameters (two-way ANOVAs) nor the variances (Bartlett's test of homogeneity of variance) were significantly ($P > 0.05$) different between disturbed and undisturbed plots. Therefore, the disturbance of the sediments during the process of nutrient enrichment apparently did not affect the growth of *H. tasmanica*. Because the means and variances were not different from each other, the results from disturbed and undisturbed plots have been combined in this report and labelled "control".

INTERSTITIAL NITROGEN AND PHOSPHORUS

There was no seasonal trend in the ammonium and reactive phosphorus concentration in the sediments. Therefore, data from all months have been combined and are presented in Table I. The levels in the sediments are lower than reported for

TABLE I

Ammonium and reactive phosphorus in experimental plots sampled from November, 1977 through February, 1978: means ± SE ($n = 10$–24) of interstitial water not significantly ($P < 0.05$) different from each other by the (non-parametric) Wilcoxon–Mann–Whitney multiple comparison test are indicated by the same superscript letter.

Treatment	Overlying water 0–10 cm above	Sediment interstitial water	
		0–10 cm below	10–20 cm below
		NH_4^+ (μm)	
Control	2.4 ± 0.4	2.0 ± 0.4[a]	2.1 ± 0.4[a]
+N	3.8 ± 1.2	9.6 ± 2.3[b]	63 ± 26[b]
+P	1.8 ± 0.6	1.5 ± 0.4[a]	1.9 ± 0.4[a]
+N+P	1.3 ± 0.2	13.8 ± 5.4[ab]	740 ± 398[b]
		PO_4^{3-} (μm)	
Control	0.34 ± 0.06	0.37 ± 0.08[c]	0.49 ± 0.08[c]
+N	0.35 ± 0.05	0.39 ± 0.08[c]	0.39 ± 0.08[c]
+P	0.87 ± 0.18	3.01 ± 0.08[cd]	9.49 ± 2.86[d]
+N+P	0.38 ± 0.07	2.41 ± 0.92[cd]	41.9 ± 26[d]

other anaerobic marine sediments (e.g. Matisoff *et al.*, 1975; Martens *et al.*, 1978). These low values observed in the dialysis tubes after 8 days of equilibration may reflect an aerobic environment immediately around the tubes, which may have been caused by the movement of oxygen from the distilled water used to fill the tubes into the surrounding sediments. Water squeezed in the laboratory from control plot sediments had a much higher concentration of ammonium and reactive phosphorus (200–1700 μm NH_4^+ and 3–60 μm PO_4^{3-}) than was in the dialysis bags. The concentrations reported in Table I, therefore, may be low, but because all

plots were sampled by the same method the values indicate the relative availability of these nutrients. Ammonium and reactive phosphorus concentration increased with plots enriched with nitrogen and phosphorus, respectively, while the overlying water changed very little (Table I). If all of the applied nitrogen and phosphorus were retained in the sediments and if it were evenly mixed in the top 20 cm of sediment, the calculated concentration of ammonium and reactive phosphorus would be 50 to 125 times the concentration measured in water squeezed from control plots. The observed sediment enrichment was similar, 35 to 100 times the concentration in control plots (Table I). Thus, the treatment method effectively increased the ammonium and reactive phosphorus concentration of the sediments.

PLANT NITROGEN AND PHOSPHORUS

Total nitrogen of both leaves and rhizomes was higher during winter (August) and late summer (February) than during spring and early summer (Fig. 2). Total phosphorus concentration, in contrast, increased during late spring and summer after reaching a minimum in September–October.

Ammonium enrichment of the sediments did not change the seasonal pattern of total nitrogen in the leaves or rhizomes (Fig. 2). Over all sampling dates, however, the nitrogen level in the leaves and rhizomes from +N+P plots was significantly higher than the level in plants from control plots (two-way ANOVA, $P < 0.01$). Phosphorus levels in the rhizome were also significantly higher in enriched plots than in controls, but phosphorus levels in the leaves were similar in both treatments.

LEAF GROWTH RATE

From winter (August) to late summer (February) there was approximately a doubling in growth rate in all plots (Fig. 3). In two of the four treatments, growth rate was beginning to decrease in February. Other data from Western Port (unpubl.) indicate that growth gradually decreased during autumn and remained at ≈ 10 mm shoot apex$^{-1} \cdot$ day^{-1} from May to August. Superimposed on this seasonal increase in growth rate during the experiment was an additional increase in plots enriched with ammonium (+N, +N+P, Fig. 3). Three-way ANOVA of the leaf growth rates shown in Fig. 3 indicates that this response to nitrogen enrichment was highly significant (Table II). The significant time effect in Table II reflects the seasonal change in growth rate. The months also were analysed one by one in a two-way fixed model ANOVA, the factors being: A, N enrichment, $a = 2$; B, P enrichment, $b = 2$. These analyses yield F ratios for each month for the effect of nitrogen enrichment, phosphorus enrichment and the interaction of these enrichments. The probabilities for these F ratios are given in Table III, indicating which months contributed to the highly significant nitrogen effect (Table II). Although only the September F ratio has a probability < 0.05, indicating a significant effect of nitrogen enrichment on leaf growth rate, probabilities of 0.15 or less were observed during

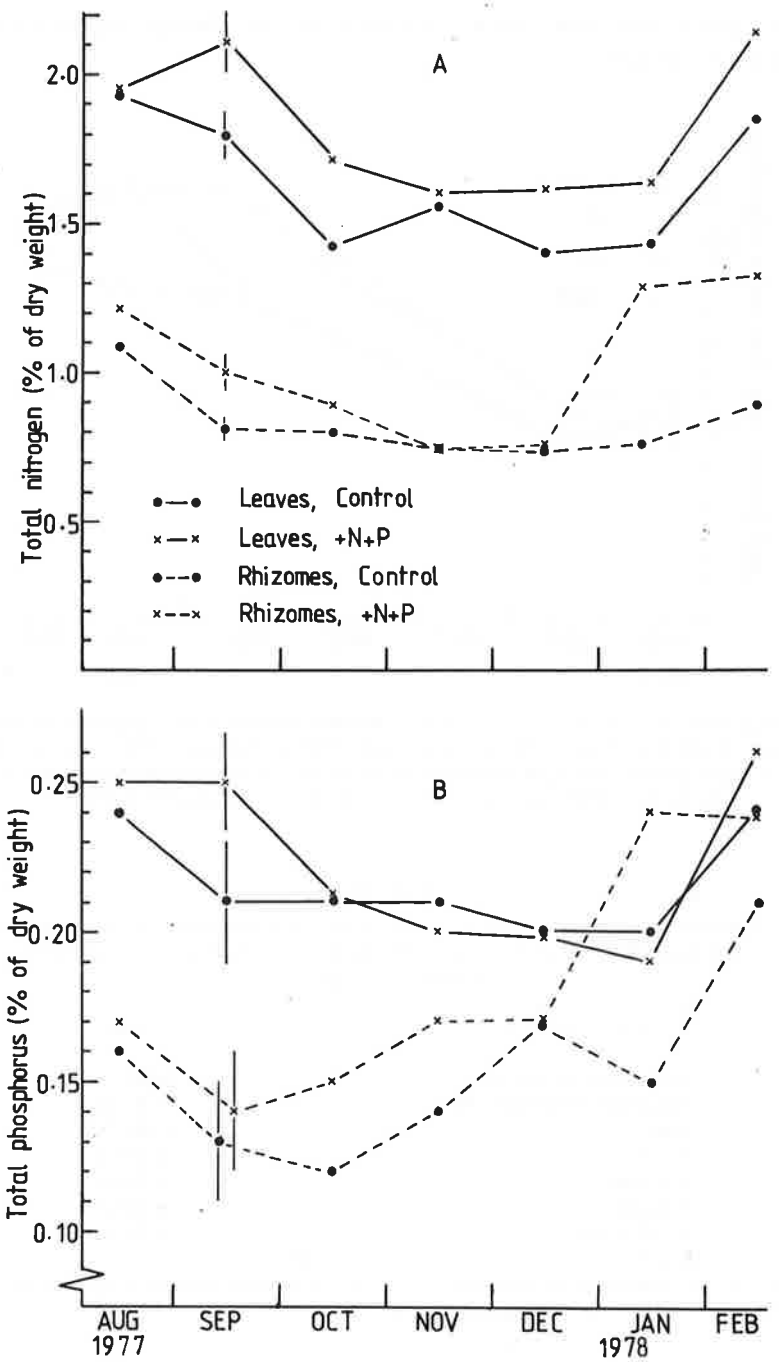

Fig. 2. Seasonal fluctuations in total nitrogen (A) and total phosphorus (B) in leaves and rhizomes of *Heterozostera tasmanica* growing in sediments enriched with ammonium and phosphate (+N+P) and unenriched (control) from August 1977 to February 1978: each point is the mean from 3 plots with the SE, which was similar each month, shown for September.

all of the spring and early summer months but not during August (winter) or February (late summer).

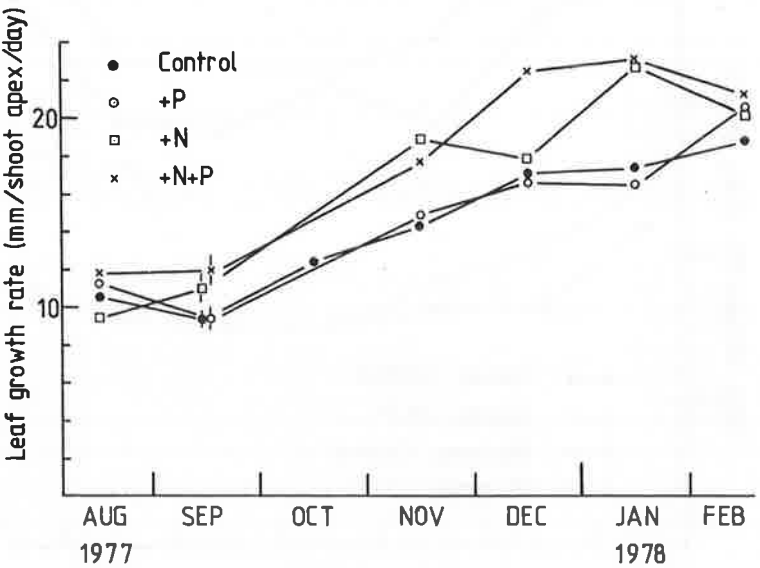

Fig. 3. Leaf growth rate of *Heterozostera tasmanica* in plots enriched with nitrogen (+ N), phosphorus (+ P), neither (Control) or both (+ N + P) from August 1977 to February 1978: values are the means from 3 plots per treatment, with each plot mean based on 5 to 10 plants each month; the SE is shown for the September data; ANOVA of all the data is presented in Table II.

TABLE II

Three-way ANOVA of leaf growth rate of *Heterozostera tasmanica* enriched by ammonium and/or phosphate from August 1977 through February 1978: the data on which this table is based are presented graphically in Fig. 3.

Source of variation	d.f.	*F* value
Ammonium enrichment (N)	1	10.392**
Phosphate enrichment (P)	1	1.461 ns
Time	5	21.802***
N × P	1	0.212 ns
N × time	5	1.264 ns
P × time	5	0.232 ns
N × P × time	5	0.515 ns
Error	48	

** $P < 0.01$, *** $P < 0.001$, ns = not significant = $P > 0.05$.

TABLE III

Probabilities for the F ratio of two-way ANOVA (A = ammonium enrichment, B = phosphate enrichment) of leaf growth rate of *Heterozostera tasmanica* enriched by ammonium and/or phosphate in the rhizosphere each month from August 1977 through February 1978.

Source of variation	Aug.	Sept.	Oct.[a]	Nov.	Dec.	Jan.	Feb.
Ammonium enrichment	>0.50	0.04	...	0.15	0.11	0.06	0.50
Phosphate enrichment	0.31	>0.50	...	0.50	0.25	>0.50	0.40
Interaction	>0.50	>0.50	...	>0.50	0.22	>0.50	>0.50

[a] Insufficient samples for analysis.

STANDING CROP

The standing crop of leaves in all plots increased about three-fold between winter and summer (Fig. 4). Maximum standing crop occurred in December or January and was followed by a sharp decline. The pattern was similar in all treatments.

TABLE IV

Maximum dry weight of leaves of *Heterozostera tasmanica* growing in sediments enriched with ammonium (+N), phosphate (+P), neither (control) or both (+N+P): mean ± 1 SE of the mean ($n = 3$); two-way ANOVA indicates no significant ($P > 0.05$) differences among the means.

Control	+N	+P	+N+P
241 ±43.3	259 ±20.5	277 ±44.3	347 ±18.0

Thus, in September, 1977 the mean standing crops for each treatment ranged from 105 to 139 $g \cdot m^{-2}$ while the maximum standing crops in December and January ranged from 239 to 304 $g \cdot m^{-2}$. Three-way ANOVA indicated no significant ($P > 0.05$) differences in standing crop due to nitrogen enrichment, phosphorus enrichment, or any of the interactions. Similarly, a two-way ANOVA of the maximum dry weight of leaves and a Student–Newman–Keuls multiple comparison test indicated no differences due to enrichment nor significant differences between any of the treatments (Table IV). At no time during the course of this study did a conspicuous development of epiphytes occur in any of the treatments.

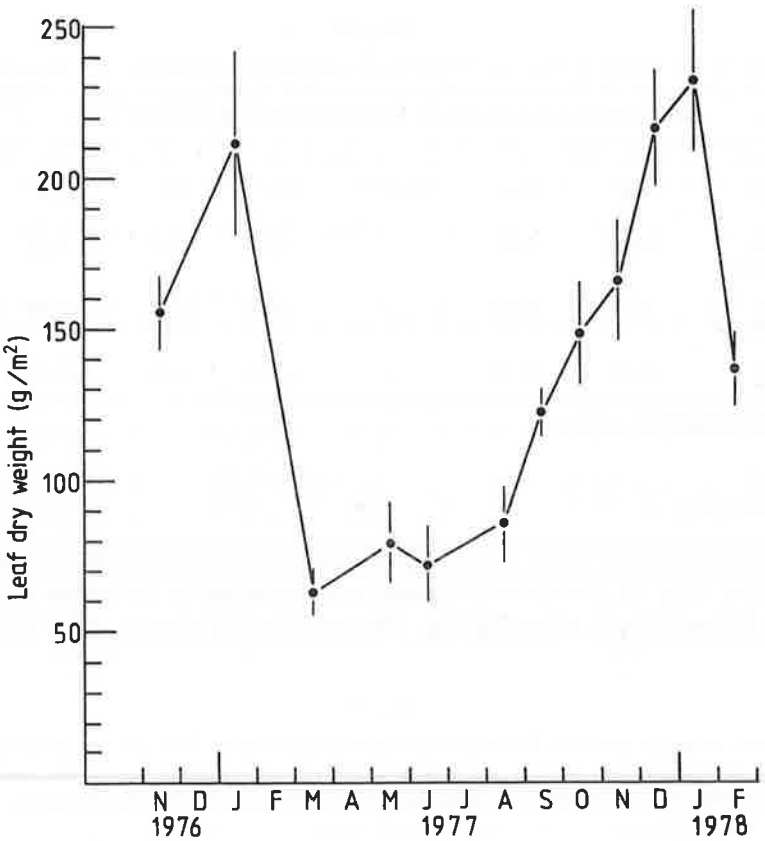

Fig. 4. Seasonal changes in the dry weight of leaves of *Heterozostera tasmanica* growing in all experimental plots in northern Western Port from November 1976 to February 1978 during the disturbance and enrichment experiments: vertical bars indicate 1 SE of the mean (n = 15–30 each month).

DENSITY

The seasonal trend of shoot density is similar to that observed for leaf standing crop (Fig. 5). There was a winter minimum of 1000–2000 apices $\cdot$ m^{-2}, a rapid increase during spring to a summer average of 5000–6000 and a decline during February–April to the winter low. Throughout the experiment all plots had similar densities. The minimum treatment means during winter ranged from 630 to 1150 apices $\cdot$ m^{-2} while summer maxima ranged from 6400 to 7700 apices $\cdot$ m^{-2}. Three-way ANOVA indicated that none of the enrichments had a significant effect on shoot density.

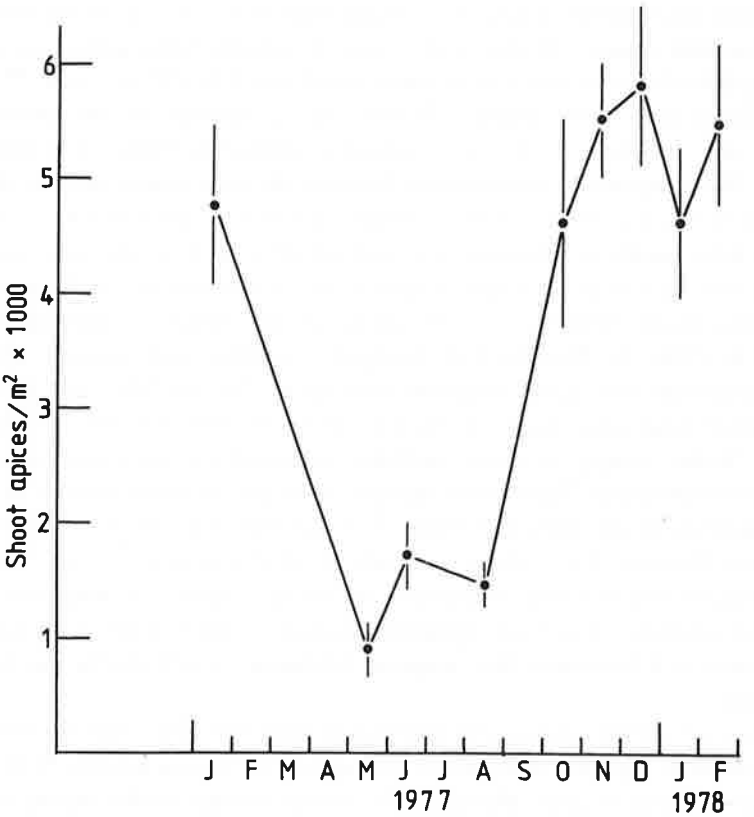

Fig. 5. Seasonal changes in the density of shoot apices of *Heterozostera tasmanica* growing in all experimental plots in northern Western Port from January 1977 to February 1978 during the disturbance and enrichment experiments: vertical bars indicate 1 SE of the mean (n = 10–30 each month).

Discussion

Raymont (1947), Buljan (1957), and Orth (1977) added fertilizer containing nitrogen, phosphorus, and various other elements to seagrass communities and reported increased growth of seagrasses. However, in Buljan's report, the dissolved oxygen increase could have been attributed to epiphytes or to the blue-green algal mat which he reported rather than to the seagrasses. Raymont did not indicate how the reported increase in *Zostera* compared with the normal summer increase. In the only other study of enrichment of seagrasses, Orth (1977), with the use of controls, reported a three-fold increase in *Zostera marina* biomass of leaves and significant increases in density and length of turions. In the present study, in contrast, there was no significant increase in either standing crop of leaves or density of *Heterozostera tasmanica* when sediments were enriched with both

nitrogen and phosphorus. These two studies had similar levels of enrichment and included similar seasons of the year – over 2 months Orth added an unnamed commercial fertilizer at a rate calculated to be 64 and 128 g $N \cdot m^{-2}$ and 57 g $P \cdot m^{-2}$ during spring and early summer. Within any 2 months in the present study 200 g $N \cdot m^{-2}$ and 40 g $P \cdot m^{-2}$ were added to sediments from late winter to late summer. The difference in the response between the two studies may be due to the potassium or trace nutrients in the commercial fertilizer used by Orth, or alternatively the two species of seagrass may respond differently to the same conditions. Differences in the natural nutrient supply to the two seagrass populations is also a likely explanation. Nutrient concentrations of the water or sediments are not reported by Orth. In Western Port inorganic nitrogen and reactive phosphorus concentrations are low in the water but were up to 1700 μm NH_4^+ and 60 μm PO_4^{3-} in interstitial water squeezed from the top 20 cm of sediment. This would provide a 30- to 50-day supply of these nutrients at maximum computed uptake rates assuming no recycling. There thus appears to be an adequate reserve of nitrogen and phosphorus in the sediments beneath *H. tasmanica* growing on intertidal flats in northern Western Port. There may not be similar reserves in the Chesapeake Bay sediments where Orth conducted his study. Further studies on sediment interstitial nutrient dynamics beneath seagrass communities and particularly measurement of Chesapeake Bay seagrass sediments, would enable this hypothesis to be tested.

Valiela *et al.* (1975) reported no increase in total standing crop the first year of enrichment of a *Spartina alterniflora* salt marsh in Massachusetts, U.S.A. There were large increases in peak biomass (2–3.5 times control levels) during the 2nd to 4th years of enrichment. However, any response of *Heterozostera tasmanica* to nutrient enrichment in the present study would have been expected during the first season of growth as has been reported for other seagrasses (Raymont, 1947; Orth, 1977) freshwater submerged macrophytes (Moss, 1976) and for *Spartina alterniflora* salt marshes at latitudes similar to Western Port (Sullivan & Daiber, 1974; Patrick & Delaune, 1976; Haines, 1979; Buresh *et al.*, 1980).

Although there was no change in leaf standing crop or plant density, there was a significant 20% increase in leaf growth rate of *Heterozostera tasmanica* when enriched with ammonium (Fig. 2, Table II). Thus, growth of *H. tasmanica* on intertidal flats in northern Western Port may be nitrogen limited since nitrogen addition resulted in an increase in growth (cf. Odum, 1959). There is an indication that this nitrogen limitation of *H. tasmanica* occurred only during the spring and early summer months, the time of maximum growth (Table III). Although ammonium was always present in the sediments, nitrogen limited growth may result from microgradients of nutrient depletion around the roots. Such microgradients have been described for phosphorus and potassium in agricultural soils (Bhat & Nye, 1974; Mengel & Kirkby, 1978) and are most likely to develop when demand for a nutrient is fairly high and nutrients are transported through the soil by diffusion

(Mengel & Kirkby, 1978). Diffusion would be expected to supply most of the nutrients to plant roots in these submerged sediments and nutrient demand would presumably be highest during spring and early summer, the time of highest leaf growth rate. This was also the time at which leaf growth rate appeared nitrogen limited. The large increase in ammonium (5- to 100-fold) in the +N and +N+P plots then, would have increased the rate of ammonium diffusion across such gradients and thus sustain higher average leaf growth rates.

The 20% increase in leaf growth rate with ammonium enrichment would have been expected to result in a similar increase in leaf standing crop. However, such an increase would not have been detected by the method used to measure leaf standing crop. That is, leaf standing crop was highly variable and although three to six replicate measurements per treatment were made each month, the minimum difference between treatments that could be declared significant ($P < 0.05$) would have been a 35% or greater increase or decrease. Thus, the increased leaf growth rate may have increased the standing crop by 20% but this was masked by the natural variance and not detected in this study, or may have been balanced by a similar increase in leaf loss so that leaf turnover rate increased while leaf standing crop remained constant, or may have produced leaves with a lower dry weight to length ratio (e.g. narrower leaves) and thus kept leaf dry weight constant. The last possibility seems unlikely since leaf size and shape appeared similar in all treatments. Thus, the lack of a significant difference in leaf standing crop between treatments is not inconsistent with the 20% significant increase in leaf growth rate with ammonium enrichment.

The level of total nitrogen in the leaves also gives an indication that *H. tasmanica* may be nitrogen limited during spring and early summer. Gerloff & Krumbholz (1966) have suggested that for several submerged freshwater angiosperms a concentration in the leaves below 1.4% nitrogen and 0.13% phosphorus may indicate growth limitation by these nutrients respectively. If the "critical concentrations" for *H. tasmanica* are similar, nitrogen is a potential growth limiting nutrient since leaf concentration averaged 1.5% nitrogen in control plots during spring and early summer (September to January) with a minimum of 1.4% (Fig. 2). Leaf phosphorus, on the other hand, averaged 0.20% with a minimum of 0.17%.

Total nitrogen and total phosphorus concentration in the rhizomes and total nitrogen concentration in the leaves increased when the sediments were enriched with ammonium and/or phosphate (Fig. 2). Thus, there appears to have been an increase in the uptake of nitrogen and phosphorus by the roots of *H. tasmanica* and an increase in the amount of nitrogen in the leaves. *H. tasmanica* is thus similar to the seagrass, *Zostera marina*, and numerous submerged freshwater angiosperms in which absorption of nutrients from the sediments and translocation from roots to leaves have been demonstrated (McRoy & Barsdate, 1970; Bristow & Whitcombe, 1971; McRoy & Alexander, 1975; Twilley *et al.*, 1977).

The present study indicates that a 5 to 100 times increase in the spring and

summer supply of nitrogen and phosphorus to the rhizosphere of *Heterozostera tasmanica* in northern Western Port would not be expected to increase total summer standing crop of this seagrass and would only slightly increase leaf growth rate during spring. This study, however, has concentrated only on the direct effects of sediment introduced nitrogen and phosphorus on *H. tasmanica*. Increased nitrogen and phosphorus levels in Western Port waters, in contrast, could enhance phytoplankton and/or other algal growth which could deleteriously affect growth of seagrasses indirectly as has been postulated for freshwater angiosperms (Jupp & Spence, 1977; Phillips *et al.*, 1978).

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Chapter 4
Rhodophyta—systematics and biology

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4.1 Introduction

The division Rhodophyta includes about 4100 species in 675 genera, 95 per cent of which are marine. Australasia, with at least 1100 species and 370 genera, contains a greater diversity of red algae than any other comparably sized region on earth. Over 70 per cent of the recorded species appear to be endemic, as are some 110 genera and 4–5 entire families. Because long stretches of the Australasian coastline remain virtually unexplored phycologically, these figures are only estimates and may have to be revised upwards when more data become available.

Red algae commonly are overshadowed in conspicuousness by the larger green and brown algae in intertidal and shallow subtidal habitats, but their importance and dominance in deeper waters is becoming increasingly clear, especially since the advent of SCUBA equipment which has enabled detailed *in situ* studies of subtidal ecosystems. Available data from these studies and from drift specimens washed ashore after storms suggest that 70–75 per cent of the entire Australasian marine benthic flora is composed of red algae.

Unfortunately, there is no comprehensive up-to-date floristic account of Australasian Rhodophyta. Most information is widely scattered in journals and concerns mainly New Zealand or southern Australia. Some of the older works by Harvey and Kützing (see Chapter 1) are beautifully illustrated and valuable for identifying species even today, but they cover only a small proportion of our flora and often depict species whose names have been changed since.

Recent publications on New Zealand red algae include four sections of a proposed comprehensive flora (Chapman, 1969a, 1979; Chapman and Dromgoole, 1970; Chapman and Parkinson, 1974) and checklists for several regions (Adams, 1972; Adams et al., 1974., Naylor, 1954; South and Adams, 1976a).

Data on tropical and subtropical Australian Rhodophyta are scant. Since the appearance of Sonder's (1871) account, some information has been published for Arnhem Land (Womersley, 1958); for Queensland (Bailey, 1913; Cribb, 1954c, 1956, 1958a, 1961, 1966; Lucas, 1931a; May, 1951; Price et al., 1976; Ngan and Price, 1979a, b); and for Lord Howe Island off New South Wales (Lucas, 1935; Zanardini, 1874). May (1965) has provided a partial summary of species records for tropical and subtropical Australia in her census of Australian Rhodophyta. In southern Australia, detailed information for many groups of Rhodophyta is contained in a series of monographs published since the floristic account of Lucas and Perrin in 1947. To date less than half of the total flora has been treated monographically, although checklists have appeared for localised areas in South Australia (Shepherd and Womersley, 1980; 1971, 1976; Womersley, 1948, 1950) and Victoria (Davey and Woelkerling, 1980, Ducker et al., 1977b; Garnet, 1971; King et al., 1971; Womersley, 1966).

This chapter first considers the basic morphology and anatomy of red algae and then reviews Australasian red algal systematics. In both parts, frequent reference is made to a series of figures (with accompanying detailed legends) which illustrate many distinctive features found in species from this region. Sections 4.4, 4.7 and the texts of 4.5 and 4.6 were prepared by the first author; sections 4.2 and 4.3 were written by the second author and the tabular data in sections 4.5 and 4.6 and the bibliography were compiled jointly.

It is our belief that an appreciation of red algae can be frustrated by the practical difficulties people have in trying to observe and apply the seemingly esoteric criteria used to classify them; it is hoped that this review will help avoid such initial problems.

4.2 Structure and reproduction

The vegetative system

Four types of thallus construction occur in red algae: unicellular, colonial, parenchymatous, and filamentous. The first three are found only in a small minority of species, all assignable to the subclass Bangiophycidae. The filamentous type of construction is characteristic of over 95 per cent of the known species, including all members of the subclass Florideophycidae.

Unicellular taxa (Kylin, 1956: pp. 50–52) rarely have been collected *in situ* in marine environments, have not been recorded from Australasia and will not be considered further. Colonial aggregates of cells, sometimes forming thread-like colonies, are characteristic of a few genera such as *Asterocytis* and *Goniotrichum* (Fig. 4.3J) which are worldwide in distribution. The thread-like colonies are sometimes referred to as 'filaments'. However, they do not possess a filamentous type of construction, because when cell division occurs, the resulting cells sooner or later become enclosed by completely new cell walls of their own. When, in contrast, cell division occurs in plants with a true filamentous (or parenchymatous) construction, a new wall is laid down between the divided protoplasts and becomes joined at either end to the old parent cell wall which never ruptures or gelatinises.

Parenchymatous construction occurs in the family Bangiaceae, which includes the widely distributed genera *Bangia* (Fig. 4.3L), and *Porphyra*. *Porphyra* is sheet-like, up to 40 cm long and 30 cm wide, and composed of one (Fig. 4.5F) or two cell layers. The fundamental characteristic distinguishing parenchymatous thalli from filamentous thalli is that cell division can occur in two or three planes in the former but is restricted to a single plane in the latter.

The range in filamentous construction among red algae is considerable. In some genera, the various filamentous branches of the plant remain free from one another (Fig. 4.3D, F). In other genera, they become interconnected in a more or less defined manner (Fig. 4.3E). In still other genera, amalgamation of filaments occurs to such an extent that the thallus appears to be parenchymatous (Figs 4.3B,C, 4.5C). These three categories represent points along an intergrading series of morphological variants in red algae. Where consolidation of filaments occurs, the thallus may be encrusting (Figs 4.3H, 4.5E) or erect in form and cylindrical (Fig. 4.3B,C), compressed (Fig. 4.3E) or foliose (Fig. 4.2A, H) in appearance.

Branch apices possess either a uniaxial or a multiaxial organisation. In uniaxial construction, a single axial (central) filament is present (Fig. 4.3A,B,D–F) and gives rise to lateral filaments or cells in various ways. In multiaxial construction (Fig. 4.3C,I), the single axial filament is replaced by a central core of axial filaments, all capable of producing lateral branches. The type of apical organisation present becomes difficult to recognise in some taxa with a parenchyma-like thallus.

Often several more or less distinct regions are evident in cross-sections of thalli possessing a number of cell layers, and these include a centrally located medulla and a surrounding cortex (Fig. 4.5C, D,G,I). Characteristic differences in cell size, cell arrangement, degree of amalgamation and other anatomical features of the medulla and cortex provide important clues as to a plant's taxomonic affinities.

In a number of uniaxial red algae, cells of the axial filament are encircled by a distinct layer of pericentral or periaxial cells. Pericentral cells are usually evident in cross section (Fig. 4.5A,B) and in many species can be seen in surface view as well

(Fig. 4.3D,E). When formed, each pericentral cell typically is the same length as the axial cell from which it was derived, and commonly the pericentral cells are arranged in distinct tiers (Fig. 4.3D,E). Periaxial cells also arise from cells of the central axis but do not match the central cells in length (Figs 4.3F, 4.5I).

Consecutive cells of filaments in most red algae are joined by more or less conspicuous primary pit-connections (Fig. 4.11G,E) which can vary greatly in diameter from one species to another. In some species secondary pit-connections also occur between cells of adjacent filaments (Fig. 4.5J). Finally, adjacent vegetative cells of some red algae, including many members of the Corallinaceae, can undergo varying degrees of fusion (Fig. 4.5K). Such fusions occur independently of those associated with carposporophyte development (see below).

Gametic reproduction

Gametic reproduction in red algae is oogamous and involves formation of gametic nuclei within specialised structures. The 'carpogonium', or female gamete, usually consists of an enlarged basal portion and a more or less elongate 'trichogyne' which functions as a receptor for male gametes (Fig. 4.6A–D). In some species carpogonia are sessile or borne on an unspecialised stalk cell, but in most species they terminate more or less specialised filaments known as 'carpogonial branches' (Fig. 4.6A,B). The carpogonial branch may be composed of a definite or variable number of cells, depending on the taxonomic group, and the cells usually differ to varying degrees from ordinary vegetative cells in size and shape and in the diminution or absence of pigmentation. Carpogonial branch cells also commonly stain more intensely than ordinary vegetative cells. The cell from which a carpogonial branch arises is termed a 'supporting cell'.

Male gametes, or 'spermatia', are non-flagellated and are produced within 'spermatangia'. The spermatangia of most red algae are aggregated into clusters on specialised branch systems and consist of more or less non-pigmented cells smaller in size than ordinary vegetative cells (Fig. 4.9). At maturity male cells are released and carried passively to trichogynes where they adhere (Fig. 4.6D). After plasmogamy (fusion of the male and female gametes), karyogamy occurs, resulting in formation of a single diploid zygotic nucleus.

The carposporophyte

One unique feature of red algae belonging to the subclass Florideophycidae is the development of a 'carposporophyte' after karyogamy. The carposporophyte is a somatic generation initiated from the zygote (that is, the fertilised carpogonium). It remains permanently attached to the haploid parent plant (which is much larger in size), and ultimately gives rise to 'gonimoblasts' or filaments of cells which either bear or become reproductive bodies called 'carposporangia' (Figs 4.7, 4.8). In most cases carposporangia contain a single 'carpospore' which arises mitotically, although in a few species the carposporangium contains a presumably meiotic tetrad at maturity. The significance of the carposporophyte in red algal life histories is discussed below and is considered in greater detail by Drew (1954).

Differences in the mode of carposporophyte development have been assigned considerable taxonomic importance, as noted in the section on systematics. In some cases, gonimoblast filaments arise directly from the fertilised carpogonium (Fig. 4.7A,E). In other cases, the zygotic nucleus or its derivatives is transferred from

the fertilised carpogonium to specified cells of the gametophyte known as 'auxiliary' cells, from which gonimoblast filaments subsequently arise. When present, auxiliary cells may (Fig. 4.6J) or may not become evident before fertilisation. The auxiliary cells in some taxa occur on the same branch system as the carpogonium, and the two structures show a consistent spatial relationship. In the Ceramiales, for example, the auxiliary cell is normally borne on the cell which gives rise to the carpogonial branch (the 'supporting' cell). When a defined spatial relationship is present and a common branch system is involved, the entire female gamete–auxiliary cell structure is referred to as a 'procarp'. Auxiliary cells also may occur within specialised accessory branches (Fig. 4.6G,J) or as part of ordinary vegetative filaments.

Auxiliary cells may be situated near to or remote from carpogonia. Transfer of the zygotic nucleus or its derivatives from the fertilised carpogonium to the auxiliary cell is effected in most cases by development of a connecting cell or tube which arises from the carpogonium (Fig. 4.6F,I) and fuses with the auxiliary cell. In some species, a single connecting tube can fuse successively with a number of auxiliary cells, and a number of separate gonimoblasts can result from a single fertilised carpogonium.

Depending on the species, either the fertilised carpogonium or a 'diploidised' auxiliary cell may fuse with certain adjacent cells. These can include such haploid cells as the supporting cell and cells of the carpogonial (Fig. 4.6E) or auxiliary cell branch (Fig. 4.6K), or various 'nutritive' cells surrounding the fertile area, as well as (at times) some of the earliest-formed diploid gonimoblast cells (Fig. 4.8C,D). Such fusion cells, when present, are thought to function in a nutritive capacity for developing gonimoblast filaments. Cells of gonimoblast filaments also may fuse with cells of the haploid progenitor plant to form a complex nutritive tissue (Fig. 4.6M) which Kraft (1977a) terms a 'placenta'.

4.3 Life History

Reliable data relating to red algal life histories are meagre, and detailed studies based on laboratory cultures have been published for less than 5 per cent of the described species of Rhodophyta. Moreover, available information is attended by differences in the terminology used to describe life histories. In addition, much of the existing 'evidence' upon which important life history generalisations are based requires verification, and the potential variability present within the life histories of individual species remains largely unknown. Dixon (1973) and Drew (1955) provide further documentation on these points.

In this account, the term 'life history' is used to denote the recurring sequence of events resulting in the production of successive generations of plants. As such, the life history usually includes both a sexual cycle which involves gametic reproduction (gametogenesis, plasmogamy, karyogamy), and any apomictic cycles in which gametic reproduction does not take place. Only one type of sexual cycle can occur within a given species as far as we know, but one or more apomictic cycles also may be present.

Florideophycidae

At least four different sexual cycles are known to occur within the subclass Florideophycidae, and others may exist. Each is characterised by a particular sequence of morphological stages which include a haploid gamete-producing stage and one or

two distinct diploid stages. The first diploid stage (the carposporophyte) develops from the zygote and in all known cases remains permanently attached to the haploid parent plant (Figs 4.7, 4.8), from which it always differs markedly in appearance. The second diploid stage, when present, develops from carpospores produced mitotically by the first diploid stage, and it always grows independently of its progenitor. This second diploid stage invariably differs in appearance from the first diploid stage but may or may not possess a morphology identical to that of the haploid plant body. Thus a single sexual cycle involves two or three morphological stages, at least two of which differ dramatically in structure.

In all four sexual cycles, karyogamy involves the fusion of male and female gametic nuclei produced respectively within carpogonia and spermatangia. Zygote formation occurs within the carpogonium. Meiosis subsequently may occur during formation of spores or within ordinary vegetative cells, depending upon the species involved. The distinctive features of the four sexual cycles (Fig. 4.12) are outlined below.

The most documented (in terms of culture studies and cytological investigations) of the sexual cycles involves a 'free-living' haploid gametangial phase, a diploid carposporangial phase of markedly different morphology which remains attached to the haploid phase, and a 'free-living' diploid meiosporangial phase with a morphology similar to that of the haploid, gamete-producing plant (Fig. 4.12A). Spermatangia and carpogonia may be produced on the same haploid plant, but more commonly they occur on separate plants. The carposporangial phase or carposporophyte may be entirely embedded within the tissue of its haploid progenitor or it may protrude above the surface of the gametangial plant to varying degrees. Often the carposporophyte is surrounded by a 'pericarp,' a sterile envelope of haploid tissue derived from the haploid parent plant (Fig. 4.7D, G,H,I). The carposporophyte and the pericarp collectively are referred to as a 'cystocarp'.

Ultimately, this stage produces diploid carpospores by mitosis which germinate and develop into mature meiosporangial plants, or 'tetrasporophytes'. Meiosis occurs within developing sporangia, and in most cases four haploid spores are produced. Depending upon the species, spores may be arranged zonately, cruciately, tetrahedrally or irregularly within the sporangium (Fig. 4.10A-J). In a few species, the four meiotically formed spores divide further by mitosis to produce as many as 32 haploid spores within a single sporangium (Fig. 4.10K,L). The terms 'tetrasporangia' and 'tetraspores' generally are used where only four spores are involved; the terms 'polysporangia' and 'polyspores' apply when more than four spores are involved.

The cytological details for this type of sexual cycle were established first by Yamanouchi (1906) for the genus *Polysiphonia*, and the morphological sequence in *Polysiphonia* was confirmed in subsequent culture studies by Edwards (1968) and others. Parallel cytological and/or culture data based on northern hemisphere studies exist for a number of other genera, but to date no cytological data have been obtained for the Australasian region. However, the complete morphological sequence has been established in culture for *Dasya clavigera* (Womersley) Parsons and *Mazoyerella arachnoides* (Harvey) Gordon-Mills & Womersley, both of which are endemic to southern Australia (Gordon-Mills and Womersley, 1974; Parsons, 1975). For the majority of red algae, gametangial and meiosporangial plants of similar morphology occur, and it is presumed that all of these species exhibit the '*Polysiphonia*-type' of sexual cycle. Future culture and cytological studies will determine the validity of that presumption.

The other sexual cycles will be considered more briefly since fewer species are involved and many details require confirmation. One of these cycles is essentially similar to that of *Polysiphonia* except that the gametangial, carposporangial and meiosporangial stages all possess dissimilar morphologies (Fig. 4.12B). Examples possessing this type of sexual cycle include some northern hemisphere species of *Acrosymphyton* (Cortel-Breeman and Van den Hoek, 1970), *Asparagopsis* (Feldmann and Feldmann, 1939a), *Bonnemaisonia* (Feldmann and Feldmann, 1939b), *Gigartina* (West, 1972; West et al., 1977) and *Pseudogloiophloea* (Ramus, 1969); Dixon (1970a) summarises other examples. This type of sexual cycle is thought to occur in a number of Nemalionales and some Cryptonemiales and Gigartinales for which the gametangial or meiosporangial stages are unknown presently. In most cases confirming culture studies have yet to be undertaken. The Australasian flora contains a number of taxa which probably possess this type of sexual cycle (species of *Asparagopsis*, *Liagora* *Acrosymphyton*, *Nemastoma*), but to date no published accounts of cytological or culture studies based on material from this region have appeared.

The other two sexual cycles in the Florideophycidae involve only two stages: a haploid gametangial stage and a morphologically dissimilar diploid carposporophyte which remains attached to the haploid progenitor. In one cycle (Fig. 4.12C) the sporangial phase ultimately produces tetraspores, which in one species, *Helminthocladia senegalensis* (Bodard, 1971), are known to form meiotically; these presumably give rise to gametangial plants. The only known species from the Australasian region suspected of having this sexual cycle is *Liagora harveyana* Zeh (Womersley, 1965b). In the other cycle (Fig. 4.12D), the diploid carposporophyte produces diploid carpospores by mitosis. Upon germination these spores give rise to a 'juvenile' stage of prostrate filaments from which the adult gametangial phase arises. Meiosis occurs in the apical cell of the upright filament which gives rise to the gametangial plant. This cycle is known in species of *Lemanea* (Magne, 1967) and *Batrachospermum* (von Stosch and Theil, 1979), both freshwater genera. Much additional work is needed to confirm and fully establish the nature of these last two sexual cycles.

Bangiophycidae

The occurrence of a sexual cycle within the subclass Bangiophycidae has been a subject of considerable debate and interest (Drew, 1956), especially since diploid stages analogous to the carposporophyte and tetrasporophyte are not known to occur. As noted by Dixon (1973: p. 205), existing data are attended by many uncertainties and by some apparent contradictions. Hawkes (1978) has provided convincing evidence for the occurrence of a sexual cycle in one species of *Porphyra*. Male and female gametes develop within apparently ordinary vegetative cells. Spermatangia are formed from mitotic divisions of a protoplast, while the female gamete is formed within a carpogonium-like cell which differs from an ordinary cell only in producing a bulge thought to be a rudimentary trichogyne. Following plasmogamy and karyogamy, the zygotic protoplast divides to produce directly two presumably diploid spores without formation of gonimoblasts. The fate of these spores and precise details related to the time and place of meiosis remain uncertain, but it may be presumed that the spores give rise to a minute filamentous thallus (the so-called *Conchocelis* phase). Giraud and Magne (1968) suggest the meiosis may be somatic and occur prior to formation of spores by the filamentous thallus. The presumably haploid spores then give rise to foliose gamete-producing plants.

Apomictic cycles

In addition to sexual cycles, various apomictic cycles involving spore production also occur. In most cases, the spores give rise to the same type of plant as that from which they were derived. Monospores (spores produced singly within a sporangium) occur in a number of genera (Fig. 4.11 I,J) including *Audouinella* (Woelkerling, 1970, 1971) and *Monosporus* (Baldock, 1976) from Australasia. In *Audouinella*, monosporangia may form on the same plants with gametangia or meiosporangia, or plants may bear monosporangia exclusively. In *Monosporus* these spores constitute the only known mode of reproduction.

Various other spore types have been recorded in field and culture populations of red algae. These include bispores,non-meiotic tetraspores, and paraspores (Fig. 4.11L) which have been recorded by Drew (1939), Ganesan and West (1975), Suneson (1950), West and Norris (1966), West (1970) and others.

Polanshek and West (1977) also have discovered an apomictic cycle involving parthenogenesis in cultures of *Gigartina papillata* from North America. Female plants grown in the absence of male plants produced carpogonia. These subsequently developed into carposporophytes without fertilisation taking place, and the carpospores ultimately developed exclusively into female plants. All stages were presumed to be haploid.

Most of these phenomena have yet to be demonstrated in Australasian Rhodophyta, and when such studies are undertaken (especially on taxa endemic to this region), many as yet unknown aspects of red algal life histories may emerge and ultimately provide a better basis for formulating generalisations.

4.4 Systematics

The basic structural unit of red algae is the branched, often heterotrichous, filament derived from divisions of apical cells, although some species lack meristems and a few (mostly non-marine forms) are colonial or unicellular. Chloroplasts (Fig. 6.19A,B) are characterised by single, unstacked thylakoids on which organelles called 'phycobilisomes' are arranged which contain the characteristic bilin pigments. Food reserves are grains within the cytoplasm (Fig. 4.5J) related to the starch products of higher plants and termed 'Floridean' starch. Cells walls have inner cellulosic layers and pectic outer layers of varying composition and thickness. Flagellated vegetative and reproductive cells are completely absent from the division and appear never to have evolved in it. The Rhodophyta consists of the single class Rhodophyceae and two primary subdivisions, the subclasses Florideophycidae and Bangiophycidae.

In the treatment that follows, the characteristics of the major taxonomic subdivisions are given, together with a rundown of their Australasian numbers, endemic genera, and recent literature pertaining to Australasian members of the groups.

We want to emphasise that the presently accepted grouping of red algae into orders and, in some cases, families is neither static nor a finished achievement. Many workers feel that the system is liable to major modification as more becomes known for a greater proportion of the Division than now exists. The criteria by which red algae are classified below the subclass level are still almost wholly morphological and based on observations and intuitions made from light microscopy. Although major

advances are being made to knowledge of red algal life histories, ultrastructure, biochemistry and genetics, these new data have scarcely touched fundamental taxonomy and phylogenetic theory. The expectation is that they eventually may do so.

The classification scheme that we follow is that of Kylin (1956), modified by recent fine tuning of his widely employed system. The counts of genera and species given are composites of Kylin, Dawson (1962), recent Australasian monographic works, and unpublished data. These are approximations and probably nobody else repeating the exercise would exactly match our numbers (cf. Chapter 9).

4.5 Subclass Florideophycidae

Plants of this group are composed of filaments derived from apical meristems (Fig. 4.3), although some secondarily develop intercalary, diffuse or marginal (Fig. 4.3G) growth. Thalli are uniaxial or multiaxial, either remaining filamentous (Fig. 4.5D) or compacting into pseudoparenchyma (Fig. 4.5C). Cells are linked by primary pit-connections when they are adjacent members of the same filament (Fig. 4.5E), and may or may not form secondary pit-connections (Fig. 4.5J) or partial fusions (Fig. 4.5K) with contiguous cells on separate filaments. Sexual reproduction is of the specialised oogamous type described previously.

The Florideophycidae is further divided into from 5 to 10 orders, based on rather esoteric and often fleeting features of the sexual cycle and initiation of the zygote. Precise information on these phenomena is presently known only for a minority of the red algae, however. Dawson (1966) notes that in most species taxonomically crucial events such as auxiliary cell formation have never been observed and that actual placement of such taxa into orders more or less strongly rests on the use of 'numerous alternative clues' (which tend to suggest themselves mainly to 'experts'). As a practical as well as phylogenetic system, the classification scheme presently in use has its drawbacks (cf. Searles, 1968: 78, for an excellent summary), a major one being that keys to orders and families based on it are almost totally unworkable to non-specialists. Such keys are omitted here, but examples can be found in Abbott and Hollenberg (1976), Bold and Wynne (1978), Dawson (1966) and Kylin (1956). The following six-order scheme is followed in this work.

Order 1: Nemalionales

This is a very heterogeneous group of both freshwater and marine species. It contains some seven families, 30 genera and roughly 375 species of marine plants, plus three freshwater families of about eight genera and 145 species (Bourrelly, 1970). The genus *Audouinella* (Figs 4.2F, 4.7E) has both freshwater and marine representatives. Plants may be either uniaxial or multiaxial depending on the family, and most are clearly filamentous in internal structure. Several members of the group are slimy and worm-like, and a few are calcified. The carposporophyte arises either directly from the fertilised carpogonium, or from the cell of the carpogonial branch directly beneath the carpogonium into which the zygote nucleus migrates. Tetrasporophytes are often unknown; where present they may be isomorphic to the gametophytes (*Audouinella*, *Delisea*), heteromorphic but macroscopic (*Galaxaura*, *Asparagopsis*), or microscopic filaments (*Liagora*). Division of the tetrasporangia is regularly (Fig. 4.10F) or

irregularly (Fig. 4.10J) cruciate. In some species of *Liagora* (Womersley, 1965b) the terminal cells of the carposporophyte, instead of forming carposporangia, apparently undergo meiosis to form 'carpotetraspores'.

The Nemalionales is well represented in Australia and New Zealand, with 21 genera and about 90 marine species present.

Endemic genera: *Leptophyllis*, *Nothocladus* (freshwater)

Relevant literature:

Order or family	References	Genera treated
Nemalionales	Chapman (1969a)	General survey (NZ)
	Levring (1953)	General survey (Aust.)
	Levring (1955)	General survey (NZ)
Acrochaeticaceae	Woelkerling (1970)	*Audouinella* (as *Acrochaetium*)
	Woelkerling (1971)	*Audouinella*, *Colaconema*
Helminthocladiaceae	Womersley (1965b)	*Helminthora*, *Helminthocladia*, *Liagora*
Naccariaceae	Womersley and Abbott (1968)	*Naccaria*
Nemalionaceae	Womersley (1965b)	*Nemalion*

Order 2: Gelidiales

The Gelidiales is a small but distinctive marine order of two families, 10 genera and about 130 species. All members are uniaxial and have filamentous thalli, but may appear pseudoparenchymatous in cross-section (Fig. 4.5C). Most species are characterised internally by 'rhizines', slender filaments with very thick walls and narrow lumens running longitudinally through either the cortex or medulla. Carposporophytes arise as lax filaments directly from the fertilised carpogonium and grow among clusters of small 'nurse' cells in the medulla to produce large egg-shaped carpospores within a distinctly swollen fruit chamber (Fig. 4.7H). The species have tetrasporophytes isomorphic to the gametophytes, and tetraspores divide in a cruciate pattern. Cystocarps are unknown in the tropical genus *Gelidiella*.

There are no endemic genera among Australia and New Zealand's six representatives, but most of the 15 or so species are endemic. The major genera of both countries are *Gelidium* and *Pterocladia*, with rarer taxa being *Beckerella* (NSW), *Gelidiella* (NSW, Qld, WA) and *Ptilophora* (WA).

Relevant literature:

Order or family	References	Genera treated
Gelidiales	Chapman (1969a)	General survey (NZ)
Gelidiaceae	Fan (1961)	*Pterocladia* (NZ), *Beckerella*, *Ptilophora*

Order 3: Cryptonemiales

This is an order of very diverse forms containing 14 families, around 130 genera and about 900 species, all marine with the exception of one or two species of *Hildenbrandia*. Plants are either uniaxial or multiaxial and can be obviously filamentous or

pseudoparenchymatous. Some are broad and leafy, others thin and wiry. Some are soft and mucilaginous, others are firm and cartilaginous, while still others are heavily calcified and rock-like. Carposporophytes do not arise from fertilised carpogonia, nor from other cells within the carpogonial branch (except in a very few anomalous North American genera), but instead originate from completely separate 'auxiliary cells' which may be close-by or distant from the carpogonia. When the auxiliary cells are distant, the zygote nucleus is conveyed to them from the carpogonium through mostly non-septate tubes called 'connecting filaments'. Whether near or far, the auxiliary cell is always located in an 'accessory' branch, meaning that the branch containing the auxiliary cell is a special lateral structure that arises after the normal vegetative architecture of the plant body has been laid down. Tetrasporophytes may be unknown, lacking altogether, isomorphic, or heteromorphic. Tetrasporangia are regularly to irregularly cruciate or zonate.

About 40 per cent of the world's genera of Cryptonemiales and about half the species belong to the family Corallinaceae, whose members are heavily calcified. Plants of this group are particularly important in the tropics where they are often the dominant structural organisms (either plant or animal) on so-called 'coral' reefs.

Australia and New Zealand have representatives of 9 families, 62 genera and around 180 species of the Cryptonemiales, with half the species being members of the Corallinaceae.

Endemic genera: *Apophloea* (NZ), *Austrophyllis*, *Blastophye*, *Dasyphloea*, *Ectophora* (NZ), *Epiphloea*, *Gelinaria*, *Glaphyrymenia*, *Hormophora*, *Mastophoropsis*, *Metagoniolithon*, *Polynema*, *Pseudoanemonia* (NZ), *Pterocladiophila* (NZ), *Rhizopogonia* (NZ).

Relevant literature:

Order or family	References	Genera treated
Cryptonemiales	Chapman and Parkinson (1974)	General survey (NZ)
Corallinaceae	Ducker (1979a)	*Metagoniolithon*
	Ducker et al. (1976)	*Jania*
	Townsend (1979)	*Synarthrophyton*
	Woelkerling (1978)	*Mastophoropsis*
	Woelkerling (1980a, 1980b)	*Metamastophora*
Cryptonemiaceae	Chiang (1970)	*Acodes* (NZ), *Carpopeltis*, *Polyopes*, *Thamnoclonium*
	Kraft (1977c)	*Grateloupia* (NZ)
Dumontiaceae	Mitchell (1966)	*Dasyphloea*, *Dudresnaya*
Hildenbrandiaceae	Denizot (1968)	*Apophloea* (NZ), *Hildenbrandia*
Kallymeniaceae	Norris (1957)	*Polycoelia*, *Pugetia* (NZ)
	Norris (1961a)	*Glaphyrymenia*
	Womersley and Norris (1971)	*Austrophyllis*, *Callophyllis*, *Cirrulicarpus*, *Glaphyrymenia*, *Hormophora*, *Kallymenia*, *Polycoelia*, *Thamnophyllis*
	Womersley (1973)	*Kallymenia*

Order or Family	References	Genera treated
Peyssonneliaceae	Denizot (1968)	*Peyssonnelia*
Pseudoanemoniaceae	Chapman (1969b)	*Pseudoanemonia* (NZ)
Pterocladiophilaceae	Fan and Papenfuss (1959)	*Pterocladiophila* (NZ)
Unknown family	Denizot (1968)	*Sonderophycus*

Order 4: Gigartinales

The Gigartinales is a very complex order with the largest profusion of families in the division. The group consists worldwide of some 28 families, 100 genera and around 700 species. Only two species are known from brackish or freshwater habitats, one being endemic to Queensland (Cribb, 1965a). Plants have a habit range almost as broad as the Cryptonemiales, although only one or two genera are calcified and there are no rock-like forms. Plants are uni-or multiaxial depending on the family, and several genera are strongly pseudoparenchymatous. Reproductive morphology is often quite similar to the Cryptonemiales, and families are occasionally switched back and forth between the two orders as opinions are formed and reformed. The defining feature of the Gigartinales is that the carposporophyte arises from an auxiliary cell which is not located in a special, accessory branch of cortical filaments in the thalli, but which is intercalary in a normal vegetative cortical cell branch. In several families the auxiliary cell itself is the cell that bears the carpogonial branch. The range of tetrasporophyte habits and tetraspore division types is similar to the Cryptonemiales.

The Gigartinales is particularly well represented in Australia and New Zealand with 18–19 families, 65 genera and some 200 species recorded. Four entire families and more than 95 per cent of the species that occur there are endemic to Australasia.

Endemic genera: *Acrotylus*, *Adelophyton*, *Amphiplexia*, *Antrocarpus*, *Areschougia*, *Austroclonium*, *Catenellopsis* (NZ), *Clavicloniun*, *Dicranema*, *Erythroclonium*, *Erythronema*, *Gloiophyllis*, *Hennedya*, *Melanema*, *Melanthalia*, *Mychodea*, *Mychodeophyllum*, *Nizymenia*, *Peltasta*, *Placentophora* (NZ), *Reptataxis*, *Rhabdonia*, *Stenocladia*, *Stictosporum*, *Tylotus*.

Relevant literature:

Order or family	References	Genera treated
Gigartinales	Chapman (1979)	General Survey (NZ)
Acrotylaceae	Kraft (1977a)	*Acrotylus*, *Amphiplexia*, *Hennedya*
Dicranemaceae	Kraft (1977b)	*Dicranema*, *Peltasta*, *Reptataxis*, *Tylotus*
Gracilariaceae	Kraft (1977d)	*Gracilaria* (NZ)
	May (1948)	*Gracilaria*
Mychodeaceae	Kraft (1978)	*Mychodea*
Mychodeophyllaceae	Kraft (1978)	*Mychodeophyllum*
Nemastomataceae	Kraft (1975a)	*Adelophyton*
	Chapman (1979)	*Catenellopsis* (NZ)
Nizymeniaceae	Searles (1968)	*Stenocladia*
	Womersley (1971b)	*Nizymenia*, *Stenocladia*
Phacelocarpaceae	Searles (1968)	*Phacelocarpus*
Phyllophoraceae	Lewis and Kraft (1979)	*Schottera*

Family	References	Genera treated
Plocamiaceae	Womersley (1971a)	*Plocamium*
Rhabdoniaceae	Min-Thein and Womersley (1976)	*Areschougia*, *Catenella*, *Erythroclonium*, *Melanema*, *Rhabdonia*
	Searles (1968)	*Caulacanthus* (NZ), *Tayloro-phycus* (NZ)
Rhodophyllidaceae	Min-Thein and Womersley (1976)	*Austroclonium*, *Calliblepharis*, *Craspedocarpus*, *Gloiophyllis*, *Rhodophyllis*
	Searles (1968)	*Stictosporum*
Sarcodiaceae	Rasmussen (1964)	*Sarcodia* (NZ)
Solieriaceae	Kraft (1975b)	*Placentophora* (NZ)
	Min-Thein and Womersley (1976)	*Callophycus*, *Solieria*

Order 5: Rhodymeniales

This is a distinctive and exclusively marine order of four families, 42 genera and around 280 species. All members are multiaxial, and several are pseudoparenchymatous. Most species are fairly firm in texture, but several have hollow parts (Figs 4.2E, 4.11A) and some are partitioned into chambers by regular diaphragms (Fig. 4.3I). The carposporophyte grows from an auxiliary cell which terminates a short lateral branch adjacent to the carpogonium and which is formed before union of the gametes takes place. The mature carposporophyte is prominently encased in a dome-shaped, ostiolate pericarp and usually consists of several dense lobes of carposporangia borne on a distinct stalk cell that elevates it above the floor of the cystocarp cavity (Fig. 4.7F). Tetrasporangia are usually borne on tetrasporophytes isomorphic to the gametophytes and are cruciately or tetrahedrally divided, although two northern hemisphere genera (*Gastroclonium*, *Coeloseira*) form polyspores.

The group is well represented in Australasia, with three families, 24 genera and around 60 species being recorded.

Endemic genera: *Cenacrum* (Snares, Auckland I. [NZ]; Macquarie I. [Tas.]), *Faucheopsis*, *Gloiocolax* (NZ), *Gloiodermatopsis* (NZ), *Gloiosaccion*, *Webervanbossea*.

Relevant literature:

Order or family	References	Genera treated
Rhodymeniales	Chapman and Dromgoole (1970)	General survey (NZ)
Rhodymeniaceae	Ricker and Kraft (1979)	*Cenacrum*
	Sparling (1957)	*Gloioderma* (NZ)
		Gloiocolax (NZ)
		Hymenocladia
Champiaceae	Reedman and Womersley (1976)	*Champia*, *Chylocladia*

Order 6: Ceramiales

With some 325 genera and 1500 species in its four component families, the Ceramiales contains nearly half the genera and over a third of the world's red algal species. Only eight or nine species occur in fresh water (Bourrelly, 1970). This is the largest and reproductively most uniform of the orders, and has obviously been the most successful in terms of sheer numbers. The range of vegetative forms is extensive, and while most members are plainly uniaxial, pseudoparenchyma is common in some groups and a few leafy forms disguise their initial uniaxial construction by later marginal meristems and intercalary cell divisions (Fig. 4.3G). The carposporophyte grows from an auxiliary cell which is generally cut off from the supporting cell of the carpogonial branch very soon after fertilisation. Tetrasporophytes are usually isomorphic with gametophytes, the normal meiotic spore pattern being tetrahedral, occasionally cruciate, or rarely polysporangial (Fig. 4.10K,L).

The distinctiveness and size of the individual families warrants their individual consideration.

Family 1: Ceramiaceae

A family of some 100 genera and 500 species, the Ceramiaceae is particularly abundant in Australasia, where over 60 genera and 200 species occur. Plants of this group are usually composed of a single row of axial cells (Figs 4.3F, 4.7B, 4.10A) (with a few exceptions like the spongy genus *Haloplegma*), from each of which determinate lateral branchlets may develop in whorls of three or more, in pairs, or singly (although they may be lacking altogether). Carposporophytes are usually unprotected (Fig. 4.7B) or loosely surrounded by adjacent branchlets (Fig. 4.7C), as opposed to being encased in a flask-shaped pericarp (the one exception being the genus *Lejolisea*). While plants of the Ceramiaceae are usually thin and delicate, some become quite substantial and robust due to layers of corticating filaments or rhizoids that develop around the axes (Fig. 4.5H).

The Ceramiaceae is subdivided into some 18 tribes, based on details of reproductive and vegetative structure.

Endemic genera: *Amoenothamnion*, *Dasythamnion*, *Diapse*, *Dreviana*, *Euptiloclaclia*, *Gulsonia*, *Heterothamnion*, *Interthamnion*, *Involucrana*, *Lasiothalia*, *Lomathamnion*, *Lophothamnion*, *Macrothamnion*, *Mazoyerella*, *Perischelia*, *Perithamnion*, *Radiathamnion*, *Rhodocallis*, *Shepleya*, *Spencerella*, *Spongoclonium*, *Tetrathamnion*, *Thamnocarpus*, *Trithamnion*, *Warrenia*, *Wollastoniella*.

Relevant literature:

Tribe	References	Genera treated
Antithamnieae	Wollaston (1968)	*Acrothamnion*, *Antithamnion*, *Ballia* *Macrothamnion*, *Platythamnion*
	Wollaston (1974)	*Ballia*
	Wollaston (1977a)	*Acrothamnion*
	Wollaston (1978)	*Platythamnion*
Ceramieae	Womersley (1978)	*Ceramium*

Tribe	References	Genera treated
Compsothamnieae	Gordon-Mills and Womersley (1974)	*Mazoyerella*
Crouanieae	Wollaston (1968)	*Crouania*, *Euptilocladia*, *Gattya*, *Gulsonia* *Ptilocladia*
	Wollaston and Womersley (1959)	*Gulsonia*
Dasyphilieae	Wollaston (1972)	*Muellerena*
	Wollaston (1977b)	*Dasyphila*, *Muellerena*
Griffithsieae	Baldock (1976)	*Anotrichium*, *Griffithsia*, *Monosporus*
Heterothamnieae	Wollaston (1968)	*Amoenothamnion*, *Antithamnionella*, *Heterothamnion*, *Perithamnion*, *Tetrathamnion*, *Trithamnion*
Ptilotieae	Erskine (1955)	*Dasyptilon* (NZ)
Radiathamnieae	Gordon-Mills and Kraft (1980)	*Radiathamnion*
Spermothamnieae	Gordon (1972)	*Interthamnion*, *Lejolisea*, *Lomathamnion*, *Ptilothamnion*, *Spermothamnion*, *Tiffaniella*
Sphondylothamnieae	Baldock and Womersley (1968)	*Involucrana*
	Gordon (1972)	*Drewiana*, *Involucrana*, *Medeiothamnion*, *Shepleya*, *Wollastoniella*
Spyridieae	Womersley and Cartledge (1975)	*Spyridia*
Warrenieae	Wollaston (1971)	*Warrenia*
Wrangelieae	Gordon (1972)	*Wrangelia*
Unplaced Ceramiaceae	Baldock and Womersley (1968)	*Bornetia*

Family 2: Delesseriaceae

This family contains leafy forms that are among the most artistic and beautiful of all the red algae (Figs 4.2D, 4.3E, 4.4C). It is composed of some 20 tribes, 90 genera and 300 species, of which around 30 genera and 60 species occur in Australasia. New Zealand is blessed with spectacular representatives of this group to a far greater extent than Australia. Although all the species begin as uniaxial plants, a number lose this type of apical growth and exhibit marginal meristems or diffuse cell divisions at maturity (Fig. 4.3G), anomalies that are thought to be highly evolved conditions in the Florideophycidae. In many species, cells of the central filament divide longitudinally to

form four parallel-lying cells of equal length (Fig. 4.3E), called 'pericentral' cells. Derivatives of the lateral pericentral cells coalesce to form leafy blades, which may show various features such as veins and cortication. Cystocarps are either formed on the midribs or veins, the blade surfaces, or in special lateral leaflets and are surrounded by a protective flask, or 'pericarp' (Fig. 4.2D). Tetrasporangia are tetrahedrally divided and are borne on the blade surface (Fig. 4.10D), on marginal lobes or small leaflets, often in distinct patches called 'sori'.

Endemic genera: *Abroteia* (NZ), *Crassilingua*, *Halicnide*, *Hemineura*, *Heterodoxia*, *Phitymophora*, *Rhodoseris*, *Sympodophyllum*, *Womersleya*.

Relevant literature:

Family or tribe	References	Genera treated
Delesseriaceae	Kylin (1929)	General survey (NZ)
Delesserieae	Wagner (1954)	*Laingia* (NZ), *Marionella* (NZ)
	Mikami (1978)	*Laingia* (NZ)
Hypoglossieae	Wagner (1954)	*Phitymophora* (NZ)
Myriogrammieae	Wagner (1954)	*Abroteia* (NZ)
Cryptopleurieae	Wagner (1954)	*Gonimophyllum* (NZ)
Sympodophyllieae	Shepley and Womersley (1959)	*Sympodophyllum*

Family 3: Dasyaceae

The Dasyaceae is a small but distinct family of 12 genera and around 100 species. Australia seems to be a major centre of occurrence for the group, and Australasia has four or five genera and about 45 mostly endemic species. Plants of the Dasyaceae are prominently uniaxial and produce from four to 11+ pericentral cells around the main axial filaments. Further cortication can result in thick and robust plants. Pigmented, monosiphonous filaments called 'pseudolaterals' characterise most species, and the growth pattern of the apex is of a distinctive type called 'sympodial' (Fig. 4.3K) in which the apical cells of the first-formed lateral branches regularly and repeatedly overtop the shoot apex and take over as the main growing points. Carposporophytes are surrounded by a well developed pericarp, and the tetrahedrally divided tetrasporangia are produced in distinctive spear-shaped short branchlets called 'stichidia'.

There are no endemic genera of Dasyaceae in Australasia, although the bulk of the region's species are endemic. The two most common genera are *Dasya* and *Heterosiphonia*, although the unusually formed *Thuretia* (Fig. 4.2K) is also common at times in Australia.

Relevant literature:

Family	Reference	Genera treated
Dasyaceae	Parsons (1975)	*Dasya*, *Heterosiphonia*, *Thuretia*

Family 4: Rhodomelaceae

This is the most morphologically diverse family of the Ceramiales. It is divided into some 15–16 tribes and contains around 130 genera and 600 species. Roughly 70 genera

and 250 species occur in Australasia, making this one of the main centres of the family's distribution. Plants are composed of variously branched main axes surrounded by four or more pericentral cells and covered externally with greater or lesser amounts of cortication. Unlike the Dasyaceae, the apical growth pattern is 'monopodial', with lateral branches produced in spiral, alternating, or distichous order along percurrent axes. Plants may be erect or prostrate, filamentous or leafy, soft and flexible or tough and cartilaginous, depending on the elaboration of the axes and degree of cortication. Gametangia are normally associated with unpigmented, deciduous hairs called 'trichoblasts', and carposporophytes are borne within flask-like pericarps (Fig. 4.71D). Tetrahedral tetrasporangia are borne in stichidia (Fig. 4.10G) or in rows within the main branches and axes (Fig. 4.10B).

Endemic genera: *Aphanocladia*, *Chiracanthia*, *Cladhymenia*, *Cladurus*, *Cliftonea*, *Coeloclonium*, *Diplocladia*, *Dolichoscelis*, *Doxodasya*, *Echinosporangium*, *Echinothamnion*, *Gonatogenia*, *Haplodasya*, *Herpopteros*, *Heterocladia*, *Holotrichia*, *Husseyella*, *Jeanneretia*, *Lembergia* (NZ), *Lenormandia*, *Lophothalia*, *Metamorphe* (NZ), *Osmundaria*, *Pityophykos*, *Pleurostichidium* (NZ), *Rhodolophia*, *Sarcomenia*, *Sarcotrichia*, *Sonderella*, *Thaumatella*, *Triginea*, *Tylocolax*, *Wilsonea*.

Relevant literature: The bulk of Australasia's rich hoard of endemic genera is still known mainly through the classic monograph of the family by Falkenberg (1901), in which many are illustrated and most discussed.

Tribe	References	Genera treated
Amansieae	Saenger and Ducker (1971)	*Lenormandia*
	Womersley (1965a)	*Sonderella*
Bostrychieae	Hommersand (1963)	*Bostrychia* (NZ)
	De Berg (1949)	*Bostrychia* (NZ)
	Post (1963, 1964)	*Bostrychia*
Brongniartellieae	Parsons (1975)	*Brongniartella*
	Parsons (1980)	*Brongniartella*
Chondrieae	Kraft (1979)	*Acanthophora* *Cladhymenia* (NZ)
	Saenger et al. (1971)	*Cladhymenia*
Herposiphonieae	Scagel (1953)	*Metamorphe* (NZ)
Laurencieae	Cribb (1958a)	*Laurencia*
	Saito and Womersley (1974)	*Laurencia*
Lophosiphonieae	Cribb (1956)	*Lophosiphonia*
Lophothalieae	Parsons (1975)	*Doxodasya*, *Haplodasya*, *Lophothalia*
Polysiphonieae	Cribb (1956)	*Polysiphonia*
	Womersley (1979)	*Polysiphonia*
Polyzonieae	Scagel (1953)	*Dasyclonium* (as *Euzoniella*)
	Scagel (1962)	*Dasyclonium*
	Scagel and Chihara (1968)	*Leveillea*

Tribe	References	Genera treated
Sarcomenieae	Saenger et al. (1971) Womersley and Shepley (1959)	*Lembergia* (NZ) *Malaconema*, *Platysiphonia*, *Sarcomenia*, *Sarcotrichia*

4.6 Subclass Bangiophycidae

This is a rather small group of 4–5 orders, about 30 genera and 110 species of which some 13 genera and 28–30 species are terrestrial or freshwater (Bourrelly, 1970). The Porphyridiales contains six genera and about 12–13 species of unicellular algae found on damp soil, subaerially and in freshwater as well as marine habitats. The Rhodochaetiales has but a single marine genus and species and exhibits the only consistent apical growth of the subclass. The remainder of the group are multicellular filaments, tubes or sheets of diffuse growth. The Compsopogonales consists of two strictly freshwater genera and 8–10 species, while the Goniotrichales is roughly evenly divided between marine and freshwater species. The Bangiales is primarily marine.

Algae of the Bangiophycidae are mostly characterised by lack of certain features of the Florideophycidae: carposporophytes, tetrasporophytes and pit-connections. In the few cases where pits have been observed, only certain stages of the life cycle possess them. Most reproduction is by vegetative fission or through monospores, sex being confirmed in only a few members, as described earlier.

Two orders with marine species are recorded from Australasia.

Order 1: Goniotrichales

This small group of two families, ten genera and around 20 species is represented by two genera (*Asterocytis* and *Goniotrichum*) and three species in our region. Plants of the order do not reproduce sexually, but propagate from monospores which form from entire vegetative cells and escape with the breakdown of the plant body. Thalli are composed of branched chains (Fig. 4.3J) that are generally uniseriate or irregularly arranged into multiseriate strands. Representatives from Australia have been surveyed by Levring (1953), and from New Zealand by Levring (1955) and Chapman (1969a).

Order 2: Bangiales

This is a marine and freshwater group of three families, nine genera and around 70 species, over half of which belong to the worldwide genus *Porphyra*. Two families, five genera and about 10 species are known in Australasia. In the Erythropeltidaceae, with its Australasian representatives *Erythrocladia* and *Erythotrichia* (Fig. 4.2J), reproduction is accomplished by monospores which divide off from a parent cell, as opposed to being formed by conversion of the entire cell as in the Goniotrichales. Plants are small epiphytic discs, unbranched uniseriate filaments or small leaflets. The family Bangiaceae reproduces by both monospores and sexually, the latter process involving an alternation of dissimilar generations and a number of different types of spores. Carpospores form by mitotic divisions within the fertilised carpogonium, and

possibly give rise to *Conchocelis* stages, although no species have been grown through their complete life cycle in Australasia. *Bangia* (Fig. 4.3L) and *Porphyra* gametophytes are generally high intertidal winter annuals in our region.

Relevant literature:

Order	References	Genera treated
Bangiales	Chapman (1969a), Levring (1953) and Levring (1955)	*Bangia*, *Erythrocladia*, *Erythrotrichia*, *Porphyra*
	South and Adams (1976b)	*Erythrotrichia* (NZ)
	Womersley and Conway (1975)	*Porphyra*, *Porphyropsis*

4.7 Morphological and anatomical diversity (Figs 4.1–4.11)

The following plates are only a small sampling of the great diversity shown by red algae. Although the plants or sections in each figure are credited to a collection locality (NSW = New South Wales; NZ = New Zealand; Qld = Queensland; SA = South Australia; Tas. = Tasmania; Vic. = Victoria; WA = Western Australia), the Australian species are seldom confined to just that region cited but may occur in several states. All slides and specimens illustrated are on file at the University of Melbourne or LaTrobe University.

Acknowledgements

The authors would like to thank Jean Turner, La Trobe University, for the sections of *Lithoporella* (Figs 4.8B, 4.9F), Alan Millar, Melbourne University, for the material of *Herposiphonia* (Fig. 4.4F), Robert Ricker, Melbourne University, for the material and photographs of *Cenacrum* (Figs 4.6E, 4.9J), and Dr Richard Wetherbee, Melbourne University, for the photographs of *Holmsella* (Fig. 4.1G) and *Polysiphonia* (Fig. 4.7D).

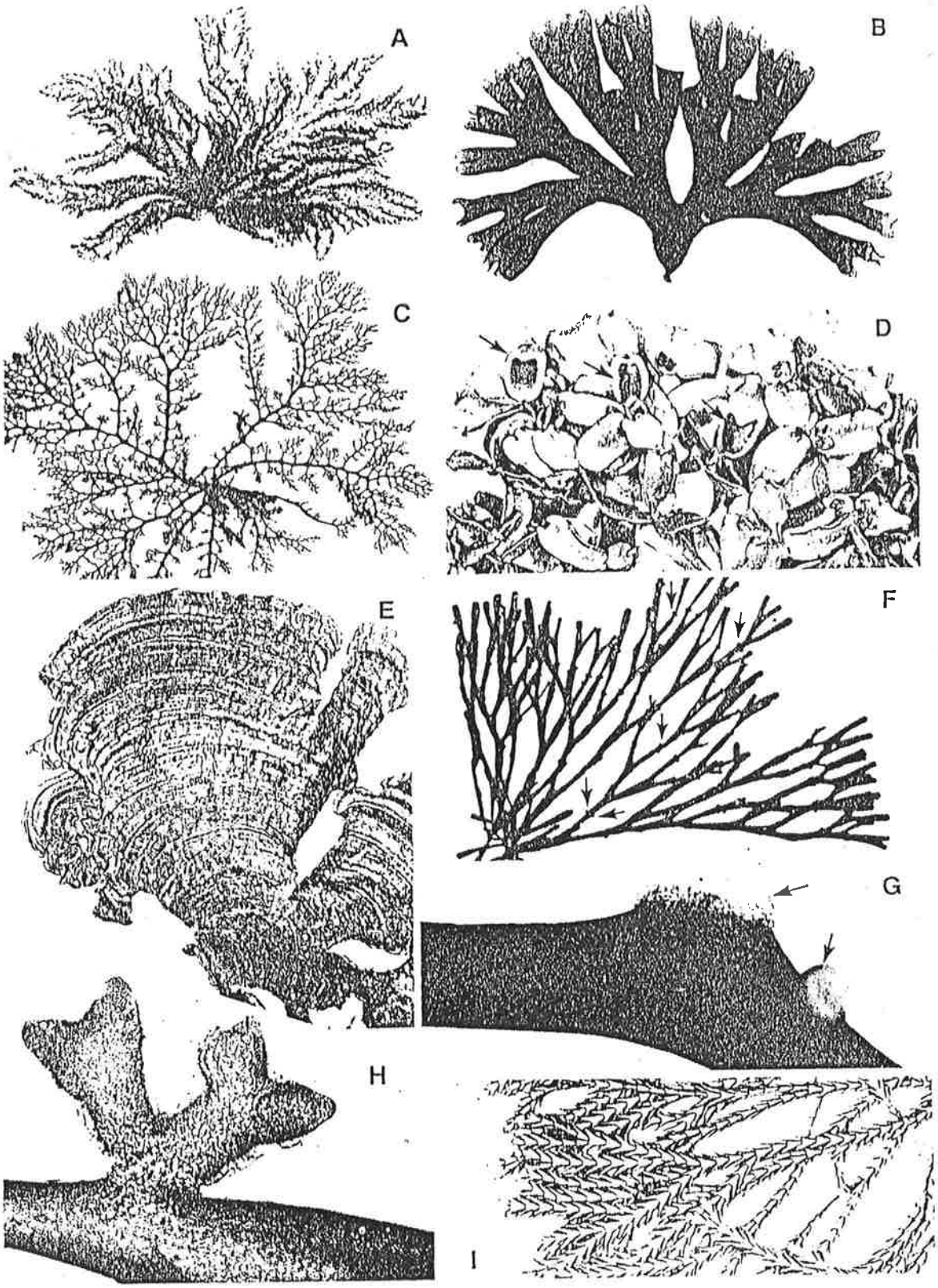
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Figure 4.1 Habits and growth forms (i)
The variety of plant forms and branch patterns in the red algae is very rich, encompassing a range from microscopic filaments and minute epiphytes and parasites on the one extreme, to hard calcified crusts and large leafy blades on the other. The following examples are not necessarily the most common species, but they represent a fair sample of the red algal spectrum.
A Many 'primitive' red algae consist of gelatinous axes in which photosynthetic filaments are rather loosely arranged, giving a shaggy appearance to dried specimens, as in this species of *Dudresnaya* (NSW). x1.
B A few species, such as this *Halymenia* (NSW), are firmly membranous dichotomous tubes mostly filled with a low-viscosity mucilage. x0.9.
C A number of red algae in several different groups are cartilaginous in texture and finely divided into several orders of pinnate branching. *Chondrococcus* (NSW) is common on tropical coral reefs. x0.9.
D One of the most unusual of the calcium carbonate impregnated species is *Rhodopeltis* (SA), which consists of flattened leaflets joined in branched series by flexible uncalcified joints. The cystocarps are contained within non-calcified cushions (arrows) on the 'leaf' faces. x1.5.
E Encrusting forms may be either calcified or non-calcified. The enigmatic *Sonderophycus* (SA), with its concentric growth lines and prostrate habit, resembles a shelf fungus. Despite the large size it attains, reproductive structures of any sort are unknown for this alga. x0.6.
F Wiry, dichotomous axes characterise a number of red algae. In *Melanthalia* (Vic) the branches are slightly flattened and can have hemispherical cystocarps (arrows) along the edges. x0.8.
G Among the most specialised reds are the parasites which infect certain other red algae that act as specific hosts. In *Holmsella* (Vic) the frond is composed of microscopic filaments that grow within the host *Gracilaria* plant and erupt into colourless pustules (arrows) that bear the reproductive structures. x20.
H A parasite with somewhat more elaborate morphology than *Holmsella* is *Hypneocolax* (Vic), which infects the genus *Hypnea*. *Hypneocolax* is called an 'adelphoparasite', meaning that it is taxonomically close to its host, whereas *Holmsella* is an 'alloparasite', belonging to a different family than its host, *Gracilaria*. x30.
I Most non-crustose calcified red algae consist of regular stoney units (called 'intergeniculae') which are separated by flexible joints, or 'geniculae'. The segments of *Cheilosporum* (Vic) form a series of interlocking arrowheads. x1.3.

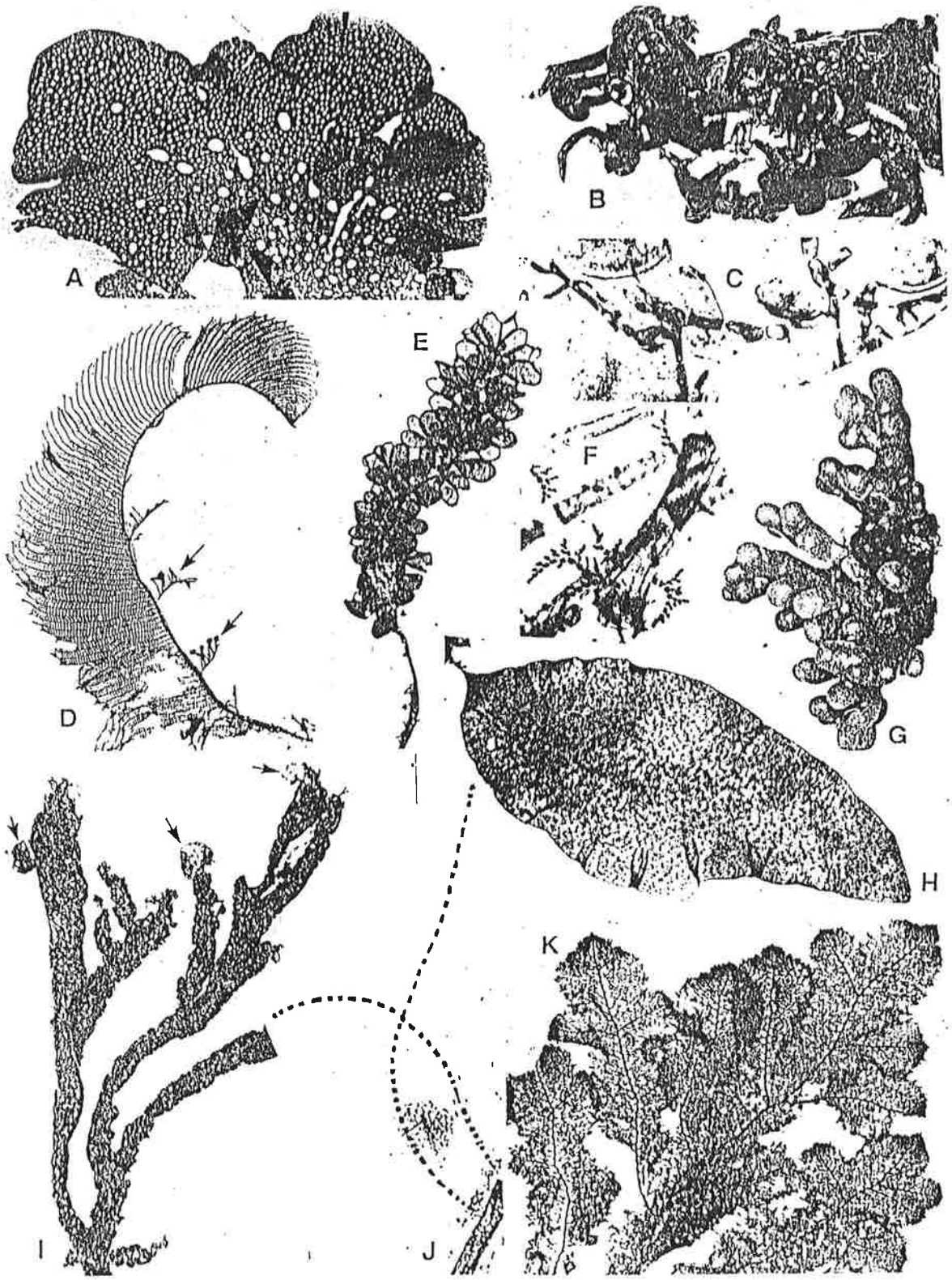
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Figure 4.2 Habits and growth forms (ii)
A Many red algae form leafy membranes and a few, such as this *Kallymenia* species (SA), seem programmed to produce regular perforations or holes. The cystocarps can be seen as dark dots on the lower frond. x0.5.
B Some reds are coarse and almost rubbery in texture, with irregular outlines often caused by wound response to fish or invertebrate grazing. The genus *Eucheuma* (NSW) is one of the commercially important carrageenan weeds which is farmed and harvested in other parts of the world. x1.
C A very few red algal species are 'endophytes', producing pigmented filaments within the tissues of other algae but not parasitising the host. This *Colaconema* (Vic) is growing between the utricles of the green seaweed *Codium*. Some *Colaconema*-type reds also grow 'endozooically', or within the tissues or hard parts of certain invertebrates. x120.
D One of the most striking algal habits is that of *Claudea* (Vic), which produces feathery fronds of net-like branch orders and rows of club-shaped cystocarps (arrows). x0.9.
E In the genus *Botryocladia* (NSW), clusters of liquid-filled bladders surround a cartilaginous central stalk. x1.
F Many red algae are 'epiphytes', meaning that they are anchored to other marine plants but carry out their own photosynthesis. These *Audouinella* thalli (Vic) are tiny epiphytes of a larger red alga. x155.
G This species of the unusual genus *Apophloea* forms crusts and stubby erect axes on high intertidal rocks in northern New Zealand. x2.4.
H An example of the leafy habit adopted by many reds is *Lenormandiopsis* (SA), whose blade surface is dotted with islands of tiny hair tufts. x0.6.
I Several red algae form consistent associations with various invertebrates such as hydrozoans, tunicates or, in the case of *Thamnoclonium* (Vic), with sponges. The small blades housing reproductive structures (arrows) are borne on axes of which the outer surface is a mixture of sponge and algal tissue. x1.4.
J One of the most simply-constructed of all the marine red algae is *Erythrotrichia* (Vic). The unbranched filaments lack pit-connections and grow epiphytically on other algae. x100.
K An elaborate and intricate body plan is exhibited by *Thuretia* (SA), which forms spongy leaflets of interconnecting filaments along the sides of its prominent central axes. x1.

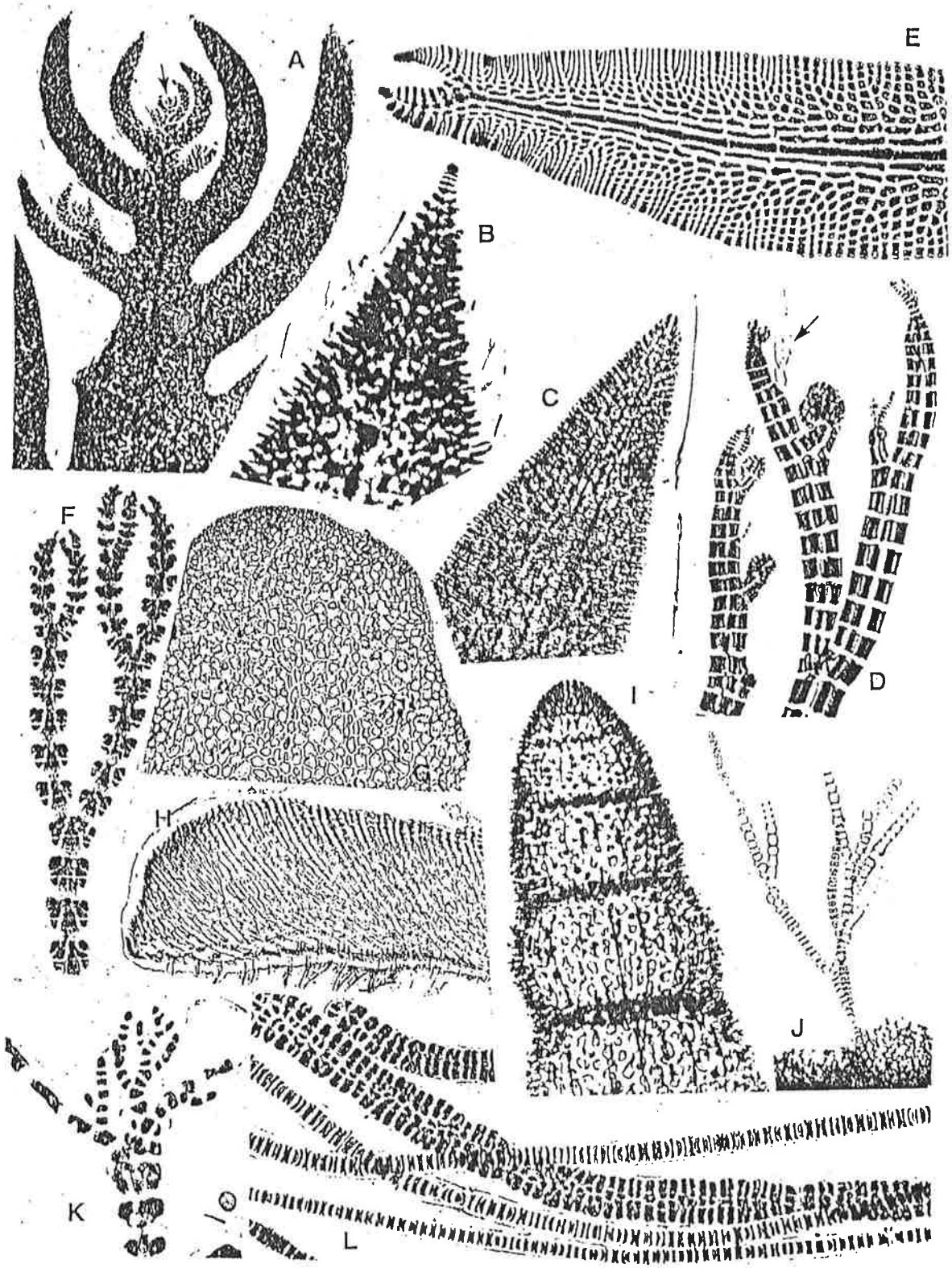
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Figure 4.3 Apices and axes

With few exceptions, the basis of plant organisation in the red algae is the branched, apically-growing filament. Within the group there are many variations on this theme, and one of the first observations to be made in trying to identify a red alga is its apical structure.

A The elaborate frond of *Delisea* (Vic) grows from a single apical cell (arrow) from which the central axis and surrounding branch orders are ultimately derived. x120.

B In *Dasyphloea* (Vic) the central filament derived from the single apical cell becomes surrounded by a girth of corticating filaments and cells. A number of hair cells are borne on the outer cortex. x280.

C *Solieria* (Qld) is an example of a multiaxial apex in which the thallus is derived from several distinct apical cells, each of which gives rise to central filaments and exterior cortication. x170.

D In *Polysiphonia* (NSW) and its relatives, the corticating cells surrounding the filaments derived from the single apical cells of the branch orders all reach equal lengths, resulting in the distinctively tiered, or 'polysiphonous' appearance. Colourless hairs borne on such axes (arrow) are called 'trichoblasts', x120.

E Distantly related to *Polysiphonia* but having a leafy thallus is *Caloglossa* (Vic). This widespread alga occurs in high-intertidal marine habitats, is a characteristic epiphyte of mangrove pneumatophores and is even found (as in this case) in freshwater streams. x140.

F In the uniaxial alga *Ceramium* (NSW), cells of the central axis become encircled by narrow cortical bands at the nodes, resulting in a distinctive pattern of incomplete cortication. x140.

G An exception to the rule that red algal growth is both filamentous and apical is *Acrosorium* (Vic), which not only has a marginal meristem of dividing cells but also intercalary cell divisions within the two-cell thick, leafy frond. x90.

H Prostrate or encrusting algae such as *Peyssonnelia* (SA) grow from a margin of apical cells that produce horizontal filaments emitting anchoring rhizoids to the underside and a palisade of arching, apically-growing lateral filaments above. x100.

I Some multiaxial reds have hollow interiors lined by longitudinally-running medullary filaments derived from the cluster of apical initials. In *Champia* (NSW) the hollow centre is regularly traversed by cellular diaphragms. x90.

J An alga of very simple structure without apical growth is *Goniotrichum* (NSW), whose cells lack pit-connections and divide intercalarily to form branched chains. x150.

K *Dasya* (Qld) and a few other genera display a distinctive apical pattern termed 'sympodial growth' in which the apical cells of the first-formed lateral branchlets regularly and repeatedly grow out to overtop the shoot apex and take over as the main growing points. This growth is in contrast to the 'monopodial' pattern displayed by the other uniaxial algae illustrated in this plate in which regular overtopping does not occur. x180.

L The genus *Bangia* (NSW) forms either uniseriate or multiseriate filaments lacking pit-connected cells and apical growth. Division of the cells occurs in 1–3 planes throughout the filaments. *Bangia* is a winter annual growing on very high intertidal rocks subject to long periods of drying. x145.

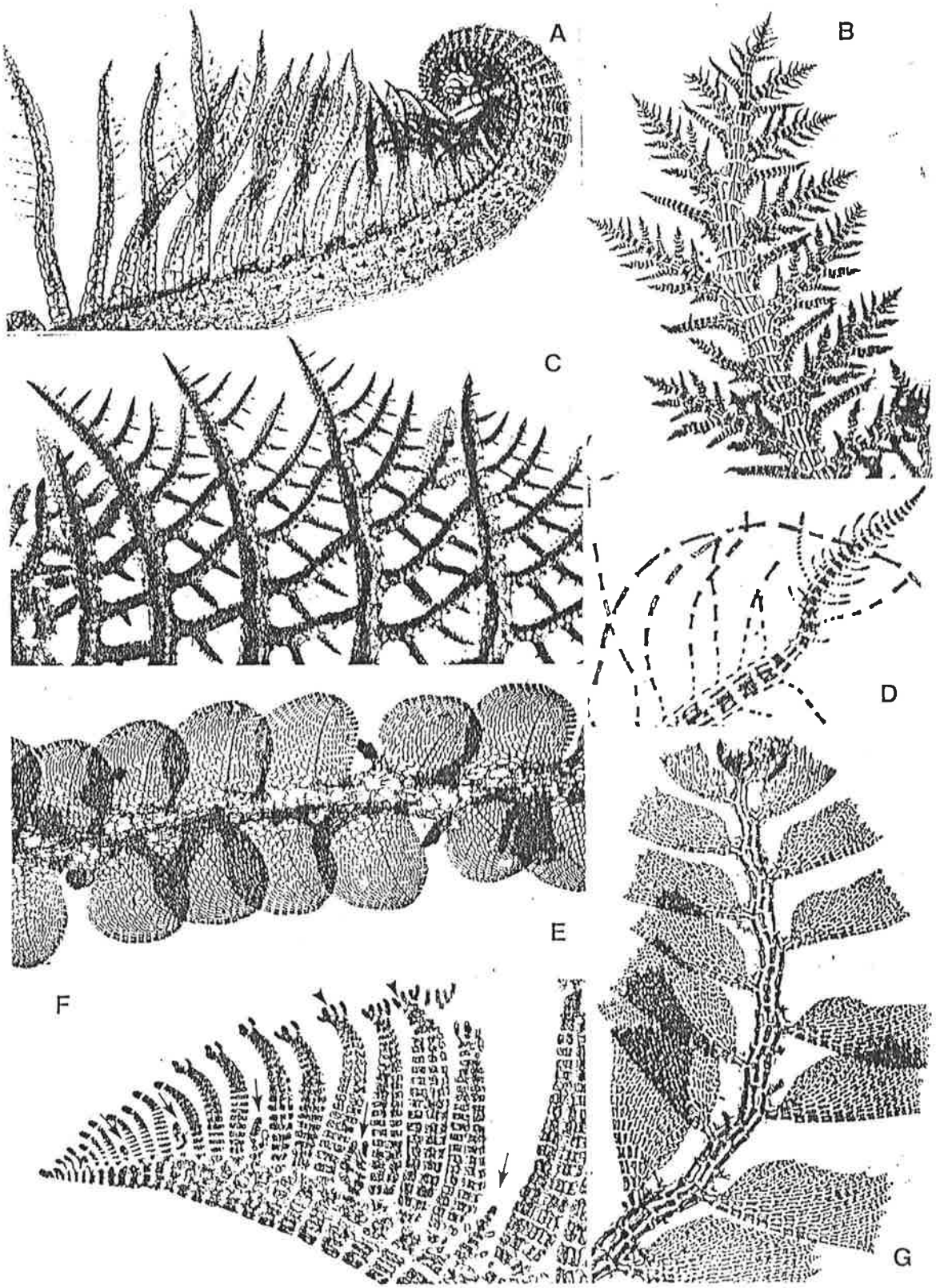
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Fig. 4.4 Patternings
Once the pattern of growth has been set at the tip in a red alga, it is often carried through with great precision, regularity and beauty.
A The crozier-tip of *Cliftonea* (SA) unfolds to produce feathery fronds of comb-like teeth fringed with finely branched hairs. x32.
B. The lateral branchlets of *Dipterosiphonia* (NZ) alternate in pairs along both sides of the creeping main axis. The lowermost of each pair in this species generally remains unbranched. x34.
C The net-like fronds of *Vanvoorstia* (Qld) are formed when successive orders of branchlets arise at right angles from the previous order and fuse where they touch a neighbour. x26.
D The regular pattern of *Sarcotrichia* (SA) arises from the growth of monosiphonous filaments from opposite sides of the main axes. x105.
E The superficial resemblance of this alga to certain leafy liverworts is so striking that the species has been named *Leveillea jungermannioides* (NSW). A tropical alga, it is found across northern Australia from NSW to Perth. x30.
F *Herposiphonia* (Vic.) produces two distinctive types of lateral structure along the one side of its major axes. Indeterminate branches (arrows), capable of growing out into new main axes, alternate regularly with groups of three branchlets of limited growth (determinate laterals) which produce trichoblasts (arrowheads) and bear the reproductive structures (x160.0).
G The paddle-like lateral branchlets of this species of *Dasyclonium* (NZ) arise alternately from opposite sides of the main axis. x30.

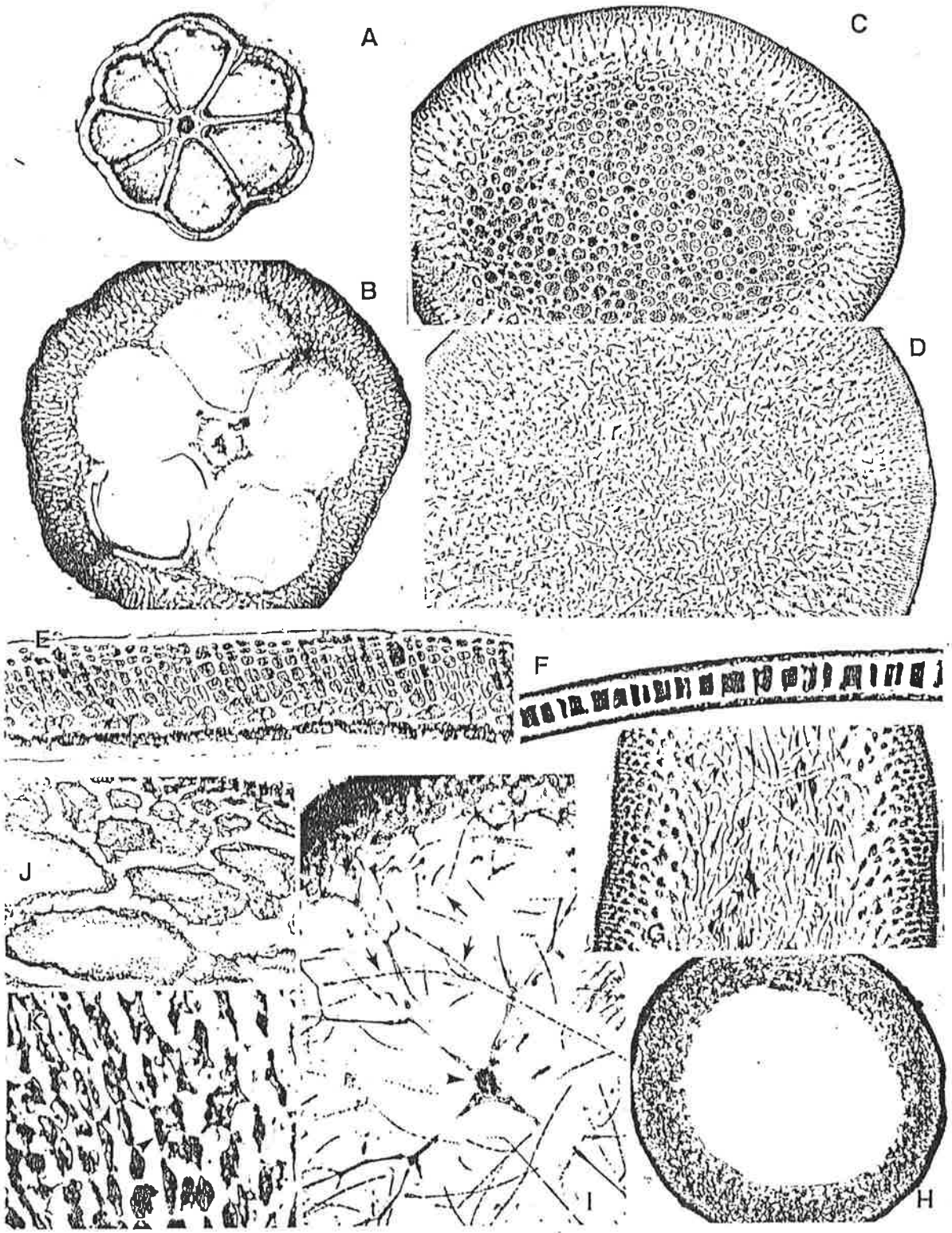
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Figure 4.5 Cross-sections and internal structures
The type of apical or other meristematic growth, cell elongation and enlargement, cortication and/or internal filament production all combine in the red algae to produce what are usually characteristic cross and longitudinal sections. Medulla and cortex are often sharply delimited and of dissimilar structure, so that red algal identification is often helped by making sections as well as by examining the apices.
A The cross section of a lower axis in this species of *Polysiphonia* (Vic) shows that the central filament is surrounded by seven 'pericentral' cells with no outside cortication. x40.
B The central filament in *Cladurus* (Vic) is separated from its 5 pericentral cells by some surrounding filaments, while the pericentral cells themselves are encased in a thick outer layer of cortical filaments. x30.
C The cross section of this *Gelidium* (Vic) shows a filamentous inner cortex and a medulla that is termed 'pseudoparenchymatous' because the swollen appearance of the cells belies their derivation from filaments. x100.
D The cross section of *Gigartina* (NSW) is uniformly filamentous, with medulla and cortex distinguishable mainly by the right-angle orientation of the outer filaments. x90.
E A section through an encrusting red such as *Peyssonnelia* (NSW) shows the basement layer supporting parallel columns of apically-growing upright filaments. x190.
F A section of the one-layer thick blade of this species of *Porphyra* (NZ) shows the non-pit-connected cells arranged in the plant's gelatinous matrix. x170.
G A very common type of cross- or longitudinal section in the fleshy red algae is one in which a medulla of narrow longitudinal filaments gives way fairly abruptly to a pseudoparenchymatous cortex of isodiametric cells, as in *Placentophora* (NZ). x150.
H In genera like *Perischelia* (WA), cells of the single central axial filament become very large in diameter and are surrounded directly by narrow corticating filaments rather than by pericentral cells. x50.
I In other uniaxial species such as *Dasyphloea* (Vic), the central axial filament (arrowhead) remains narrow, but gives rise to (in this case 4) 'periaxial' filaments which span the mostly cell-free space of the medulla and grade into the isodiametric cells of the inner cortex. Numbers of slender rhizoidal filaments (arrows) also grow from the periaxial filaments to fill the medulla. x145.
J Pseudoparenchymatous medullary cells of *Gracilaria* (NZ) are often filled with grains of floridean starch and are connected to adjacent cells by a myriad of secondary pit-connections. x210.
K As well as forming secondary pits, neighbouring cells of genera like *Peltasta* (SA) fuse laterally along much of their lengths (arrows). x600.

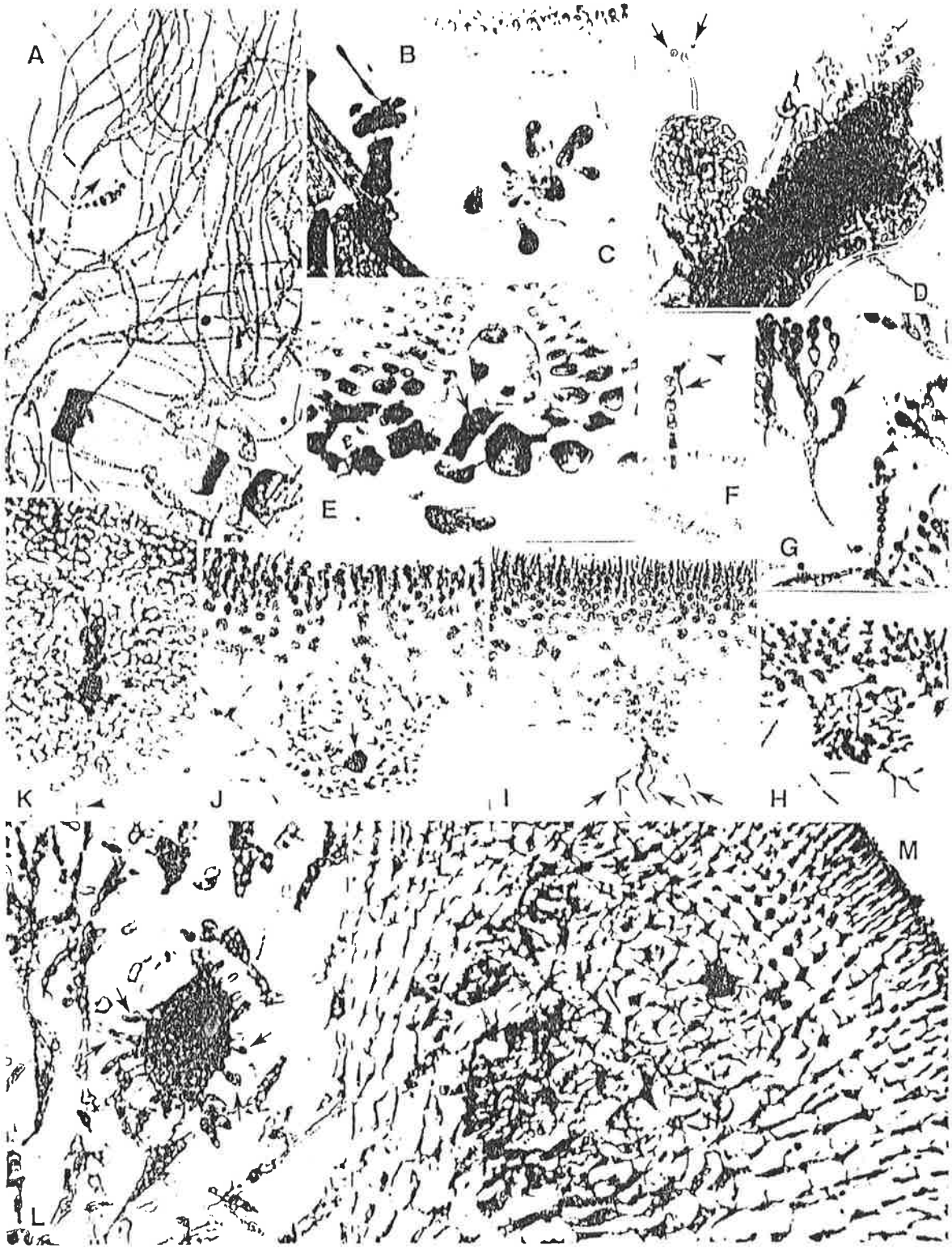
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Figure 4.6 Female gametes, connecting filaments, auxiliary cells and gonimoblast initials
The various ways by which carposporophytes are initiated and formed are thought to be among the most conservative processes operating in the red algae and are the reasons behind what is difficult about much of their classification. Although the range of female gamete and carposporophyte morphology is less than that of free-living plant habits and internal cell architectures, there is still considerable variation, of which these illustrations show only a few examples.

A An 8-celled carpogonial branch with its carpogonium and trichogyne (arrow) is borne on a lateral branchlet of the uniaxial alga *Dudresnaya* (Qld). x120.

B The compact 4-celled carpogonial branch of *Medeiothamnion* (SA) is borne in an exposed site near a branch apex. x220.

C In *Kallymenia* (NSW) several carpogonial branches (four in this case) are borne on a single supporting cell formed in the inner cortex of the leafy thallus. The dark elongate cells are the lower-most cells of the carpogonial branches, which are three cells in length. x300.

D In *Polysiphonia* and its relatives, such as *Echinothamnion* (SA), the carpogonial branch is protected by a pericarp before fertilisation, with only the trichogyne protruding to receive the male gametes (arrows). x250.

E The fertilised carpogonium passes the zygote nucleus to an auxiliary cell in *Cenacrum* (Tas) by means of a bridging cell (arrow) between the carpogonium and auxiliary cell. x440.

F The zygote nucleus is passed to an auxiliary cell in *Dudresnaya* by means of a connecting filament (arrow), shown being initiated from the carpogonium while the trichogyne (arrowhead) withers away. Although the material pictured is from Hawaii, the same species also occurs in Qld and NSW. x100.

G The auxiliary cell (arrow) is borne at the tip of a special auxiliary-cell filament in *Acrosymphyton* (NSW). The gonimoblast initial (arrowhead) arises following contact with a connecting filament derived from a fertilised carpogonium. x100.

H Carpogonial branches are contained within flask-like networks of filaments within the centre of the thallus in *Grateloupia* (NZ). x 360.

I In the same *Grateloupia* species, fertilisation results in numerous (six or more) connecting filaments (arrows) arising from the carpogonium and each apparently conveying a nucleus derived mitotically from the zygote. x260.

J Target for the connecting filaments in the New Zealand *Grateloupia* is an auxiliary cell (arrow), which lies in its own basket of internal filaments separate from ones with carpogonial branches. x380.

K Initiation of the gonimoblast (arrow) in the same *Grateloupia* occurs when a single connecting filament (arrowhead) fuses with an auxiliary cell within its proliferating network of surrounding filaments. x340.

L The auxiliary cell of *Mychodea* (SA) fuses with a fertilised carpogonium belonging to a carpogonial branch borne on the auxiliary cell itself. Although several carpogonial branches occur on each auxiliary cell, only one carpogonium passes its zygote nucleus, which results in numerous gonimoblast initials (arrows) being formed as arm-like outgrowths. x420.

M The early development of the gonimoblast reaches great complexity in the genus *Dicranema* (SA). The auxiliary cell and some adjacent cells combine to form a small fusion cell (arrow) from which numerous gonimoblast filaments grow through the parent tissue towards the centre of the thallus. Such features are key elements in the classification of red algae. x330.

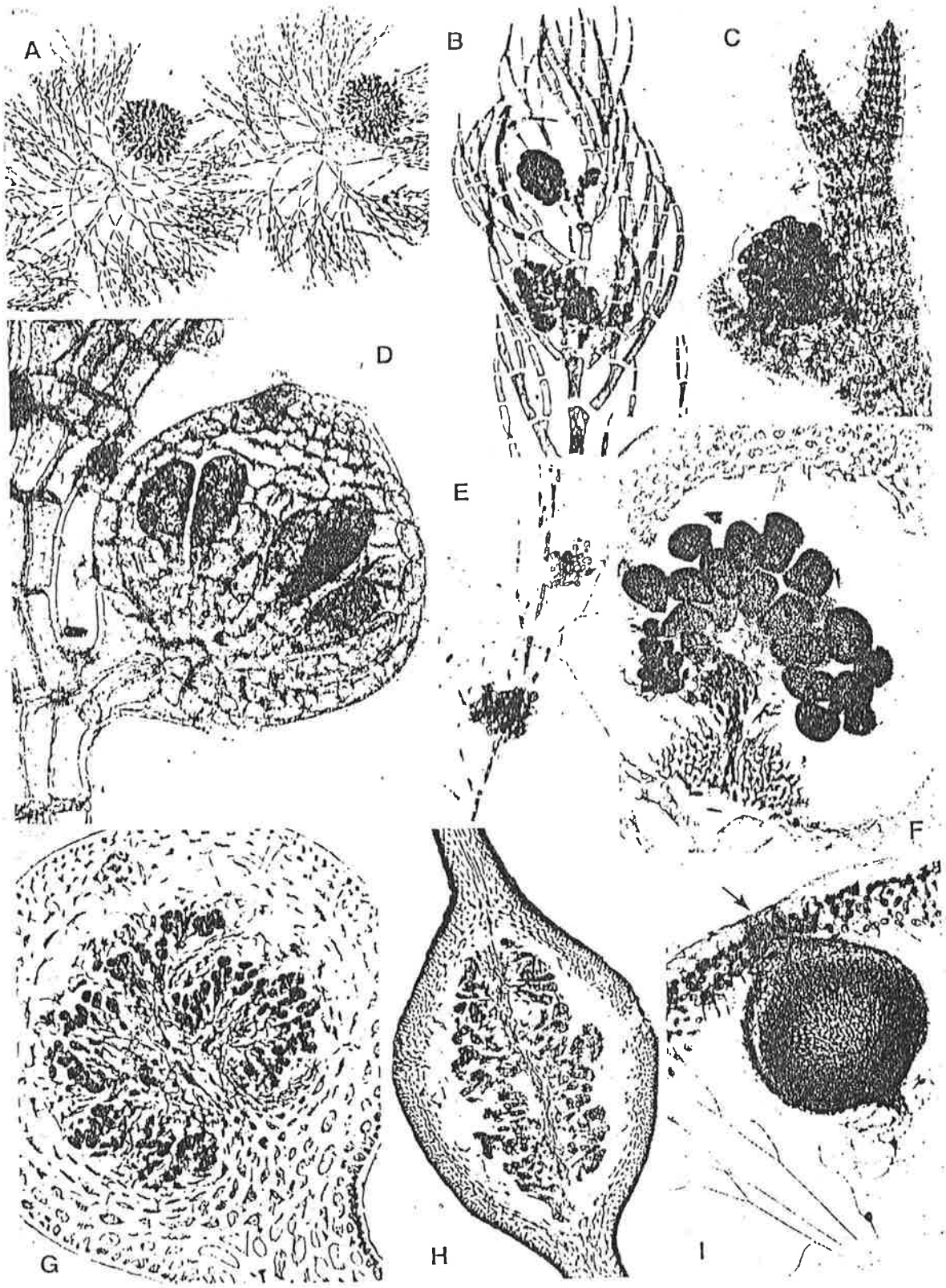
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Figure 4.7 Carposporophytes, cystocarps and carpospores (i)
The end products of most carposporophytes are diploid carpospores which, on release from carposporangia, germinate into free-living tetrasporophytes. Although much red algal taxonomy is based on the supposedly conservative processes by which the carposporophyte is initiated, mature cystocarp morphologies are usually characteristic of particular genera, families and at times even orders.
A The globular carposporophytes of *Batrachospermum* (NSW) nestle within the whorls of vegetative branchlets occurring at nodes along the axis. *Batrachospermum* is restricted to freshwater, and this particular species may be the highest-growing in Australia, having been collected from a stream near Mt. Kosiusko at 1500 m elevation. x125.
B Among the simplest type of carposporophyte is that of *Callithamnion* (NSW), consisting of unprotected clusters of carposporangia at various points on the main axis. x100.
C The dense carposporophyte of *Ceramium* (SA) is somewhat protected by its position in the axil of a lateral branch. x95.
D The cystocarp of *Polysiphonia* (Vic) and its relatives consists of an outer sterile jacket or 'pericarp' supplied by the gametophyte and an inner carposporophyte with large terminal carpospores. x185.
E The vegetatively simple genus *Audouinella* (SA) has diminutive carposporophytes with relatively few terminal carposporangia. x100.
F The cystocarp of *Hymenocladia* (WA) is typical of its family and consists of an outer sterile pericarp and an inner hollow chamber into which the carposporophyte protrudes on an elongate fusion cell. x90.
G In *Calliblepharis* (WA) a cystocarp cross-section shows a mixture of sterile and sporogenous tissue within a thick pericarp wall. x90.
H Typical of the genus *Gelidium* and other members of its family such as this *Beckerella* is a cystocarp in which pear-shaped carpospores line both sides of a central cell layer within a domed, perforated pericarp. x126.
I The unusual cystocarp of *Scinaia* (Qld) consists of a flask-like sterile jacket submerged in the mostly hollow branches and containing a carposporophyte that releases carpospores through the narrow opening (arrow) to the outside. x110.

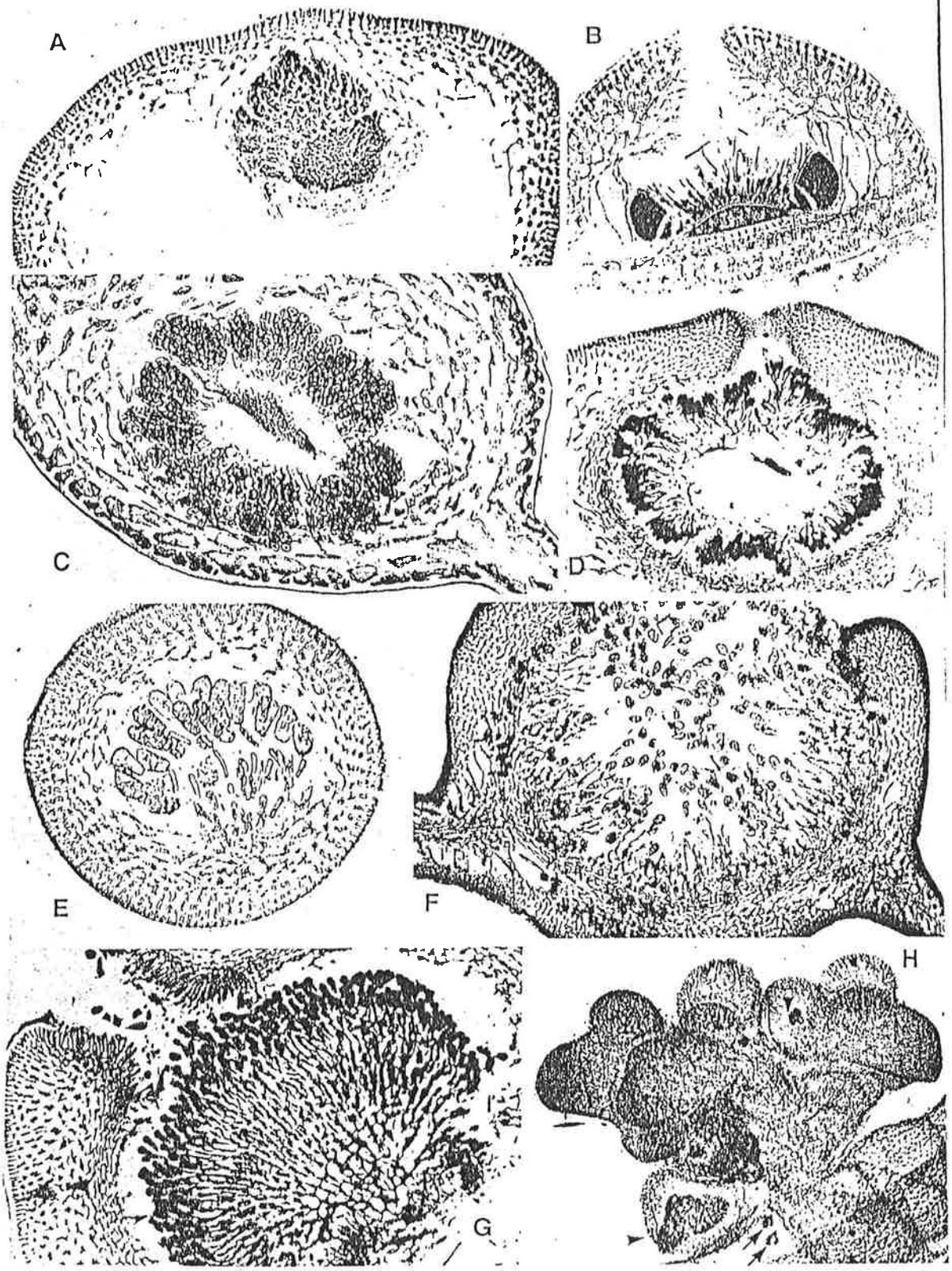
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Figure 4.8 Carposporophytes, cystocarps and carpospores (ii)
Some further illustrations of mature red algal 'fruit' promote the theme of its great diversity.
A The carposporophyte of *Grateloupia* (NZ) grows into the central hollow of the plant but lacks a coherent protective jacket or an exit pore to the surface. x150.
B As is generally the case, calcified algae such as *Lithoporella* (NSW) produce peripheral squat chains of carpospores within a conceptacle. Both carposporangial chains and a central mass of 'unused' carpogonial branches are borne on a lens-shaped fusion cell. x80.
C Many red algae produce fusion cells as part of their cystocarp. In *Rhodophyllis* (NZ) the chains of carpospores radiate from a fusion cell composed of several gametophytic and carposporophytic cells. x140.
D In *Solieria* (SA) the central fusion cell mostly disintegrates, leaving the centre of the carposporophyte hollow. The inner layers of the carposporophyte are sterile, only the outer one producing carpospores, and a prominent pore (called the 'ostiole') links the fruit with the surface. x50.
E The genus *Dicranema* (SA) is unusual in that the carposporophyte starts growing in the inner cortex and develops towards the centre of the branch before producing large terminal carpospores. The spores are shed when the branch tissue above the cavity wears away. x100.
F The cystocarp of *Hennedya* (WA) consists of a cavity into which the carposporophyte and terminal carpospores grow centripetally. x130.
G The carposporophyte of *Sarcodia* (NZ) consists of a basally anchored hemisphere of sterile tissue bearing peripheral carpospores that are shed through a wide ostiole in the thick pericarp. x90.
H A most unusual cystocarp occurs on this species of *Champia* (SA). The lobed structure appears to be a dwarf plant (bearing both male and female gametes and cystocarps [arrowheads]) that is apparently derived from the *in situ* germination of meiotic spore tetrads (arrows) within the cortex of the host tetrasporophyte. A phenomenon that is recorded in a few Northern Hemisphere species of other genera, this is the only suspected instance of it so far in Australasia. x20.

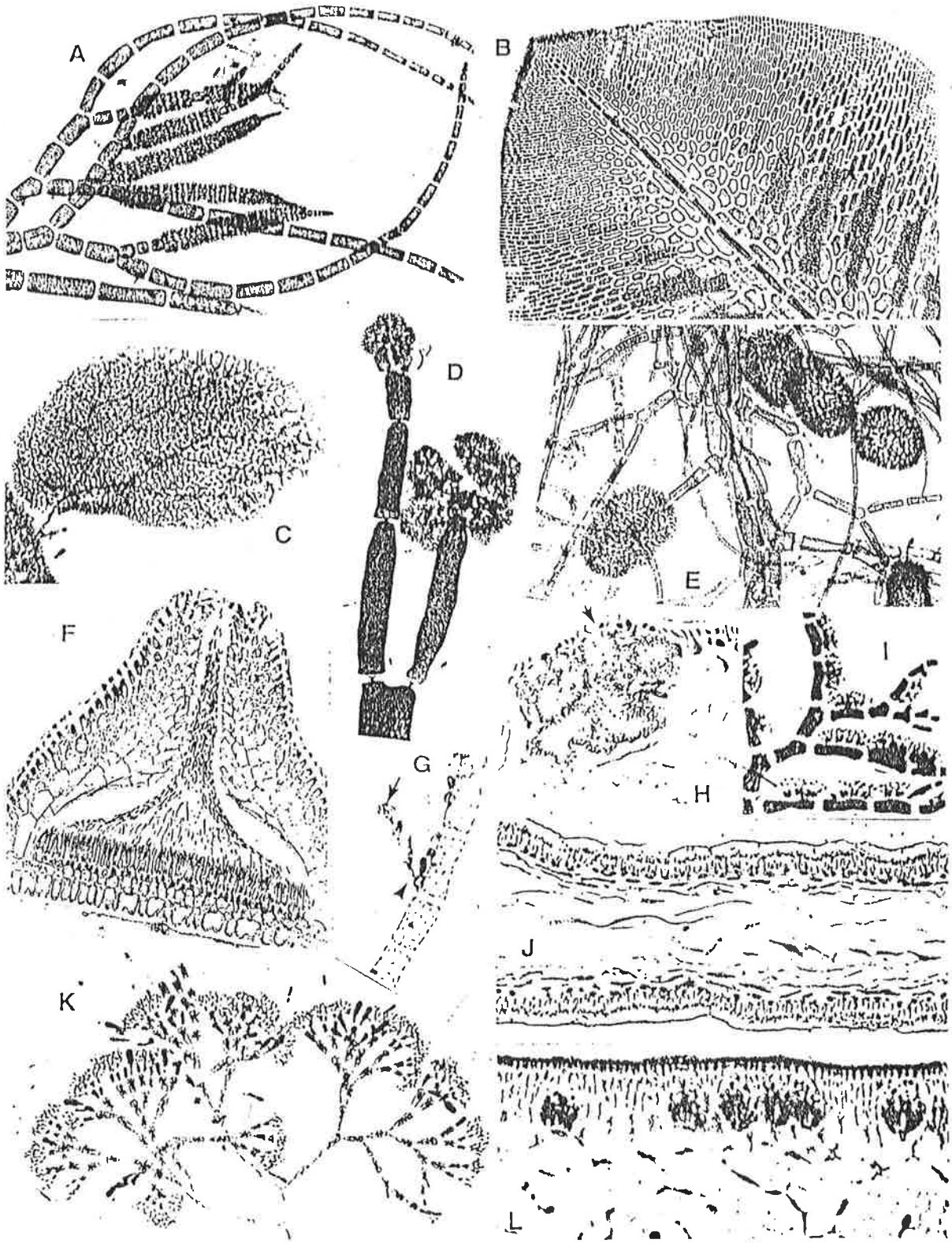
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Figure 4.9 Spermatangial branchlets, patches, pits and clusters
The non-motile male gametes, or 'spermatia', of red algae are diminutive structures usually produced in dense aggregations that are distinctive for a given family or tribe. Spermatia may occur on the same plant as carpogonia (that is, on a 'monoecious' gametophyte), or on separate plants from those bearing female gametes, (i.e. dioecious' gametophytes).
A The spermatangia of *Dasya* (Qld) form brush-like collars along parts of the hair-like monosiphonous laterals. x100.
B Spermatangia occur in isolated patches on the surfaces of leafy algae such as *Hypoglossum* (Qld). x100.
C The spermatangial platelets that characterise *Chondria* (NZ) and its relatives have a skeletal structure provided by a branched trichoblast and produce spermatangia within a margin of sterile cells. x80.
D Spermatangia form dense heads at the tips of the uncorticated axes of *Anotrichium* (Qld). x100.
E The spermatangial clusters of *Thaumatella* (SA) form rounded heads capping monosiphonous filaments. x100.
F *Lithoporella* (NSW) and other Corallinaceae produce spermatia in conceptacles with a pore opening to the surface. x96.
G One of the very smallest red algae to produce spermatia is this species of *Audouinella* (NZ), a plant less than 10 cells in length with spermatangia at the tip (arrow). The base (arrowhead) is epiphytic on a hair cell of the brown alga *Desmarestia*. x180.
H Some species of *Gracilaria* (WA) produce elaborate compound pits that are lined with spermatia which escape through a surface pore (arrow). x180.
I The rather simple male structures of *Callithamnion* (NSW) are composed of a line of bearing-cells and spermatangia confined to the adaxial sides of lateral branchlets. x210.
J In some reds the spermatangia are produced over wide patches on both sides of the frond, as in *Cenacrum* (Tas). x200.
K Clusters of spermatangia grow on the outermost cells of the cortical filaments in some of the mucilaginous algae such as *Helminthocladia* (Vic). x170.
L Catenate (chain-like) clusters of spermatangia are rare in the red algae, but are a distinctive feature in the inner cortex of the monoecious genus *Dicranema* (SA). x280.

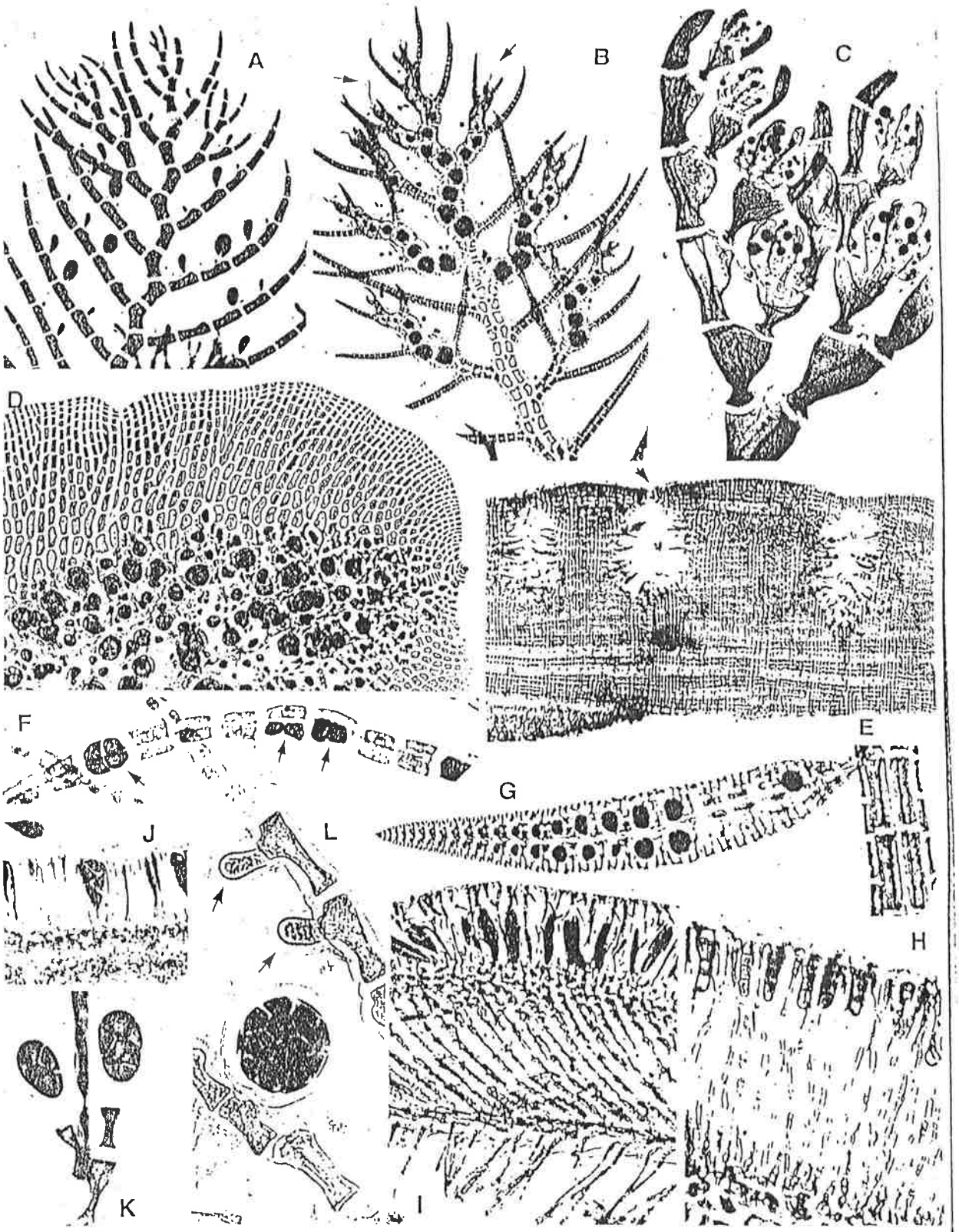
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Figure 4.10 Tetrasporophytes and tetrasporangia
The meiotic divisions which precede the formation of haploid gametes in red algae generally take place on free-living diploid plants called tetrasporophytes and give rise to reproductive spores which germinate into free-living haploid gametophytic plants.
A Tetrasporangia borne unprotectedly on the adaxial sides of lateral branchlets characterise many of the most delicately formed red algae, such as *Callithamnion* (NSW). x90.
B Tetrasporangia are borne within the axes and protected by overlying pericentral cells in *Polysiphonia* and its relatives, such as this creeping *Metamorphe* (NZ). The apices of the branches bearing tetrasporangia produce hair-like structures called 'trichoblasts' (arrows). x30.
C In some uniaxial forms, such as *Bornetia* (Vic), the groups of tetrasporangia are protected by involucres of branchlets. x24.
D Leafy forms such as *Hypoglossum* (NSW) produce tetrahedrally-divided tetrasporangia in localised patches on the frond surface. x110.
E Many of the encrusting forms of red algae, whether or not calcified, produce zonate tetrasporangia in pits called 'conceptacles' which open by pores (arrow) to the surface. The non-calcified *Hildenbrandia* (Vic) forms closely adherent crusts on rocks and shells. x145.
F Cruciate tetrasporangia are formed by conversion of entire pericentral cells (arrows) in the *Falkenbergia* stage of *Asparagopsis* (Vic). x180.
G Several genera of red algae devote special short shoots, called 'stichidia', to the production of tetrasporangia, as in the case of *Platysiphonia* (Vic). x110.
H Tetrasporangia formed within localised pustule-like swellings on a red alga are said to be in 'nemathecia'. The nemathecia of *Tylotus* (SA) produce zonate tetrasporangia directly beneath the surface cuticle. x420.
I In the prostrate genus *Peyssonnelia* (SA), cruciate tetrasporangia differentiate in nemathecia on top of the frond while uniseriate rhizoids arising from the underside anchor the plant to the substrate. x165.
J In a very few species, division patterns of the tetrasporangia, unlike the standard three patterns of most reds, are intermediate, such as this irregularly-cruciate tetrasporangium of *Delisea* (Vic). x220.
K In one species of *Spermothamnion* (NSW), a single mitotic division follows meiosis in the sporangium resulting in the formation of an 'octosporangium'. x200.
L In a few genera, such as *Lophothamnion* (SA), meiosis in the sporangial primordia (arrows) is followed by two or more mitoses of the division products, leading to 'polysporangia' containing 'polyspores'. x240.

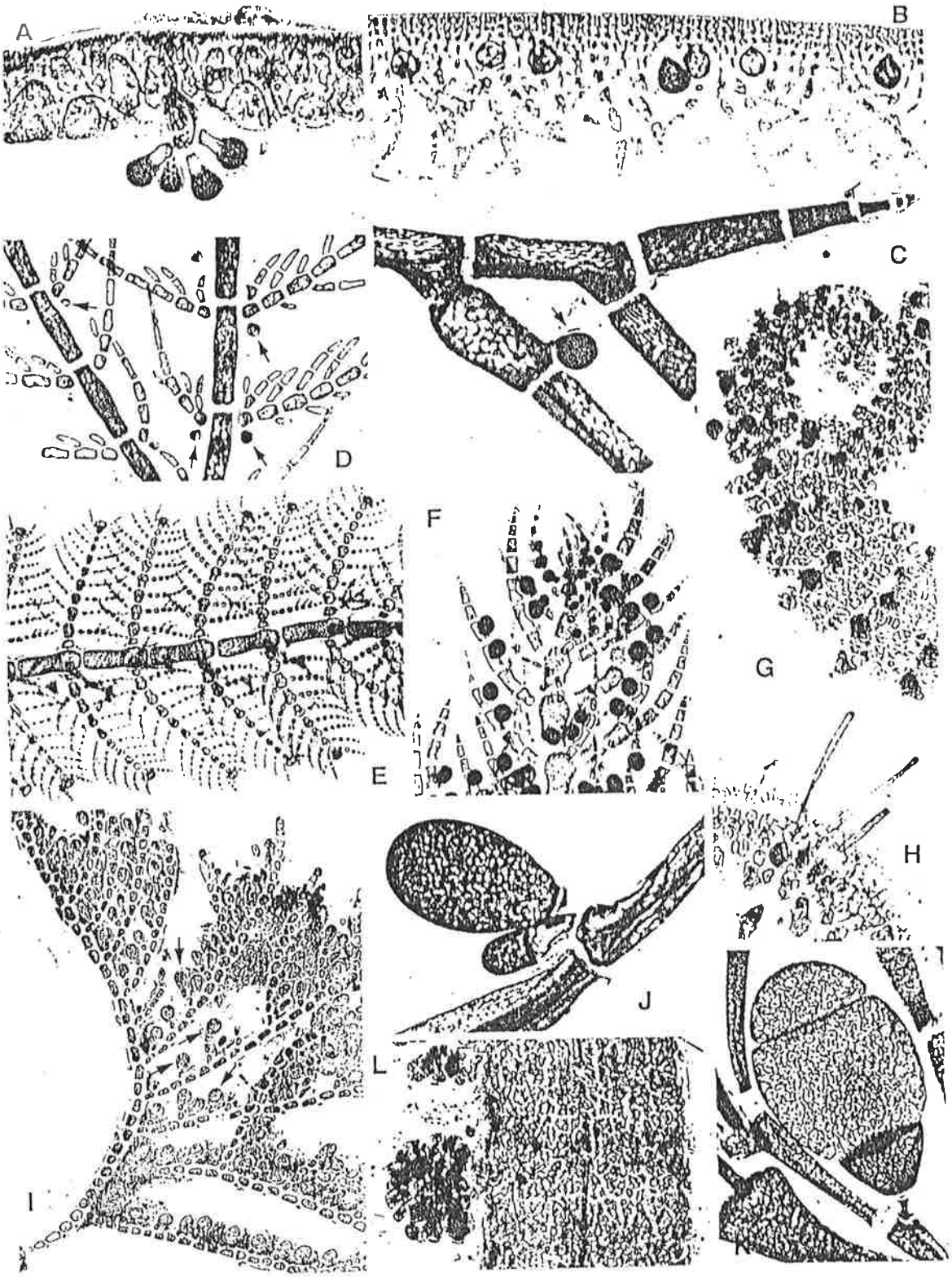
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Figure 4.11 Gland cells, propagules and other unusual happenings
Red algae produce a number of unique cell types and structures that are not bound up in the sexual process or the meiotic stages preceding gametogenesis.
A Although the purpose of so-called 'gland cells' of red algae is not precisely known in all cases, some appear to function as excretors of carbohydrate slimes. The glands of *Botryocladia* (Vic) protrude in clusters into the interiors of the hollow branches and probably generate much of the slime that fills them. x220.
B Some gland cells have proteinaceous contents and appear to act as storage structures. This is probably the case with *Adelophyton* (SA), in which numerous glands occur singly in the inner cortex of solidly constructed axes. x230.
C A gland cell in *Macrothamnion* (Vic) arises on a short lateral shoot and swells to become much larger than the tiny cell (arrow) that bears it. x210.
D Gland cells (arrows) in the tropical genus *Balliella* (Qld) are unusually situated in that they 'dangle' from the abaxial side of the lowermost cells of lateral branchlets. x210.
E The attractive genus *Acrothamnion* (NSW) is easily distinguished by the location of its gland cells at the tips of each determinate lateral branchlet. x110.
F Gland cells in *Platythamnion* (NZ) can occur in large numbers along the adaxial sides of the lateral branchlets. x110.
G In some species of *Ceramium* (NSW), gland cells stand out from ordinary cortical cells by their slightly larger size and denser contents. x200.
H Many red algae produce vegetative hairs, which have nothing to do with reproduction but can look confusingly like the receptive trichogynes of female gametes. In this species of *Gracilaria* (Vic), such hairs are associated with gland cells in the outer cortex. x200.
I 'Monosporangia' liberate 'monospores' which form new plants of the same ploidy level as the parent. In some genera, such as *Colaconema* (SA), such monosporangia (arrows) are the only reproductive structures known. Spaces between many of the branchlets in the plant illustrated are filled with bacteria. x90.
J The 'monosporangia' of *Monosporus* NSW) swell and become densely packed with floridean starch grains before being released. x170.
K The propagule of this still undescribed species from Victoria divides into three pit-connected parts and germinates as a unit, the apical cell producing an upright axis and the basal cell giving rise to an anchoring rhizoid. x160.
L Structures superficially resembling cystocarps but formed without preceding sexual fusion of gametes are called 'parasporangia', each cell of the clump producing a single 'paraspore'. As found in this species of *Ceramium* (SA), the paraspores presumably give rise to plants of the same ploidy level as the parent. x110.

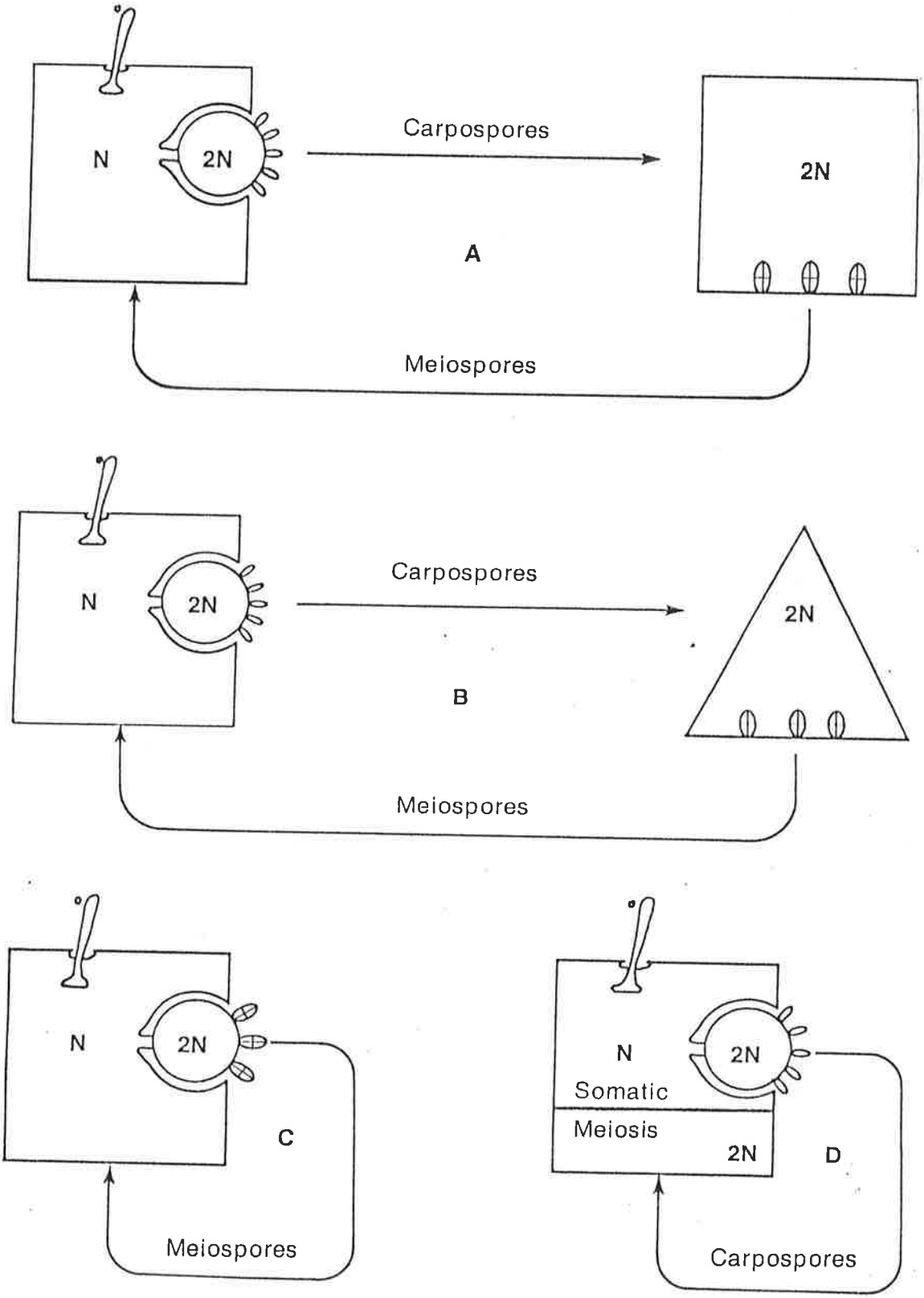
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Figure 4.12 Diagrammatic summary of sexual cycles known to occur in the subclass Florideophycidae
A Free-living tetrasporophyte present and isomorphic with gamete-bearing plant; meiosis sporic.
B Free-living tetrasporophyte present and heteromorphic with gamete-bearing plant; meiosis sporic.
C Free-living tetrasporophyte absent; meiosis sporic.
D Free-living tetrasporophyte absent; meiosis somatic.
All sexual cycles involve a diploid carposporophyte stage (circles) parasitic on the gamete producing plant.

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STUDIES ON AUSTRALIAN MANGROVE ALGAE: II. COMPOSITION AND GEOGRAPHIC DISTRIBUTION OF COMMUNITIES IN SPENCER GULF, SOUTH AUSTRALIA

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ABSTRACT: This study of algal communities associated with the temperate mangrove ecosystems of Spencer Gulf, South Australia documents the occurrence of 49 species including 10 Chlorophyta, 2 Cyanophyta, 9 Phaeophyta, and 28 Rhodophyta. Pertinent morphosystematic and distributional data are presented for each species. The Spencer Gulf mangrove algal flora is far more diverse than previously thought but is pedestrian and depauperate compared with the southern Australian marine algal flora as a whole. Most species are widespread on a global basis, although several typically tropical taxa also occur on Spencer Gulf mangroves and possible explanations for their occurrence are provided. Frequency data indicate that *Caloglossa leprieurii* occurs most commonly but that most species found occur only rarely or sporadically. Comparisons of the Spencer Gulf mangrove algal flora with those of mangrove ecosystems elsewhere in Australia suggest that the Spencer Gulf flora is comparatively species rich and shows distinct similarities to and differences from the mangrove algal flora in Victoria.

Data on Australian tropical and warm temperate mangrove algal communities are scant and pertain mainly to scattered floristic records (and one biomass production estimate) in Queensland and New South Wales (Cribb 1979, King 1981a, 1981b, 1981c, Saenger *et al.* 1977). Along the cool temperate southern Australian coast, mangrove ecosystems occur as geographically disjunct stands within Victoria, South Australia, and Western Australia (Fig. 1), but the only detailed account (Davey & Woelkerling 1980) of associated mangrove algae deals with community composition and geographic distribution in Victoria. Data for Western Australia are lacking entirely.

Within South Australian mangrove ecosystems, *Cladophora* sp., *Enteromorpha compressa* (Linnaeus) Greville, *Hormosira banksii* (Turner) Decaisne, *Ulva lactuca* Linnaeus and various diatoms have been regarded as common (Butler *et al.* 1977a, 1977b, Specht 1972, Womersley & Edmonds 1958, Wood 1937), whereas *Bostrychia* and *Caloglossa*, two of the most characteristic and cosmopolitan genera of mangrove algae (Post 1963), have been reported as apparently absent (Womersley & Thomas 1976, Womersley 1981a). Based on these isolated records, mangrove algal communities in South Australia would appear to differ markedly from those in Victoria where species of *Bostrychia* and *Caloglossa* are the most frequently occurring algae, species of *Enteromorpha* and *Ulva* tend to occur only sporadically, *Cladophora* occurs only rarely and *Hormosira* appears to be absent (Davey & Woelkerling 1980). The dearth of detailed data from South Australia has precluded a more thorough comparative assessment of these apparent differences.

Among those regions in South Australia where mangrove ecosystems occur (Fig. 1), Spencer Gulf has been regarded as noteworthy (Womersley 1981b) in the sense that at least three typically tropical benthic algae (*Acetabularia calyculus* Quoy et Gaimard, *Hormophysa triquetra* (Lamouroux) Kuetzing, *Sargassum decurrens* J. Agardh) are present, presumably because summer water temperatures are high enough for a sufficient period to allow survival (Womersley 1981c). Whether Spencer Gulf mangrove ecosystems also harbour typically tropical macroscopic algae has remained unknown as has the extent to which the algal communities in Spencer Gulf mangroves contrast with those in more tropical regions of Australia.

This account presents results of detailed studies on the floristic composition, frequency of species occurrence and geographic distribution of mangrove algal communities of Spencer Gulf, South Australia. It also examines the extent to which Spencer Gulf mangrove algal communities differ from those in Victoria and those in more tropical regions of Australia, and it includes comparisons of mangrove and open coast algal communities in terms of composition, diversity, and occurrences of endemic taxa.

STUDY SITES

The 10 mangrove algal communities (Fig. 2) selected for detailed study included the southern-most stands on both the eastern (Wallaroo) and western (Tumby Bay) shores, three stands in the far north (Blanche Harbour, Port Augusta, Red Cliff), two stands along tidal creeks (Arno Bay, Port Davis) and three other larger stands (Cowleds Landing, Franklin Harbour, Port Broughton).

In the two tidal creeks, pneumatophores occurred in permanently submerged areas only at Arno Bay (Fig. 4). Spencer Gulf mangrove ecosystems, like others in southern Australia (Macnae 1966), are based primarily in the mid to upper eulittoral zone, are dominated solely by *Avicennia marina* (Forster) Vierhapper, and usually are associated with a salt-marsh in the littoral-fringe (Butler *et al.* 1977a, 1977b). Data relating to tree height and stand size at the study sites are

REPORTED DISTRIBUTION: From King George Sound, Western Australia, around southern Australia; New South Wales; Lord Howe Island; Norfolk Island; New Zealand.
SPECIMENS EXAMINED: LTB 12166, 12199, 12224, 12225, 12326, 12329, 12347.
REMARKS: Plants up to 25 cm tall with swollen vesicles, were attached to the lower half of pneumatophores and loose lying on mud surfaces at Wallaroo, Red Cliff, Franklin Harbour, and Cowleds Landing. The loose lying form was also encountered at Tumby Bay. King (1981a, 1981b, 1981c) provided data on an extensive loose lying community of *H. banksii* within the mangroves of southern Botany Bay in New South Wales; he estimated that mean dry weight biomass ranged from 280 g m^{-2} in late winter (August) to 638 g m^{-2} in mid-summer and suggested an annual biomass production rate of approximatley 400 g m^{-2}. Clark & Womersley (1981, p. 500) reported an unattached population of plants occurring among mangroves at Port Arthur, South Australia at the north end of St. Vincent Gulf. Individuals up to 50 cm long were encountered.

Division RHODOPHYTA
Order BANGIALES
Family ERYTHROPELTIDACEAE
Genus **Asterocytis** (Hansgirg) Schmitz 1896.

A. ornata (C. Agardh) Hamel 1925: 40.
A. ramosa (Thwaites) Schmitz 1896: 314. Abbott & Hollenberg 1976: 283. Taylor 1960: 287.
TYPE LOCALITY: British Isles.
RECORDED DISTRIBUTION: Widespread in temperate seas.
SPECIMENS EXAMINED: LTB 12211, 12257, 12302, 12340, 12358, 12364.
REMARKS: *A. ornata* was attached to pneumatophores in the sun-exposed seaward margin at Port Broughton and Cowleds Landing and occurred at Wallaroo in June but not in March. Plants were also encountered as epiphytes on *Chondria* sp. at Arno Bay and Wallaroo, on *Polysiphonia teges* and *Sphacelaria furcigera* at Red Cliff, and on *Cystophyllum onustum* at Cowleds Landing.

Genus **Erythrotrichia** Areschoug 1850

E. carnea (Dillwyn) J. Agardh 1883: 15. Abbott & Hollenberg 1976: 286, fig. 228. Newton 1931: 242. Taylor 1960: 291.
TYPE LOCALITY: Wales, Gt. Britain.
REPORTED DISTRIBUTION: Widespread.
SPECIMEN EXAMINED: LTB 12247.
REMARKS: *E. carnea* grew on pneumatophores, on *Ulva lactuca* and on *Chondria* sp.

Order NEMALIONALES
Family ACROCHAETIACEAE
Genus **Audouinella** Bory 1823

A. botryocarpa (Harvey) Woelkerling 1971: 37. Searles & Schneider 1978: 100.
TYPE LOCALITY: King George Sound, W. Australia.
REPORTED DISTRIBUTION: Bunbury, Western Australia to Point Lonsdale, Victoria, and Tasmania; New Zealand; North Carolina.
SPECIMEN EXAMINED: LTB 12248.
REMARKS: Plants were attached both to continually submerged and mud-flat pneumatophores at Arno Bay, and usually bore monospores. Woelkerling (1970) provided a detailed account of this alga.
A. daviesii (Dillwyn) Woelkerling 1971: 28, figs 7A-J, 22A-B; 1973: 550, fig. 32-43.
TYPE LOCALITY: Bantry Bay, Ireland.
REPORTED DISTRIBUTION: Widespread.
SPECIMENS EXAMINED: LTB 12249, 12365.
REMARKS: Plants of *A. daviesii* grew attached to continually submerged and mud-flat pneumatophores and also on *Ulva lactuca* at Arno Bay. Plants were encountered at Wallaroo in June but not in March.
A. savianna (Meneghini) Woelkerling 1973: 560-565, figs 56-60.
TYPE LOCALITY: Genoa, Italy.
REPORTED DISTRIBUTION: Widespread.
SPECIMEN EXAMINED: LTB 12250.
REMARKS: Monosporangial plants were found attached to continually submerged and mud-flat pneumatophores at Arno Bay. A detailed account of this taxon in southern Australia was provided by Woelkerling (1971) using the name *A. thuretii* (Bornet) Woelk. Subsequent comparisons of the type collections of *A. savianna* and *A. thuretii* (Woelkerling 1973) indicated that the two taxa were conspecific, with *A. savianna* having priority.

Order GELIDIALES
Family GELIDIACEAE
Genus **Gelidiella** Feldmann & Hamel 1934

G. nigrescens (Feldmann) Feldmann & Hamel 1934: 533. Feldmann & Hamel 1937: 222, fig. 7.
TYPE LOCALITY: Algeria.
REPORTED DISTRIBUTION: Uncertain.
SPECIMENS EXAMINED: LTB 12175, 12323.
REMARKS: Dense stands of tetrasporangial plants colonized the lower half of pneumatophores at Wallaroo. Plants were more common under the canopy than in sun-exposed regions. A single plant also was collected at Franklin Harbour. The two species of *Gelidiella* recorded in this study closely fit the reproductive and morphological descriptions in Feldmann and Hamel (1934, 1937), and apparently have not been recorded previously from southern Australia.
G. tenuissima Feldmann & Hamel 1937: 226, figs 11, 12A-E.
= *G. panosa* (Bornet) Feldmann & Hamel 1934: 534.
TYPE LOCALITY: Biarritz, France.
REPORTED DISTRIBUTION: Uncertain.
SPECIMENS EXAMINED: LTB 12173, 12207, 12238, 12335, 12366.
REMARKS: *G. tenuissima* was common under the *Avicennia* canopy at Wallaroo and Arno Bay and occurred infrequently at Cowleds Landing, Port Augusta and Red

Cliff. Plants were usually fertile and bore either cystocarps or tetrasporangia.

Genus **Gelidium** Lamouroux 1813

G. pusillum (Stackhouse) Le Jolis 1863: 139. Chapman 1969: 89. Dixon & Irvine 1977: 129, fig. 48A-J. May 1965: 371.
TYPE LOCALITY: England.
REPORTED DISTRIBUTION: Widely distributed in tropical and temperate waters.
SPECIMEN EXAMINED: LTB 12367.
REMARKS: Sterile plants occurred infrequently on pneumatophores under the *Avicennia* canopy.

Order CRYPTONEMIALES
Family CORALLINACEAE

REMARKS: With few exceptions, southern Australian representatives of this family are poorly known and never have been the subject of monographic studies. Moreover, species concepts among nongeniculate taxa generally are rather confused and many questions concerning generic concepts also remain unanswered. Consequently the corallines found during the study have not been identified to species, and placement into genera is based on concepts presented by Johansen (1981).

Genus **Heteroderma** Foslie 1909

Heteroderma sp.
SPECIMENS EXAMINED: LTB 12368, 12369.
REMARKS: *Heteroderma* sp. was common on pneumatophores at Wallaroo, and occurred infrequently at Cowleds Landing. Many plants possessed either female or tetrasporangial conceptacles.

Genus **Jania** Lamouroux 1812

Jania sp.
SPECIMEN EXAMINED: LTB 12372.
REMARKS: One small sterile plant, 5 mm tall, was found at Wallaroo in July.

Genus **Lithothamnium** Philippi 1837

Lithothamnium sp.
SPECIMEN EXAMINED: LTB 12318.
REMARKS: Specimens occurred on the lower portion of pneumatophores under the canopy at Franklin Harbour. Most plants bore either female or tetrasporangial conceptacles. The concept of *Lithothamnium* as a genus is under review (Woelkerling 1981).

Genus **Neogoniolithon** Setchell & Mason 1943

Neogoniolithon sp.
SPECIMENS EXAMINED: LTB 12370, 12371.
REMARKS: Crusts up to 4 mm thick occurred on pneumatophores in sun-exposed and shaded regions. Most plants had male or female or tetrasporangial conceptacles.

Genus **Phymatolithon** Foslie 1898

Phymatolithon sp.
SPECIMEN EXAMINED: LTB 12373.
REMARKS: Tetrasporangial plants encrusted the lower portions of pneumatophores.

Order CERAMIALES
Family CERAMIACEAE
Genus **Centroceras** Kuetzing 1841

C. clavulatum (C. Agardh) Montagne 1846: 140. Abbott & Hollenberg 1976: 604, fig. 547. May 1965: 371. Taylor 1960: 537.
TYPE LOCALITY: Caloa, Peru.
REPORTED DISTRIBUTION: Widely distributed in tropical and temperate seas.
SPECIMENS EXAMINED: LTB 12188, 12209, 12217, 12256, 12286, 12321, 12357.
REMARKS: Sterile plants up to 3 cm tall were found entangled with other algae at Wallaroo, and attached to pneumatophores at Red Cliff, Franklin Harbour, Arno Bay and Tumby Bay. Plants were epiphytic on *Cystophyllum onustum* at Red Cliff and Cowleds Landing. No sun or shade preference was evident. Cribb (1979) recorded this species from Queensland mangroves.

Genus **Spyridia** Harvey 1833

S. filamentosa (Wulfen) Harvey 1833: 336. Womersley & Cartledge 1975: 222, fig. 1A-D.
TYPE LOCALITY: Adriatic Sea.
REPORTED DISTRIBUTION: Widespread in tropical and temperate seas.
SPECIMENS EXAMINED: LTB 12170, 12198, 12221, 12283, 12285, 12309, 12325, 12354.
REMARKS: Plants usually grew on the lower half of pneumatophores in both the sun-exposed and shaded regions of the community. *S. filamentosa* was encountered growing on mud surfaces and attached to shells at Tumby Bay and Red Cliff, and as an epiphyte on *Cystophyllum onustum* at Red Cliff and Cowleds Landing. All specimens were sterile. This species occurs on mangroves in Queensland (Cribb 1979, Saenger *et al.* 1977).

Family RHODOMELACEAE
Genus **Bostrychia** Montagne 1842

B. moritziana (Sonder in Keutzing) J. Agardh 1863: 862. Post 1963: 57; 1964: 244.
TYPE LOCALITY: French Guiana.
REPORTED DISTRIBUTION: Widespread in tropical and temperate seas.
SPECIMENS EXAMINED: LTB 12180, 12195, 12230, 12273, 12305, 12330.
REMARKS: *B. moritziana* was locally abundant at Wallaroo, Port Davis, Red Cliff, Blanche Harbour, Cowleds Landing and Franklin Harbour. Plants were most common under the *Avicennia* canopy and often were intermixed with *B. radicans*. Tetrasporangial plants were rare, and cystocarpic or male plants were not found. Davey and Woelkerling (1980) found this to be the most widely distributed species of *Bostrychia* in Victorian mangrove ecosystems, and Cribb (1979) and Saenger *et al.* (1977) recorded the species from Queensland.

B. radicans (Montagne) Montagne 1850: 286.

TYPE LOCALITY: Sinnamary, French Guiana.
REPORTED DISTRIBUTION: Widely distributed in tropical and temperate seas.
SPECIMENS EXAMINED: LTB 12177, 12194, 12229, 12236, 12272, 12287, 12306, 12334.
REMARKS: *B. radicans* was the most abundant and widespread species of *Bostrychia* in Spencer Gulf, occurring at all sites except Port Broughton and Port Augusta. Plants often formed mats on pneumatophores under the *Avicennia* canopy and in some cases bore spermatangia, cystocarps or tetrasporangia. The only previous record of this taxon in southern Australia was from the mangrove environment in Victoria (Davey & Woelkerling 1980); Saenger *et al.* (1977) and Cribb (1979) recorded this species from Queensland.

Genus **Caloglossa** J. Agardh 1876

C. leprieurii (Montagne) J. Agardh 1876: 499.
TYPE LOCALITY: Cayenne, French Guiana.
REPORTED DISTRIBUTION: Widespread in tropical and temperate seas.
SPECIMENS EXAMINED: LTB 12179, 12193, 12232, 12235, 12258, 12274, 12307, 12331.
REMARKS: *C. leprieurii* was often in association with species of *Bostrychia* and sometimes forming dense, pure stands on pneumatophores in both sun-exposed and shaded regions. Tetrasporangial and cystocarpic plants were found on occasions. This species occurs commonly on mangrove pneumatophores elsewhere in Australia (see Cribb 1979, Davey & Woelkerling 1980).

Genus **Chondria** C. Agardh 1817

Chondria sp.
SPECIMENS EXAMINED: LTB, 12204, 12240, 12291, 12374.
REMARKS: *Chondria* sp. occurred infrequently at Wallaroo, Tumby Bay and Red Cliff. Plants were attached to pneumatophores in the sun-exposed seaward margin, and were epiphytic on *Cystophyllum onustum* at Cowleds Landing and on *Ulva lactuca* at Arno Bay. Plants were insufficiently developed for reliable species identification.

Genus **Diplocladia** Kylin 1956

D. patersonis (Sonder) Kylin 1956: 504. May 1965: 383.
TYPE LOCALITY: Cape Paterson, Victoria.
REPORTED DISTRIBUTION: South Australia, Tasmania, Victoria.
SPECIMENS EXAMINED: LTB 12171, 12290, 12324.
REMARKS: *D. patersonis* plants up to 10 cm tall were collected both in sun-exposed and shaded areas at Wallaroo, Franklin Harbour and Tumby Bay. The Wallaroo samples collected during winter (June) bore tetrasporangia. Davey & Woelkerling (1980) reported this species on mangroves at two localities in Victoria.

Genus **Herposiphonia** Nageli 1846

Herposiphonia sp.
SPECIMENS EXAMINED: LTB 12339, 12375.
REMARKS: The two collections of *Herposiphonia* obtained during this study probably are referrable to different species but both were sterile, and as noted by Abbott & Hollenberg (1976: 720) such specimens often are difficult to identify to species level with confidence. Plants (sp. "A") in the Cowleds Landing collection (LTB 12339) had determinate branches 40-60 μm in diameter, which were 7-14 segments long and had 6-7 pericentral cells. These specimens appeared to be most similar to *H. delicatula* Hollenberg (1968: 540). Plants (sp. "B") in the Wallaroo collection (LTB 12375) had determinate branches 70-80 μm in diameter which were mostly 12-18 segments long and had 8-9 pericentral cells. These specimens appeared to be most similar to *H. tenella* f. *secunda* (C. Agardh) Hollenberg (1968).

Genus **Laurencia** Lamouroux 1813

Laurencia sp.
SPECIMENS EXAMINED: LTB 12168, 12208, 12216, 12355.
REMARKS: Sterile plants up to 3 cm tall were found on pneumatophores at Wallaroo and Red Cliff, and other plants occurred epiphytically on *Cystophyllum onustum* at Red Cliff and Cowleds Landing. Species identification could not be made with certainty but these specimens appeared to be most similar to *Laurencia shepherdii* Saito & Womersley (1974).

Genus **Lophosiphonia** Falkenberg in Schmitz & Falkenberg 1897

L. subadunca (Kuetzing) Falkenberg 1901: 496, p1.9, figs. 21-24. Cribb 1956: 139. May 1965: 380. Taylor 1960: 605.
TYPE LOCALITY: Corsica.
REPORTED DISTRIBUTION: Arabia; southern Australia; Bahamas; Mediterranean; Queensland; Texas.
SPECIMEN EXAMINED: LTB 12376.
REMARKS: *L. subadunca* was common at Wallaroo in June, but absent in March. Plants were sterile, up to 2 cm tall, and occupied the lower portion of *A. marina* pneumatophores under the canopy. According to Cribb (1956) *L. subadunca* has not been recorded from southern Australia.

Genus **Polysiphonia** Greville 1824

P. infestans Harvey 1855: 539. Womersley 1979: 481, fig. 6A-E.
TYPE LOCALITY: Princess Royal Harbour, King George Sound, W. Australia.
REPORTED DISTRIBUTION: From North Beach Reef, Perth, southwards and along the southern Australia coast. Botany Bay, New South Wales.
SPECIMENS EXAMINED: LTB 12232, 12299.
REMARKS: Sterile plants up to 3 cm tall, were encountered on the lower portion of pneumatophores.

P. scopulorum Harvey 1855: 540. Womersley 1979: 467, fig. 2A-E.
TYPE LOCALITY: Rottnest Island, W. Australia.
REPORTED DISTRIBUTION: From Rottnest Island, W. Australia to Lawrence Rock, Victoria.
SPECIMENS EXAMINED: LTB 12205, 12218.

TABLE 3
MORPHOLOGIC AFFINITIES OF THE SPENCER GULF *Cladophorella* WITH OTHER DESCRIBED SPECIES

Species of *Cladophorella*	Cell dia. range (μm)	Cell length: width ratio	Cell wall structure	Cell wall dia. (μm)	Reported habitat and references
C. calcicola	23-39	3-10	Lamellate	8	Hot house walls, Cambridge Botanical Gardens (Fritsch 1944). *A. marina* mangrove environment in Queensland (Cribb 1979). Semi-marine cavern in Queensland (Cribb 1965).
C. fritschii	55-88	1½-3½	Lamellate	3-15	Freshwater environment in East Pakistan (Islam 1964).
C. sundarbanensis	15-55	2½-6	Not Lamellate	2-4	Mangrove environment in Bangladesh (Islam 1973). Brackish water in East Pakistan (Islam 1964).
C. marina	80-240	1-5	Lamellate	Not Supplied	Marine environment, New Zealand (Chapman 1956).
Spencer Gulf *Cladophorella*	140-250	1-4	Lamellate	10-50	*Avicennia marina* mangrove environment in Spencer Gulf.

REMARKS: Sterile plants, 2 cm tall, were epiphytic on *C. onustum* under the canopy, and attached to a single pneumatophore in a tidal creek, at Red Cliff. Cribb (1979) recorded this species from Queensland mangroves.

P. subtilissima Montagne 1840: 199. Womersley 1979: 469, fig. 2F-I.

TYPE LOCALITY: Cayenne, French Guiana.

REPORTED DISTRIBUTION: Tropical and sub-tropical Eastern America, French Guiana, Hawaiian Islands; in southern Australia from Coffin Bay, South Aust., to Port Phillip Bay, Victoria; Tasmania; Botany Bay, New South Wales.

SPECIMEN EXAMINED: LTB 12255.

REMARKS: Tetrasporangial plants, up to 3 cm tall, were attached to continually submerged and mud-flat pneumatophores at Arno Bay.

P. teges Womersley 1979: 494, fig. 10A-C.

TYPE LOCALITY: Frenchmans Bay, Albany, W. Australia.

REPORTED DISTRIBUTION: Type locality and Spencer Gulf, S.A.

SPECIMENS EXAMINED: LTB 12174, 12265, 12284, 12352.

REMARKS: Specimens occurred epiphytically on *Cystophyllum onustum* at Cowleds Landing and on the lower portions of pneumatophores at Wallaroo, Port Augusta, and Blanche Harbour. Tetrasporangial plants were collected at the latter two locations. The only previously known specimens from Spencer Gulf were epilithic (Womersley 1979, H. B. S. Womersley pers. comm.).

FREQUENCY DATA

Frequency data for the 42 species collected from the belt transects are summarized in Table 4. Seven taxa (*Bostrychia radicans*, *Caloglossa leprieurii*, *Cladophorella marina*, *Enteromorpha* sp., *Gelidiella tenuissima*, *Rhizoclonium riparium*, *Rivularia atra*) occurred commonly ($F = 0.50$ to 0.75) or abundantly ($F > 0.75$) at one or several localities, and based on mean frequency values [i.e. $\Sigma F/N$, where ΣF is the sum of all recorded frequencies > 0 and N is the total number of localities at which the alga occurred; see Table 4], *Caloglossa leprieurii* is the most conspicuous alga in Spencer Gulf mangrove ecosystems. Although all seven taxa were recorded from a majority of study sites, none

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Studies on the *Mastophora–Lithoporella* complex (Corallinaceae, Rhodophyta)

I. Meristems and thallus structure and development

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A comparative study of the type species of *Mastophora* and *Lithoporella* (Corallinaceae, Rhodophyta) indicates that the two genera cannot be delineated reliably using attributes of the vegetative thallus. Thallus form is influenced by the nature of the substrate, and X-ray micro-analyses show that calcification can vary considerably from plant to plant. Vegetative development in both genera is effected from a primary meristem and from two distinct secondary meristems. Perithallial tissue is produced only in discrete patches from secondary internal meristems. Branches develop from both primary and secondary meristems; the latter arise dorsally, grow out over, and become superimposed upon the subtending thallus layer. Contiguous cell fusions occur between cells of adjacent hypothallial and perithallial filaments, and adjunctive cell fusions occur between cells of non-adjacent filaments. Auto-endophytic fusions between two plants were not observed. Attachment of the thallus to the substrate is effected by hypothallial cell adhesion and/or occasional rhizoids. Trichocytes occur in both species. The naming and characterization of thallus meristems in the Corallinaceae also is considered in relation to results obtained during this study.

INTRODUCTION

Although a number of publications (Cabioch, 1972; Chamberlain, 1978; Johansen, 1976a, 1981; Lebednik, 1977; Lee, 1970; Woelkerling, 1980a) contain information on meristems and vegetative thallus development in the Corallinaceae (Rhodophyta), few data are available for *Lithoporella* and *Mastophora*, two related genera (subfamily Mastophoroideae) of distinctive morphology which are recorded commonly from Indo-West Pacific waters. Plants of *Lithoporella* have been characterized as crusts formed by an overgrowing habit, which regularly results in a number of individuals becoming superimposed on one another (Foslie, 1909; Gordon, Masaki & Akioka, 1976; Lemoine, 1970, 1974, 1976; Masaki, 1968). Plants of *Mastophora*, in contrast, have been characterized as ribbon-like and branched (Johansen, 1976a; Lemoine, 1974; Setchell, 1943). Suneson (1937, p. 69) and Johansen (1976a, p. 238, Table 2; 1981, p. 221) state that plants of *Mastophora* are attached only at one end, whereas Setchell (1943, p. 135) states that attachment is effected by a series of rhizoids. The above attributes have been used to help delineate *Mastophora* and *Lithoporella* from other genera of Corallinaceae (Cabioch, 1972, p. 365; Foslie, 1909, p. 58; Setchell, 1943) and also have been employed in taxonomic keys (Adey, 1965; Bressan, 1974; Cabioch, 1972, p. 269; Hamel & Lemoine, 1953; Johansen, 1976a; Pham-Hoang, 1969; Setchell, 1943).

Cabioch (1972) provided brief descriptions of a 'marginal meristem' in an unidentified species of *Lithoporella*, and of a 'terminal meristem' in herbarium specimens referred to *Mastophora macrocarpa*. Cabioch concluded that all vegetative tissues in both genera originate from a single meristem (presumably of a 'non-intercalary' nature—Cabioch, 1972, p. 171). Lemoine (1974)

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interpreted overgrowing as the stratification of a number of separate plants and reported up to twenty-six individual thalli forming a single crust of *Lithoporella*. This interpretation has not been documented conclusively, however, and an alternative hypothesis is that a layered crust can develop from a single, branched individual in which the branches become superimposed on one another. Such development has been recorded in several species referred to *Dermatolithon* (Cabioch, 1970, 1972; Lemoine, 1971) in the subfamily Lithophylloideae. Recently published floristic accounts of *Lithoporella* and/or *Mastophora* (Adey, 1970; Cordero, 1977; Gordon *et al.*, 1976; Hamel & Lemoine, 1953; Lemoine, 1976; Masaki, 1968) do not contain clarifying data, and questions relating to the developmental aspects of overgrowing remain unanswered.

In another study, Lemoine (1974) compared the internal vegetative structure of specimens of both *Lithoporella* and *Mastophora*, and concluded that the two taxa were concordant anatomically and could be distinguished generically only by differences in the degree of thallus calcification. Lemoine (1970, 1974) also noted superimposition of thalli and 'auto-endophytism' in both genera. Because the degree of calcification is known to vary within individual plants of other Corallinaceae (e.g. *Mastophoropsis*—Woelkerling, 1978; *Metamastophora*—Woelkerling, 1980a), the conclusions reached by Lemoine (1974) raise the question as to whether *Lithoporella* and *Mastophora* are distinct taxonomically, or really represent only one genus as was thought prior to 1909 (Foslie, 1903, 1904, 1909).

During studies on southern Australian Corallinaceae, a number of populations of *Lithoporella melobesioides* (Foslie) Foslie (the type species of *Lithoporella*) were collected, thus providing an opportunity to investigate the developmental morphology and anatomy of the genus, particularly with respect to meristems and overgrowing. Availability of liquid-preserved material of *Mastophora rosea* (C. Agardh) Setchell (the type species of *Mastophora*) enabled a comparative investigation to be undertaken to determine more precisely the nature of meristematic activity, to analyse differences in the degree of calcification and to elucidate whether any vegetative differences of potential generic significance occur. This paper summarizes results of these studies, and also presents new data on cell fusions, attachment mechanisms and trichocytes. Aspects relating to reproduction are considered separately (Turner & Woelkerling, 1982).

MATERIALS AND METHODS

Data were obtained from type specimens and from populations of plants collected in southern Australia, Guam, Indonesia, the Maldive Islands and the Philippines. Except for the type collections, all data were gathered from liquid-preserved material. Annotated voucher specimens are deposited in BM, L, LD, LTB, TRH, or UC and representative permanent slides from all collections have been retained at LTB. Microtechnique procedures follow Woelkerling (1980a); X-ray micro-analysis and scanning electron microscopy procedures are outlined by Woelkerling (1978), except that specimens for X-ray micro-analysis were coated with carbon and gold. The statistical tests are outlined in Conver (1971) and herbarium abbreviations follow Holmgren & Keuken (1974, 1977).

Terminology

Certain terms associated with the preparation of thallus sections, the naming of meristems and the planes in which meristematic cells (hereafter referred to as initials) divide require brief explanation. The anatomical appearance of the thallus varies with the plane of sectioning; thus it is important to know the precise nature of a given section for purposes of data collection. In this study, *longitudinal sections* (ls) are cut perpendicularly to the dorsal surface of the thallus and parallel with the axes of particular hypothallial filaments (Fig. 1). Such sections normally show that successive cells, within a given hypothallial filament, are joined by conspicuous primary pit-connections. *Transverse sections* (ts) are cut perpendicularly to both the dorsal surface of the thallus and the axes of particular hypothallial filaments (Fig. 1). Such sections normally show fusions between some cells of contiguous hypothallial filaments. Because of the lobed nature of some plants, single sections may contain both longitudinal and transverse portions linked by a transitional region. Paradermal sections are cut parallel with the dorsal surface of the thallus.

In this paper, the **naming** of meristems is based principally on their *relative* times of origin and subordinately on their places of origin with-

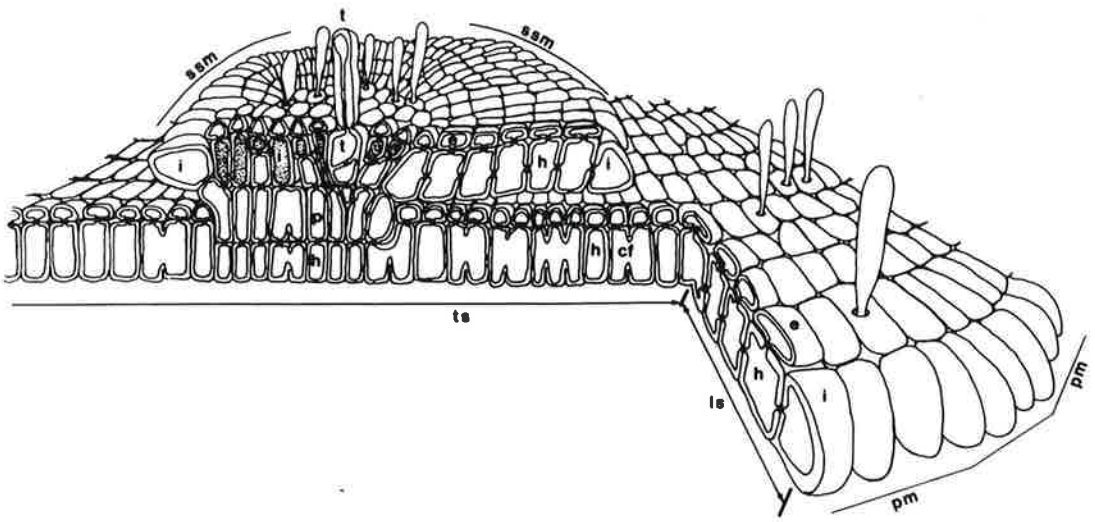


Fig. 1. Diagrammatic representation of a portion of *Lithoporella melobesioides* plant showing major morphological–anatomical features and planes of sectioning. Scale bar = 50 μm. cf = contiguous cell fusion; e = epithallial cell; h = hypothallial cell; i = initial; ls = longitudinal section (indicated for lower thallus layer); p = perithallial cell; pm = primary meristem; ssm = secondary superficial meristem; t = trichocyte; ts = transverse section (indicated for lower thallus layer). Secondary internal meristem cells are shaded.

in the plant body. Meristems may be **characterized** further, if necessary, by their location within the thallus and by the position of initials within individual thallus filaments. If the meristem arises directly after germination, it is considered *primary* (Fig. 1); if the meristem arises at a later stage, and from tissues produced by the primary meristem, it is considered *secondary* (Fig. 1). A meristem arising at the surface or periphery of the thallus is considered to have a *superficial* place of origin (Fig. 1); a meristem arising beneath the surface, and within the thallus, is considered to have an *internal* place of origin (Fig. 1). In terms of location, a superficial meristem is characterized as:

(1) *marginal,* if it is situated at the periphery of a crustose thallus or a lobose branch (Fig. 9);

(2) *apical,* if it is situated at the tip of an ascending or elongate branch; or

(3) *lateral,* if it is situated along the sides of an elongate branch (Fig. 11).

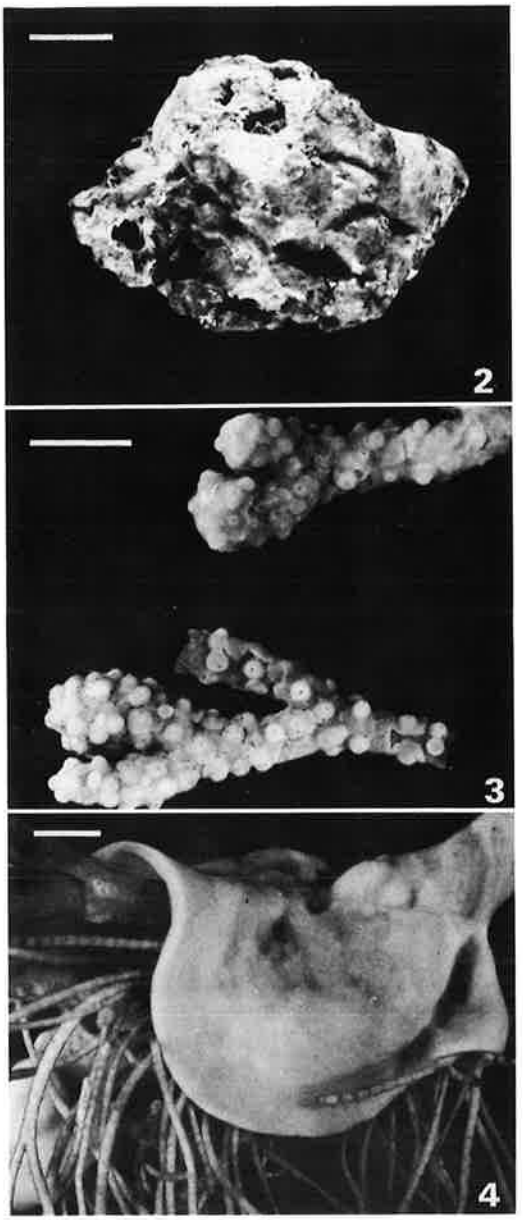
Additionally, the location of a superficial or an internal meristem may be characterized as:

(4) *dorsal,* if it is situated at, or just beneath the upper surface of a dorsiventrally-organized plant (Figs 1, 16 and 17); or

(5) *ventral,* if it is situated at or just above the lower surface of a dorsiventrally-organized plant.

Within a filament, an initial may be *terminal* or *intercalary* in position (Fig. 1) and the meristem may be characterized accordingly. At their time of origin, initials in superficial meristems occupy *terminal* positions (Figs 20 and 21), while initials in internal meristems occupy *intercalary* positions (Figs 16 and 17). Meristems are not contiguous with other meristems and never can be both primary and secondary. In at least some Corallinaceae, however, a particular meristem may be partly marginal and partly apical or lateral in location, and some initials of a given meristem may be terminal, while others are intercalary in position. The naming of meristems is considered further in the discussion.

Initials may divide in different planes to produce various types of cells or tissues. The division of a given initial may be either *periclinal* (parallel with the thallus surface) or *anticlinal* (perpendicular to the thallus surface), and may also be either *coaxial* (parallel with the axis of the relevant filament) or *transaxial* (perpendicular to the axis of the relevant filament). Within a given thallus filament, an initial may produce new cells *basipetally* (towards the base), *acrop-*



Figs 2–4. *Lithoporella melobesioides*.
Fig. 2. Holotype specimen (TRH) from Maldive Islands (substrate unknown). Scale bar = 4 mm.
Fig. 3. Compact specimens (LTB 11821) from Victoria, Australia on *Xiphophora*. Scale bar = 3 mm.
Fig. 4. Expanded specimen (LTB 12157) from Victoria, Australia on *Jania* and *Corallina*. Scale bar = 1 mm.

etally (towards the top or tip), *laterally* (towards the side), or *obliquely* (towards a distal corner).

Cell length, as used in this paper, refers to the greatest cell dimension measured in a plane, parallel with the axis of the filament in which the cell is situated (Fig. 1). Cell height, in contrast, is measured in the plane, perpendicular to the axis of the filament in which the cell occurs. Cell diameter is measured at right angles to both cell length and cell height.

RESULTS

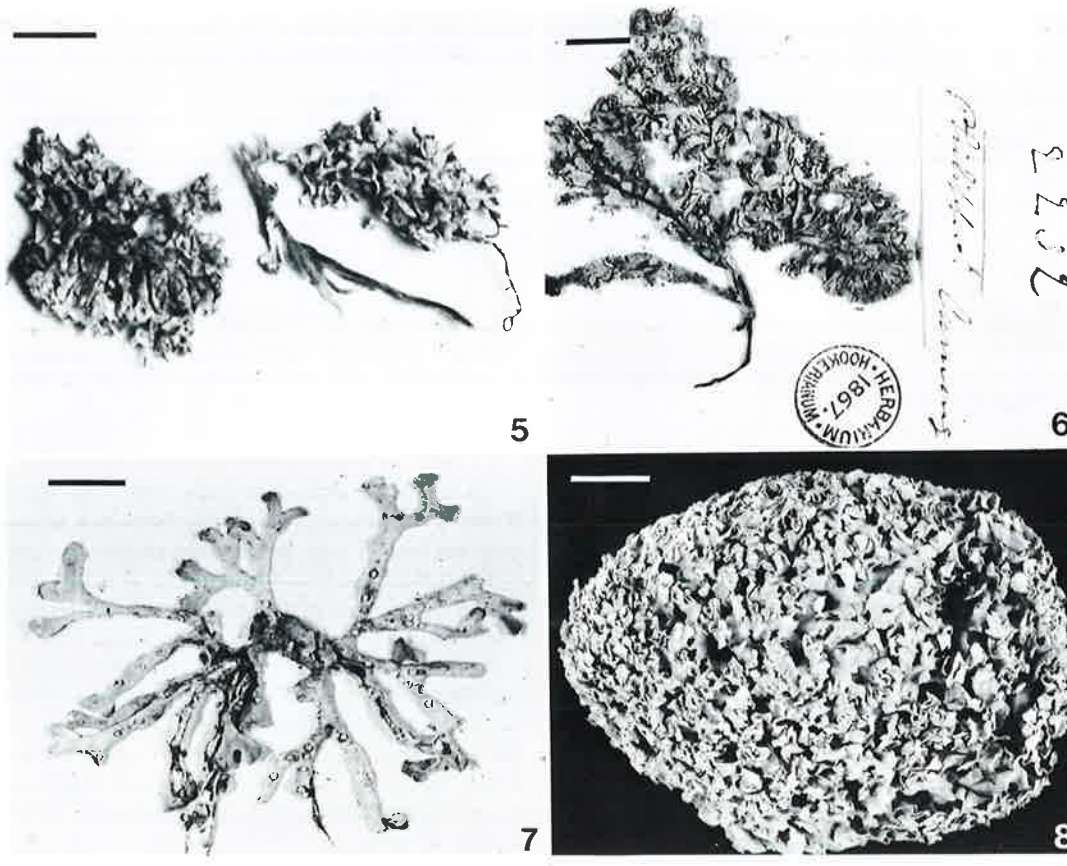
Thallus form and calcification

Thallus form and size in both *L. melobesioides* and *M. rosea* (Figs 5–8) vary considerably and appear to be influenced by the nature of the substrate and the relative amount of available growing space. Plants growing on cylindrical or narrow, compressed substrates such as axes of *Gelidium* (Rhodophyta), *Sargassum* (Phaeophyta), or *Xiphophora* (Phaeophyta) generally conform to the contours of the substrate and are relatively small and compact (Figs 3, 5 and 6). Plants growing on more expansive substrates such as other Corallinaceae, or on rock tend to be relatively large and more sprawling (Figs 3, 4 and 7). Relatively compact plants develop under more crowded conditions, and relatively sprawling plants develop when conditions are less crowded (Figs 7 and 8).

The relative degree of calcification varies from specimen to specimen. In four of the five paired samples subjected to X-ray micro-analysis during this study (Table 1), the *M. rosea* sample contained significantly greater levels of Ca^{2+} than did the paired *L. melobesioides* sample. In one case, however, no significant difference occurred. The results contrast with the observations of Lemoine (1974), who noted that *L. melobesioides* plants appeared to be more heavily calcified than those of *M. rosea*. These data suggest, therefore, that calcification can vary considerably within both species, and that differences between species may or may not be significant, depending on which individuals are involved in comparisons. Thus, relative calcification does not appear to be a reliable attribute for making taxonomic delineations.

Primary meristems and tissues

The primary meristem of younger plants in both species encompasses the contiguous apical cells distally-terminating primary hypothallial filaments, whose development started originally from a germinating spore (Fig. 9). The primary meristem thus comprises a single layer of ini-



Figs 5–8. *Mastophora rosea.*
Fig. 5. Lectotype specimen (LD 50714) from Guam. Scale bar = 10 mm.
Fig. 6. Cuming specimen (BM) from the Philippines (syntype of *M. licheniformis* Decaisne = *M. rosea*; see Setchell, 1943). Scale bar = 10 mm.
Fig. 7. Cordero specimen (UC 1463132) from the Philippines. Scale bar = 10 mm.
Fig. 8. Siboga Expedition (L943 10 00) specimen from Sula-Basi Is., Indonesia (Type specimen of *M. macrocarpa* f. *condensata* Foslie = *M. rosea* f. *condensata*; see Setchell, 1943). Scale bar = 21 mm.

tials, is marginal in location and appears to be continuous around the thallus periphery. Only one primary meristem occurs per plant. Cell elongation appears to be confined to the primary meristem (Fig. 10).

Anticlinal–coaxial divisions of primary meristem cells result in the lateral production of new primary initials, thus enlarging the size of the meristem. Filaments subsequently produced by the new initials lead to lateral expansion of the thallus or spatial replacement of senescent filaments (Figs 10 and 11). Anticlinal–coaxial divisions appear to occur randomly and asynchronously within the meristem. Anticlinal–transaxial divisions of primary meristem cells result in the production of primary hypothallial cells basipetally, thus increasing primary hypothallial filament length and outward expansion of the thallus. Within localized portions of the meristem, such divisions of contiguous initials may occur in an apparently synchronous manner, and this can result in more or less evenly radiate growth (Figs 9 and 11).

Although the primary meristem of *L. melobesioides* is, initially, entirely terminal in position, portions of it may become intercalary as the thallus develops (Fig. 10). This occurs because some contiguous initials may each undergo a periclinal division to produce a primary epithallial cell acropetally (Fig. 10). The initials are now situated between the epithallial cells and the hypothallial cells and thus occupy an intercalary position. The primary meristem may alternate, without pattern, between a ter-

Table 1. X-ray microanalysis ratios indicating relative surface calcium content in various paired samples of *Lithoporella melobesioides* and *Mastophora rosea*. Statistical significance determined from Kruskal-Wallis tests

Stub	*L. melobesioides*		*M. rosea*		Significance ($P = 0{\cdot}05$)
	n	Values*	*n*	Values*	
1	14	2·970 (0·443)	14	11·539 (1·869)	+
2	11	1·776 (0·678)	9	4·702 (1·063)	+
3	10	5·273 (1·679)	10	14·037 (3·289)	+
4	11	4·193 (1·750)	10	10·010 (2·363)	–
5	10	3·090 (0·653)	10	6·638 (0·903)	+
Pooled data	56	3·363 (0·507)	53	9·653 (1·012)	+

* Values are means ($S_{\bar{x}}$ given in parentheses) of: (Ca^+ peak-average background noise)/average background noise. Ca (K_a) window centered at 3740 eV, backgrounds at 3380 eV and 4340 eV, all window widths 180 eV, 40 s counts; irradiated area of 8600 μm^{-2}.

minal and an intercalary position. In some plants of *L. melobesioides*, and all plants of *M. rosea* examined, the primary meristem apparently remains entirely terminal.

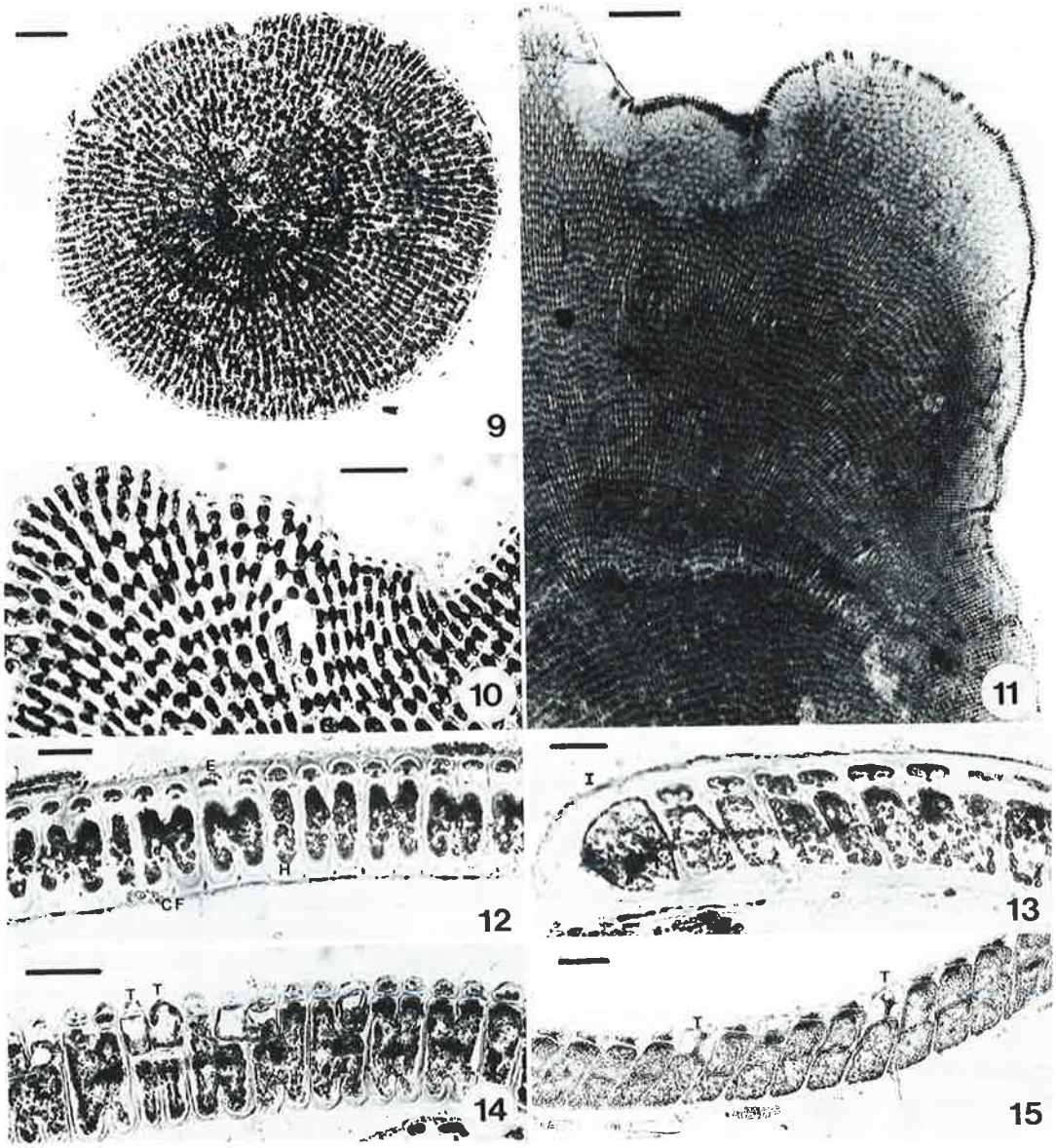
Differential activity within the primary meristem evidently leads directly to variation in thallus form. In *L. melobesioides* anticlinal–transaxial divisions in some primary meristem cells either cease, or occur less frequently than in most other primary meristem cells; this results in variable, outward expansion of the thallus and in the development of marginal lobes to varying degrees (Fig. 10). Occasionally, similar meristem activity and lobing occur in *M. rosea* (Fig. 11). More commonly however, anticlinal–transaxial divisions in certain localized groups of primary meristem cells of *M. rosea* occur far more frequently than in most others, resulting in the development of distinct, elongate branches (Fig. 7).

With the onset of branching, the primary meristem in *M. rosea* becomes divided into small active regions at the apices of developing branches and more extensive, comparatively inactive regions along the rest of the thallus periphery. As a given branch develops, initials which at first are apical in location gradually become displaced to a lateral location, as new initials are produced and the entire primary meristem increases in size (Fig. 11). Continued activity of laterally situated initials can lead to a gradual increase in branch width and commonly results in branch margins becoming involute.

Each branch may also give rise to further branches laterally. Initially branch apices become lobed, after certain hitherto active primary meristem initials become relatively inactive (Fig. 11). More active portions of the meristem, flanking both sides, continue to form new tissue and eventually two branch apices result, each with an active region at the apex. If these processes occur repeatedly, extensive branching of the thallus takes place (Figs 5, 6, 7 and 8).

At least three anatomical–morphological developments appear to be associated with localized curtailment of meristematic activity. In *M. rosea*, primary terminal meristem cells can become relatively inactive as they are displaced from branch apices to branch margins. In *L. melobesioides*, particular meristem initials may cease activity temporarily or permanently, after dividing periclinally to produce an epithallial cell. Meristematic activity in both species stops when terminal meristem cells become transformed into trichocytes (see below).

Cells of the primary hypothallium are derived basipetally from primary initials, and differ somewhat in appearance in longitudinal and transverse sections (Figs 12–15). In both species, most hypothallial cells are vertically elongate (i.e. cell height commonly is $>1{\cdot}5$ cell length or cell diameter), and the hypothallium remains unistratose throughout the plant. Some authors (Adey & MacIntyre, 1973, p. 892; Gordon *et al.*, 1976, p. 255; Johansen, 1976b, p. 395; Mason, 1953, p. 343) describe such cells as palisade-like and/or refer to the tissue as palisade hypothallium. Fusions occur between cells of contiguous, hypothallial filaments (Figs 12 and 14), but not between successive cells within the same filament (Figs 13 and 15). Epithallial cells usually arise acropetally from single, asymmetric, periclinal–coaxial divisions of hypothallial cells (Fig. 13), but occasionally they may arise from primary initials in a similar manner. The



Figs 9–15. Primary meristems and thallus structure.

Fig. 9. Young plant of *Lithoporella melobesioides* (LTB 11493) with a continuous, marginal, primary meristem. Scale bar = 100 μm.

Fig. 10. Primary meristem of older plant of *L. melobesioides* (LTB 11811) showing both terminal and intercalary initials and lateral expansion of the meristem. Scale bar = 100 μm.

Fig. 11. Primary meristem of *Mastophora rosea* (LTB 11822) showing a continuous meristem from a terminal to a lateral location and incipient branch formation. Scale bar = 250 μm.

Figs 12–13. Transverse (Fig. 12) and longitudinal (Fig. 13) sections of primary thallus of *L. melobesioides* (LTB 11811). E = epithallium; H = hypothallium; CF = contiguous cell fusion; I = primary meristem initial. Scale bar = 25 μmm.

Figs 14–15. Transverse (Fig. 14) and longitudinal (Fig. 15) sections of primary thallus of *M. rosea* (LTB 11822). T = trichocyte. Scale bar = 50 μm.

Table 2. Summary of numeric data relating to vegetative tissues of *Lithoporella melobesioides* and *Mastophora rosea*

Character	Section	*L. melobesioides* (μm)	*M. rosea* (μm)
Hypothallium			
Cell ht.	CA*	30–55 (63)‡	38–98
Cell length	CA	(12) 15–35 (69)	14–46
Ht./length	CA	1·16–2·55 (3·11)	1·53–3·00
Cell ht.	TA†	27–58	40–93
Cell diam.	TA	10–22	11–30
Ht./diam.	TA	(1·54) 2–5	(2·18) 2·50–4·86 (5·47)
Epithallium			
Cell ht.	CA	5–14	8–22
Cell length	CA	13–38	16–52
Ht./length	CA	0·40–1·13	(0·24) 0·39–0·75
Cell height	TA	5–20	8–17
Cell diam.	TA	(5) 10–20 (25)	10–22
Ht./diam.	TA	0·20–0·55 (1)	(0·53) 0·75–1·00 (1·25)
Perithallium			
Cell length	CA	14–60 (80)	27–69
Cell ht.	CA	12–27 (35)	16–35
Ht./length	CA	(0·25) 0·28–1·00 (1·45)	(0·36) 0·60–0·80

* Coaxial–anticlinal.
† Transaxial–anticlinal.
‡ Extreme values are indicated in parentheses.

epithallial cells collectively form a unistratose epithallium. Epithallial cells neither undergo fusion, nor divide again. Numeric data on cells of primary tissues are summarized in Table 2.

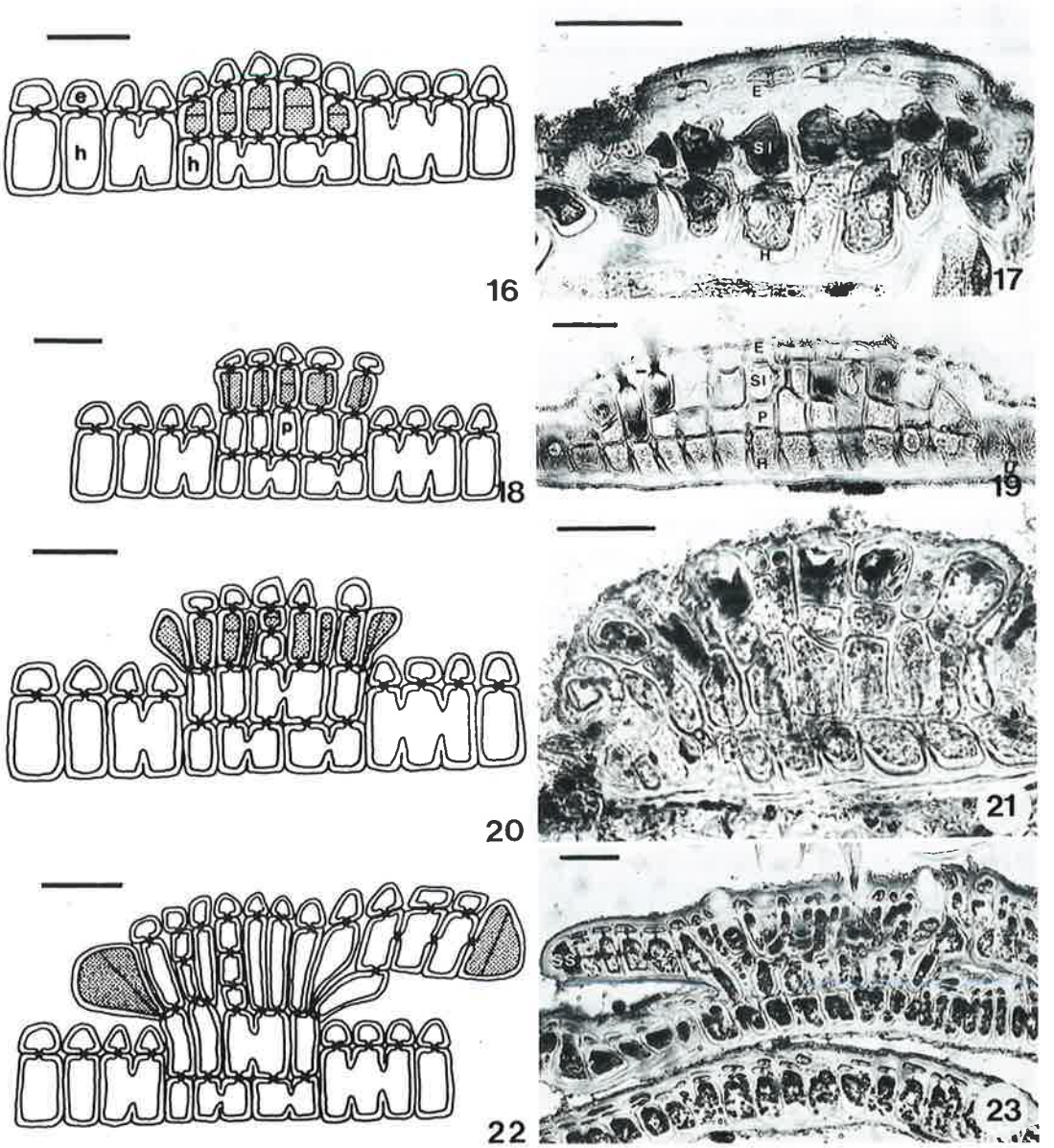
Secondary meristems and tissues

Two distinct, sequentially formed secondary meristems occur in both species. In both taxa, a secondary internal meristem develops directly beneath the epithallium when groups of primary hypothallial cells undergo single, periclinal–coaxial divisions (Figs 16–17). The basipetal products of these divisions remain non-meristematic, while the acropetal products collectively constitute a new secondary internal meristem (Figs 16–17). Within a thallus, secondary internal meristems develop independently of one another and do not amalgamate, thus producing discrete patches of secondary vegetative tissues. Secondary growth appears to be far more extensive in *L. melobesioides* than in *M. rosea*.

Production of secondary tissues in both taxa is similar and commences soon after a secondary internal meristem has formed. Initials first undergo periclinal–transaxial divisions and give rise basipetally to perithallial cells (Figs 18–19). Thus the perithallium constitutes a secondary, rather than a primary tissue in these species. The perithallium rarely becomes more than two to four cells thick, and always remains situated between the underlying hypothallium and the secondary internal meristem. Cell elongation appears to occur largely within the meristem. Cells of contiguous perithallial filaments may fuse laterally, but cells within the same filament apparently do not fuse with one another. Cell shape is similar when viewed in longitudinal and transverse thallus sections, but unlike hypothallial cells the greatest dimension is length rather than height. Numeric data on perithallial cells are summarized in Table 2.

Secondary internal meristem cells also can undergo anticlinal–coaxial divisions and give rise laterally to additional initials (Figs 20 and 21). In contrast to the progenitor initials, the newly formed meristematic derivatives do not bear epithallial cells and thus are terminal in position. If such a meristematic derivative undergoes a periclinal–transaxial division, a new epithallial cell is formed acropetally, the direction of filament growth does not change, and the initial becomes subepithallial and a contiguous part of the secondary internal meristem (Figs 20 and 21). This course of development occurs most commonly in meristematic derivatives which are not situated at the periphery of the secondary internal meristem.

Alternatively, a meristematic derivative can



Figs 16–23. Secondary meristem and tissue formation in *Lithoporella melobesioides*. In schematic drawings, meristems are shaded and solid lines within meristem cells indicate planes of subsequent division. E or e = Epithallium; H or h = hypothallium; P or p = perithallium; SI = secondary internal meristem; SS = secondary superficial meristem.

Figs 16–17. Formation of secondary internal meristem (LTB 11565). Scale bar = 40 μm (Fig. 16); Scale bar = 50 μm (Fig. 17).

Figs 18–19. Production of perithallial tissues from secondary internal meristem (LTB 11557). Scale bar = 40 μm (Fig. 18); Scale bar = 50 μm (Fig. 19).

Figs 20–21. Formation of secondary superficial meristem (LTB 11557). Scale bars = 40 μm (Fig. 20); Scale bar = 50 μm (Fig. 21).

Figs 22–23. Development of a secondary branch from the secondary superficial meristem (LTB 11811). Scale bar = 40 μm (Fig. 22); Scale bar = 50 μm (Fig. 23).

divide anticlinally, resulting in the basipetal production of a secondary hypothallial cell (Figs 22 and 23). No epithallial cell is formed, the direction of filament growth has changed and the meristematic cell remains terminal in position, but is now separated spatially from the secondary internal meristem (Figs 22 and 23). This course of development occurs commonly in contiguous meristematic derivatives situated at the periphery of the secondary internal meristem. Collectively, these meristematic cells now constitute the initials of a newly-formed, secondary superficial meristem, which is no longer contiguous with the older progenitor, secondary internal meristem.

Once formed, a secondary superficial meristem can become far more active and can produce far more tissue than the secondary internal meristem. Additional initials can be produced laterally, thereby increasing the size of the secondary meristem. The end result of this secondary tissue production is a branch which grows out over, and becomes superimposed upon part of the underlying primary thallus (Figs 22 and 23). Anatomically, secondary branches are indistinguishable from segments of the primary thallus from which they arose.

New secondary internal meristems can develop within secondary branches and ultimately result in production of another superimposed layer of branching (Figs 24 and 25). Extensive superimposition can occur in *L. melobesioides*; Lemoine (1974) records twenty-six layers. In the *M. rosea* plants examined, however, superimposition of more than two to three layers was not observed, and branch production from secondary meristems is less common (Figs 26 and 27). The secondary branches in *M. rosea* usually are small and lobose, generally are confined to older portions of the thallus and are usually greatly overshadowed in size by the elongate primary branches. Secondary branches seem to be absent in young or very small plants of *M. rosea*.

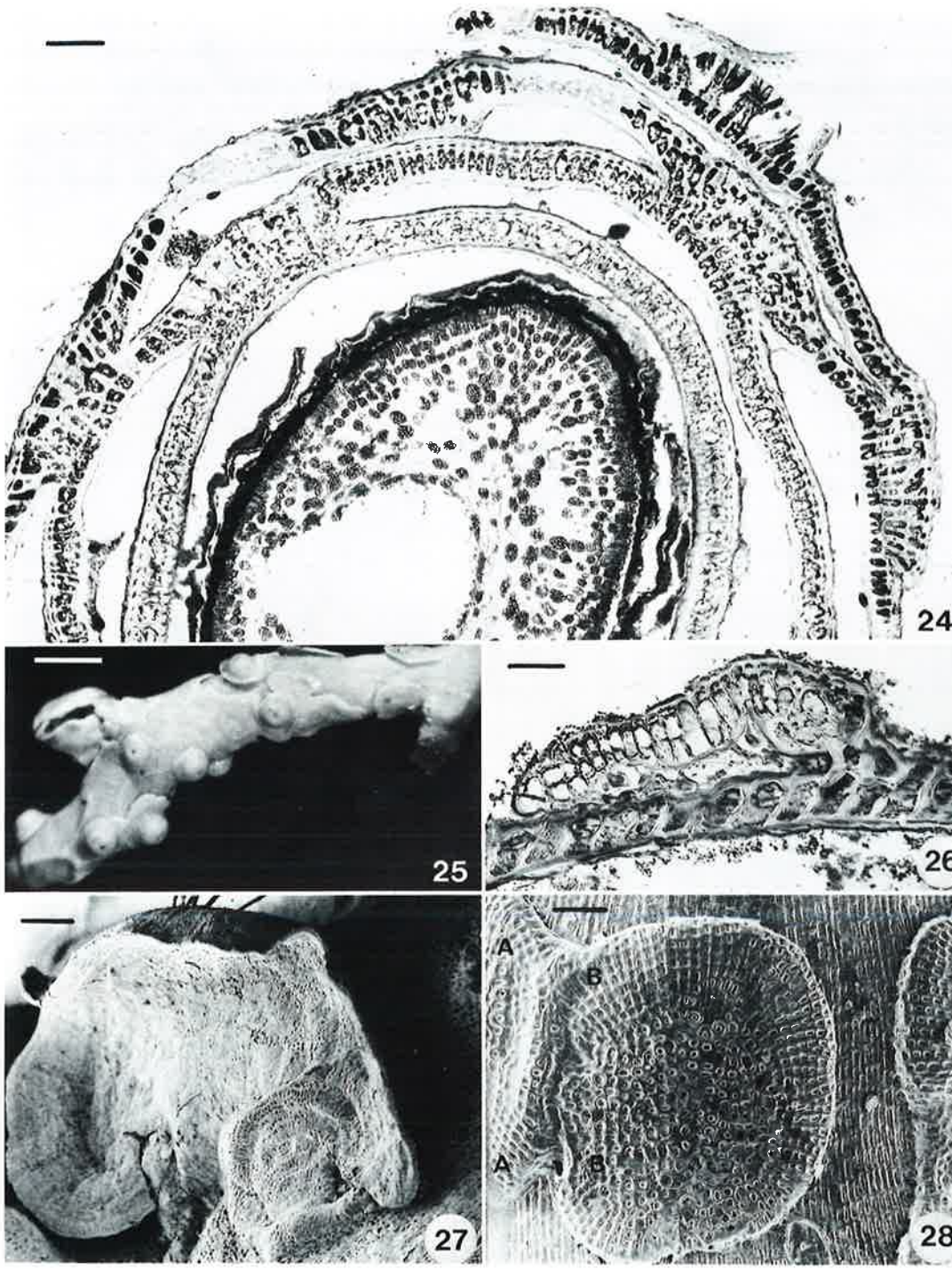
Adjunctive cell fusions

Adjunctive cell fusions occur between cells belonging to two non-contiguous filaments of the same thallus and involve at least one terminal meristem cell. Adjunctive cell fusions within individual plants apparently have not been reported previously in the taxa studied, but Lemoine (1970, 1974) described analogous 'auto-endophytic' fusions between cells presumed to belong to two different thalli of *L. melobesioides* or of *M. affinis*. Auto-endophytic fusions have not been observed unequivocally during this study.

Extensive, adjunctive cell fusions can occur both in primary and secondary tissues of *L. melobesioides*. Young plants growing epiphytically on *Xiphophora chondrophylla* (R. Brown) Harvey [Phaeophyta] often partially or entirely encircle branches of the host alga. Opposite margins of the *Lithoporella* thallus eventually come into contact with each other and adjunctive cell fusions occur between opposing primary meristem cells or between primary meristem cells and hypothallial cells (Fig. 28).

After the onset of secondary tissue production in *L. melobesioides*, numerous additional adjunctive cell fusions take place, particularly between secondary terminal meristem cells of two thallus branches which come into contact with one another (Figs 28 and 29). Further production of vegetative tissue apparently ceases where fusions have taken place. Fusions of this sort can make the thallus appear to consist of a number of concentric layers connected to one another in regions where perithallial tissue has developed (Fig. 24). Adjunctive cell fusions also can occur between a secondary terminal meristem cell of one filament and a hypothallial cell of another non-contiguous filament (Fig. 30). Fusions of this sort appear to occur less commonly.

In *M. rosea*, most adjunctive cell fusions occur between cells of, or produced by the primary meristem. Frequently, fusions occur between primary meristem cells situated along opposite lateral margins of the same branch after the margins have become involute and touch one another (Figs 31 and 32), and a portion of the branch becomes tube-like. Another type of tube-like development occurs when one lateral margin of a branch becomes involute and fuses with its own ventral surface (Fig. 33). In this case fusions occur between primary meristem cells and primary hypothallial cells. Adjunctive cell fusions also can occur between cells of two branches which then become partially confluent (Fig. 34). The branches may be part of the same branch system or belong to different branch systems. In the latter case, it may be possible that branch systems from two different plants within a *M. rosea* mat are involved and that auto-endophytism as described by Lemoine (1970, 1974) has occurred, but this has not been observed during the present study. Regardless of the type



Figs 24–28. Secondary branches.

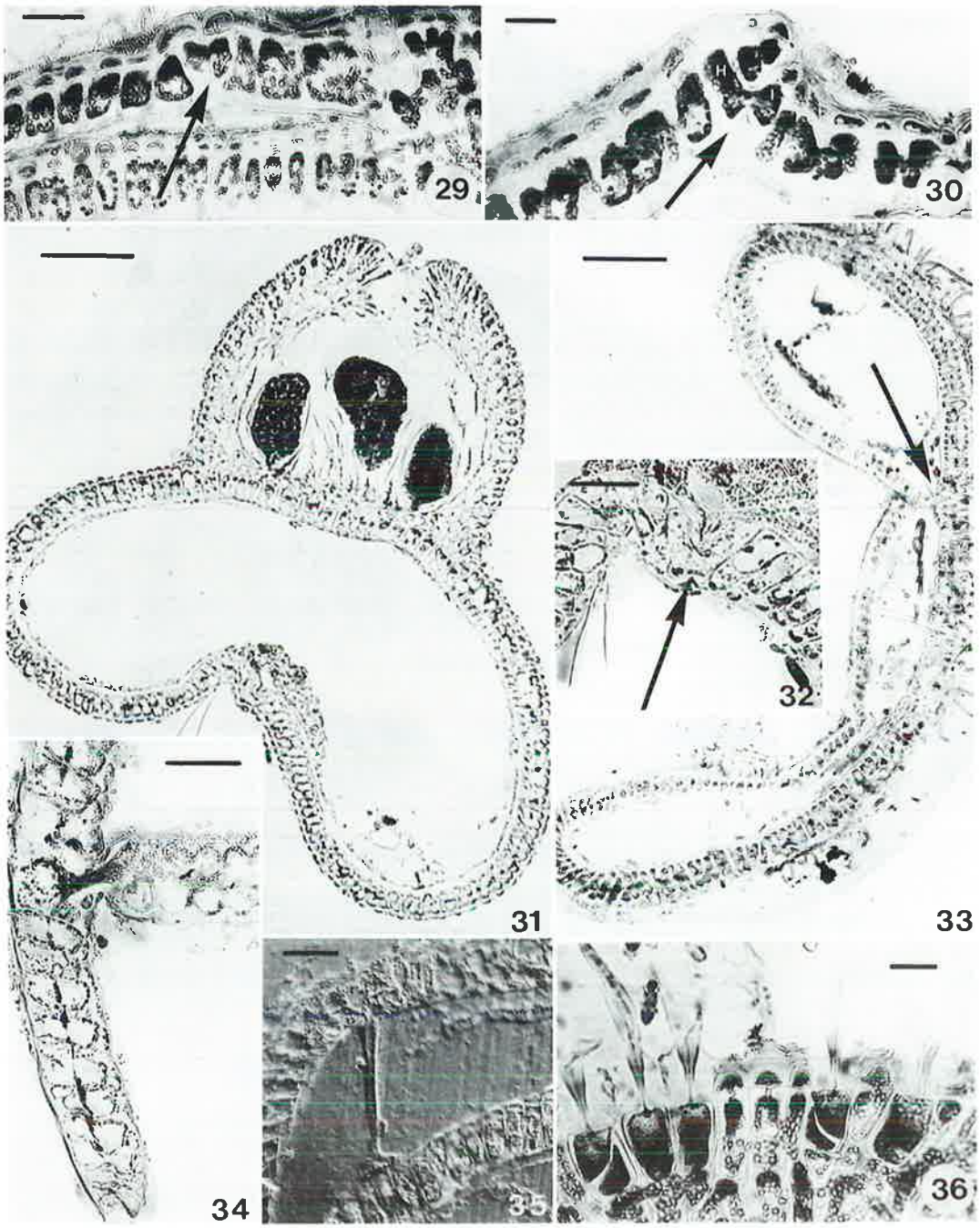
Fig. 24. Sectional view of a *Lithoporella melobesioides* plant showing several superimposed layers of branching (LTB 11811). Central host tissue is *Xiphophora*. Scale bar = 100 μm.

Fig. 25. Surface view of secondary branches of *L. melobesioides* (LTB 11811). Scale bar = 2·5 mm.

Fig. 26. Sectional view of a secondary branch in *Mastophora rosea* (LTB 11822). Scale bar = 100 μm.

Fig. 27. Surface view of a secondary branch in *M. rosea* (LTB 11824). Scale bar = 200 μm.

Fig. 28. Fusion of margins of two secondary branches (A and B) of *L. melobesioides* (LTB 11821). Scale bar = 200 μm.



Figs 29–36. Adjunctive cell fusions, rhizoids and trichocytes.
Fig. 29. Adjunctive fusion of two initials in *Lithoporella melobesioides* (LTB 11811). Scale bar = 50 μm.
Fig. 30. Adjunctive fusion of an initial (I) and a hypothallial cell (H) in *L. melobesioides* (LTB 11811). Scale bar = 25 μm.
Figs 31–32. Adjunctive fusion of two initials in *Mastophora rosea* (LTB 11822). Scale bar = 200 μm. Fig. 32 is an enlargement of fusion in Fig. 31. Scale bar = 100 μm.
Fig. 33. Adjunctive fusion of an initial and a hypothallial cell in *M. rosea* (LTB 11822). Scale bar = 200 μm.
Fig. 34. Fusion of two branches in *M. rosea* (LTB 11822). Scale bar = 50 μm.
Fig. 35. Rhizoid in *M. rosea* (LTB 11822). Scale bar = 50 μm.
Fig. 36. A group of trichocytes in *L. melobesioides* (LTB 11811). Scale bar = 25 μm.

of adjunctive cell fusion which has taken place, post-fusion meristem activity in participating cells appears to become arrested.

Attachment mechanisms

Attachment of plants to a substrate is effected through unicellular rhizoids or hypothallial cell adhesion. Rhizoids arise basipetally from single, asymmetric, periclinal–coaxial or oblique divisions of hypothallial cells and thus occur only on ventral thallus surfaces (Fig. 35). Rhizoidal cells are connected to their hypothallial progenitors by distinct primary pits and appear to be nucleate. Rhizoids not only anchor thalli to a substrate, but also anchor various parts of the same thallus to one another. Rhizoids appear neither to penetrate the substrate surface, nor become involved in adjunctive fusions. They can occur sporadically over the ventral surface of the thallus and, except in localized areas, they apparently do not develop in great numbers. In the present study, rhizoids have been found in *M. rosea* but not in *L. melobesioides*. Several other investigators (Lemoine, 1970, p. 2646, pl. 1, Fig. 4; 1974; Masaki, 1968) have recorded them in plants identified as *L. melobesioides,* and Foslie (1904, p. 74) noted [with reference to the type collection] that under some circumstances a few short rhizoids can develop. Re-examinations of small fragments from the type specimen and from a second Foslie specimen (Foslie, 1904, p. 74, Figs 30a and 30c) of *L. melobesioides,* however, have failed to confirm the occurrence of rhizoids, suggesting that rhizoidal development in this species may occur only rarely. Gordon *et al.* (1976) do not mention rhizoids in *L. melobesioides* from Guam, and Hamel & Lemoine (1953, p. 28) characterized *Lithoporella* by the absence of rhizoids.

Lithoporella melobesioides plants growing on *Xiphophora* appear to be attached via hypothallial cell adhesion. Sporelings at first seem to be attached by their entire ventral surfaces, but as the thallus develops, the central portion becomes detached from the host and hypothallial cell adhesion evidently becomes confined to peripheral areas behind the primary terminal meristem (Fig. 24). Hypothallial cell adhesion also can occur between superimposed branches of *L. melobesioides,* but has not been observed in *M. rosea* plants examined. Moreover, hypothallial cells involved in adhesion do not appear to develop thicker ventral cell walls or undergo other modification.

Attachment of entire plants to another biotic substrate by means of cell fusion has not been seen.

Trichocytes

Trichocytes (Figs 14, 15 and 36) develop in primary and secondary tissues of both species and, at some stage, bear unicellular hairs (Figs 1 and 36). Although these hairs may be shed, the remainder of the trichocyte is recognizable in thallus sections (Figs 14 and 15) and therefore would be classified as persistent (Cabioch, 1971). Mature trichocytes apparently do not bear epithallial cells but invariably are situated at the surface or margin of the thallus layer in which they occur.

Trichocytes may arise from hypothallial cells in both species (Figs 14 and 15). Such trichocytes are intercalary in position (Cabioch, 1971; Chamberlain, 1978) and do not affect meristematic activity of initials. In *L. melobesioides,* trichocytes also may arise from meristem cells (Fig. 23). Such trichocytes are terminal in position (Cabioch, 1971, p. 170, Fig. 16A; Chamberlain, 1978). When a trichocyte is formed from an intercalary meristem cell, the overlying epithallial cell is sloughed off. Meristematic activity in the relevant initial appears to be arrested permanently once a terminal trichocyte is formed. Although terminal trichocytes were not observed in *M. rosea* plants examined, further studies are required before concluding that such trichocytes do not occur.

Trichocytes in both species may occur singly, in pairs, in groups or in rows (Figs 1, 14, 15 and 36). Trichocyte density varies between plants, and some variation in trichocyte structure also has been observed. All trichocytes observed appeared to comprise one or two cells (Fig. 15). The two-celled trichocytes (regarded here as trichocyte complexes) arise from division of a progenitor cell and are contained within the old progenitor cell wall (Fig. 36). This division is more or less oblique or curved in most instances, but can be coaxial or even transaxial (Fig. 36). Coaxial divisions were observed only in intercalary trichocytes, while oblique and transaxial divisions occur in terminal trichocytes.

DISCUSSION

Morphological–anatomical implications

In a number of recent publications (Adey, Masaki & Akioka, 1974; Bold & Wynne, 1978;

Cabioch, 1972; Cardinal, Cabioch & Gendron, 1978, 1979; Chamberlain, 1978; Johansen, 1976a; Lebednik, 1977; Townsend, 1979), vegetative meristems in taxa of Corallinaceae have been classified solely on the basis of their place of occurrence. Although these authors recognize two basic types of meristems, various names have been applied to each, and clear distinctions between meristem cell position within thallus filaments (i.e. terminal or intercalary) and meristem location within the plant body (i.e. marginal, apical, lateral, etc.) have not been maintained consistently. Thus meristems comprising cells situated at the distal ends of filaments have been called terminal (Cabioch, 1972; Cardinal *et al.*, 1978, 1979), apical (Bold & Wynne, 1978; Lebednik, 1977; Townsend, 1979, p. 252), peripheral–apical (Chamberlain, 1978) and marginal (Townsend, 1979, p. 254). Meristems, comprising cells situated within filaments, have been called intercalary (Bold & Wynne, 1978; Cabioch, 1972; Cardinal *et al.*, 1978, 1979; Johansen, 1976a; Lebednik, 1977; Townsend, 1979), perithallial (Adey *et al.*, 1974) and subapical (Chamberlain, 1978). In these schemes, relative times and the places of meristem origin were not considered for purposes of classification. Woelkerling (1980a, pp. 212 and 221; 1980b, p. 237), however, attached greater importance to relative times of origin and classified the meristems of *Metamastophora flabellata* as primary and secondary, noting (1980a, p. 221) that primary and secondary meristems are not contiguous.

Results from the present study support the use of a meristem classification scheme in which relative times and places of origin are given greater weighting than meristem location and position, because such a scheme can better facilitate an overall understanding of meristem morphology and plant development. In *L. melobesioides*, the primary meristem and the secondary superficial meristems may be partly terminal and partly intercalary in position, and in *M. rosea*, they are partly apical and partly lateral in location. If these meristems were classified solely on the basis of place of occurrence (location and/or position) it would result in single, contiguous meristems arbitrarily and incorrectly being divided into two discrete tissues. Consequently, discussions of the thallus development and meristem morphology could become confused or misleading.

This also appears to be the case for non-geniculate taxa such as *Clathromorphum* (Bold & Wynne, 1978, p. 509 and Fig. 9.49a; Cardinal *et al.*, 1978; Lebednik, 1977, p. 103) and *Mesophyllum* (Bold & Wynne, 1978, p. 509 and Fig. 9.50), in which the primary meristem is partly terminal and partly intercalary in position. At first, initials are terminal within filaments located at the peripheral margins of the crust. As long as meristem cells remain so situated, they produce new cells basipetally or laterally, but not acropetally. As growth occurs, however, some of these filaments become displaced towards the dorsal surface of the thallus and the initials produce one or more epithallial cells acropetally. As a direct consequence, these initials now occupy an intercalary position. Displacement of filaments and acropetal production of epithallial cells do not spatially separate the meristem into two parts. Rather it remains a single, continuous tissue (Bold & Wynne, 1978, Fig. 9.50) and therefore must be regarded as a single meristem which is partly terminal and partly intercalary. Primary meristems of this sort also occur in geniculate members of the Corallinaceae (e.g. *Calliarthron*—Johansen, 1969); further comments are provided by Woelkerling (1980a, p. 221).

In vascular plants, meristems most commonly are classified on the basis of location within the plant body (Esau, 1965, p. 70 ff.; Fahn, 1974, p. 52 ff.) and usually are regarded as apical or lateral (parallel to the surface of the relevant plant organ). 'Primary' and 'secondary' are used subordinately, when necessary, to indicate the relative times of meristem origin. This classification scheme cannot be applied readily to the Corallinaceae, since in at least some taxa (e.g. *Calliarthron* spp., *Clathromorphum* spp., *L. melobesioides, M. rosea, Mesophyllum* spp.) different parts of the *same* meristem can occur in apical or lateral locations and in terminal or intercalary positions. A classification scheme based principally on relative times and places of origin, in contrast, can accommodate single meristems which encompass several locations and/or positions, while still maintaining meristem integrity for naming and classifying purposes.

If a meristem classification scheme, based principally on relative times and places of origin and subordinately on location and position, is employed, then the definitions of hypothallium and perithallium proposed by Woelkerling (1980a, p. 221) require modification to take account of the subordinate criteria. Thus hypo-

thallium can now be considered a tissue derived basipetally from a primary, or secondary superficial meristem, and perithallium can now be considered a tissue derived basipetally from a secondary internal meristem. The terms medulla and cortex are used for taxa in which vegetative thallus development is effected by a single, primary meristem (Woelkerling, 1980a, p. 221).

In most Corallinaceae, cell fusions apparently occur only between intercalary cells of contiguous filaments. Lemoine (1970), however, discovered that in *L. melobesioides,* cell fusions (regarded here as adjunctive cell fusions) also take place between cells of non-contiguous filaments, and later (Lemoine, 1974, p. 54) reported the same for *Mastophora.* Lemoine assumed that the non-contiguous filaments belonged to different plants and interpreted these phenomena as instances of auto-endophytism, but photographs presented by Lemoine (1970, 1974) do not demonstrate convincingly that parts of different plants, rather than different parts of one plant, are involved. All fusions between non-contiguous filaments observed during the present study occurred within individual plants, usually between cells of two branches or cells from two parts of the same branch. Lemoine's interpretation apparently rests on the assumption that overgrowing in *L. melobesioides* was the result of the superimposition of distinct thalli rather than of branches of an individual thallus. Whether auto-endophytism and attending cell fusions occur in *Lithoporella* or *Mastophora* remains uncertain, but the occurrence of these phenomena cannot be ruled out in view of the data presented by Cabioch (1972, p. 209, pl. 5, Figs 10 and 11) for a species of *Tenarea.*

Systematic implications

Distinctions between *Lithoporella* and *Mastophora* have been based primarily on apparent differences in vegetative morphology and anatomy. Foslie first erected (Foslie, 1903), and subsequently considered (Foslie, 1904, p. 73) *Lithoporella* as a subgenus of *Mastophora* Decaisne 1842, but later (Foslie, 1909, p. 58) established *Lithoporella* as a distinct genus on the grounds that the plants were crust-like rather than foliose, unbranched rather than branched, inflexible rather than flexible and grew in statified layers. Setchell (1943, p. 135), in a subsequent revision of *Mastophora,* maintained *Lithoporella* as a distinct genus on the bases that *Lithoporella* plants were devoid of marginal lobing, lacked rhizoids and proliferated to produce superimposed layers, whereas *Mastophora* plants underwent marginal lobing, possessed rhizoids and did not proliferate to produce superimposed layers. Cabioch (1972, pp. 265 and 269) delineated the two taxa solely on growth form: *Lithoporella* included taxa that were encrusting, while *Mastophora* included taxa that grew erect. Lemoine (1974, pp. 53–54) concluded that characters mentioned by Setchell (1943) could not be utilized for generic delineation and maintained the two taxa as distinct genera solely on the basis of relative differences in the degree of thallus calcification. Recently Johansen (1976a, p. 238), collating data from other studies, separated the two genera on differences in habit and substrate relations (*Lithoporella* being epilithic, sometimes becoming free; *Mastophora* being ribbon-like, branched and attached to the substrate at one end only) and on differences in tetrasporangial conceptacle roof formation. It appears, therefore, that there is no clear concensus regarding generic concepts and circumscriptions of *Lithoporella* and *Mastophora.*

Results from the present study have led to the conclusion that none of the vegetative characters used previously and/or examined during this investigation are suitable for distinguishing *Lithoporella* and *Mastophora* as genera, thus supporting and extending the conclusions reached by Lemoine (1974). Data collected from generitype specimens and numerous other plants of the two type species have led to the following conclusions for both taxa:

(1) the degree of the thallus calcification varies considerably;

(2) rhizoids can develop, but may not occur invariably;

(3) branching and marginal lobing are present;

(4) thallus stratification may occur to varying degrees as a result of secondary branch-formation;

(5) thallus appearance can vary considerably depending on the nature of the substrate and the extent of available growing space; and

(6) internal anatomy is similar.

Furthermore, *Mastophora* plants do not grow erect, as suggested by Cabioch (1972, p. 265), but rather develop in a procumbent or partially ascending manner, and become attached to a substrate by rhizoids at a number of points rather than at one end, as suggested by Johansen (1976a) and Suneson (1937).

Although branch development can vary considerably from individual to individual, many plants referable to *L. melobesioides* produce compact thalli in which branches are short and often lobose (as broad or broader than long), whereas most plants referable to *M. rosea* produce thalli which are larger, more spread out and have elongate, ribbon-like branches. In *L. melobesioides*, most branches arise from secondary meristems, whereas in *M. rosea* most branches arise from primary meristems. While these differences may provide some bases for species recognition, considerable variability occurs in both taxa and all assessments made during this study have failed to produce a consistent and reliable way in which to delineate the two genera using attributes of branching.

In the absence of suitable vegetative characteristics, continued recognition of *Lithoporella* and *Mastophora* as distinct genera rests on determining whether differences of generic significance occur in attributes associated with reproduction. This subject is considered elsewhere (Turner & Woelkerling, 1982).

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Studies on the *Mastophora–Lithoporella* complex (Corallinaceae, Rhodophyta)

II. Reproduction and generic concepts

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A comparative study of reproduction in the type species of *Mastophora* and *Lithoporella* (Corallinaceae, Rhodophyta) has revealed that differences associated with tetrasporangial conceptacle development and structure provide a reliable basis upon which to delineate the two genera. In *Lithoporella melobesioides,* tetrasporangial conceptacles are characterized in part by the presence of a layer of elongate perithallial cells, roof formation from filaments interspersed among tetrasporangia and the absence of a columella. In *Mastophora rosea,* tetrasporangial conceptacles lack a layer of elongate perithallial cells, have roofs formed from peripheral filaments surrounding fertile tissue and possess a columella. The two patterns of tetrasporangial conceptacle development differ, both from one another and from the patterns recorded for other Corallinaceae. Details of gametangial conceptacle structure and ontogeny are provided for the first time, and a number of stages of carposporophyte ontogeny are presented including transfer of diploid nuclei from carpogonium to auxiliary cell. The taxonomic implications of all results are considered, generic concepts and typification are reviewed and emended diagnoses of the two genera are presented. The relationships of *Mastophora* and *Lithoporella* to other genera of non-geniculate Corallinaceae also are discussed briefly.

INTRODUCTION

Recognition of *Mastophora* Decaisne and *Lithoporella* Foslie as distinct genera of Corallinaceae hitherto has been based on apparent differences in various vegetative characteristics (Cabioch, 1972; Foslie, 1909; Lemoine, 1974; Setchell, 1943). After a comparative study of vegetative morphology and anatomy of the type species of both genera, however, Turner & Woelkerling (1982) concluded that *Mastophora* and *Lithoporella* could not be delineated reliably on vegetative grounds and noted that continued recognition of the two taxa as distinct genera depended on whether differences of generic significance occur in attributes associated with reproduction.

Extant information on reproductive morphology and anatomy in the two genera is scant. For *Mastophora,* the only published illustrations of tetrasporangial conceptacles are those of Decaisne (1842a, pl. 17, Fig. 11; 1842c, pl. 17, Fig. 11) for *Mastophora rosea* (C. Agardh) Setchell (as *M. licheniformis* Decaisne) which appear stylized and show undivided spores. Cordero (1977) states that tetrahedral divisions occur in the tetrasporangia of *M. rosea,* but this has remained unconfirmed and contrasts sharply with the zonate mode of tetraspore formation found in other Corallinaceae (except for some species assigned to *Sporolithon*—Heydrich, 1897; Womersley & Bailey, 1970). The only account of gametic conceptacles and carposporophyte development in *Mastophora* is that of Heydrich (1907), whose results generally have been considered unreliable (Suneson, 1937, p. 64), and whose work on carposporophyte ontogeny, according to Lebednik (1977b, p. 382), has been disregarded in recent times. Data on male con-

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ceptacles presented by Johansen (1976, p. 238, Table 2) apparently is based on Suneson's (1945) paper which deals with plants of *Metamastophora* (Woelkerling, 1980a, 1980b) rather than *Mastophora*.

For *Lithoporella* there appears to be no detailed information on gametic conceptacles or carposporophyte ontogeny. Kraft & Woelkerling (1981, p. 95, Fig. 4.8B and p. 97, Fig. 4.9F) illustrate, but do not describe mature male, and carposporangial conceptacles of plants referable to *Lithoporella* (*pacifica*). Lemoine (1976) notes a possible male conceptacle in *L. antiquitas* Johnson (Johnson, 1961, p. 937, pl. 276, Fig. 2). Data on tetrasporangial conceptacles are more extensive (Gordon, Masaki & Akioka, 1976; Lemoine, 1974), but developmental information is scant (Masaki, 1968), and the possible occurrence of a columella (Lemoine, 1974, p. 51; Masaki, 1968, pl. 38, Fig. 4 and pl. 79, Figs 2 and 4) requires clarification. The mode of meiotic divisions in tetrasporangia apparently has not been illustrated for any non-fossil species of *Lithoporella*; Foslie (1903, 1904) simply describes the sporangia of *L. melobesioides* (Foslie) Foslie as four-parted.

This study provides a detailed account of reproductive morphology and anatomy in *M. rosea* and *L. melobesioides,* the type species of the two genera, and considers the morphological–anatomical, and the general systematic implications of the results. Emended descriptions of both genera are provided and possible relationships to other members of the Corallinaceae are considered.

MATERIALS AND METHODS

Procedures employed in data collection and analysis, information on species studied and terminology have been outlined previously (Turner & Woelkerling, 1982). Additional information from several collections in TCD has been included in the present study.

RESULTS

Conceptacle morphology

Conceptacles (Figs 1–6) in both species occur singly or in irregularly disposed groups. Orientation is strictly dorsiventral with the uniporate conceptacle roofs always arising from the dorsal thallus surface. Male conceptacles of *M. rosea* usually possess a distinctive conoidal–rostriform shape and protrude up to 675 μm above the thallus surface (Fig. 1). The single pore is normally bordered by a ring of at least twenty heavily calcified cells. Male conceptacles of *L. melobesioides,* in contrast, usualy are frustoconiform and rarely protrude more than 200 μm above the thallus surface (Fig. 2). The single pore normally is bounded by twelve or less cells and rests within a slight apical depression.

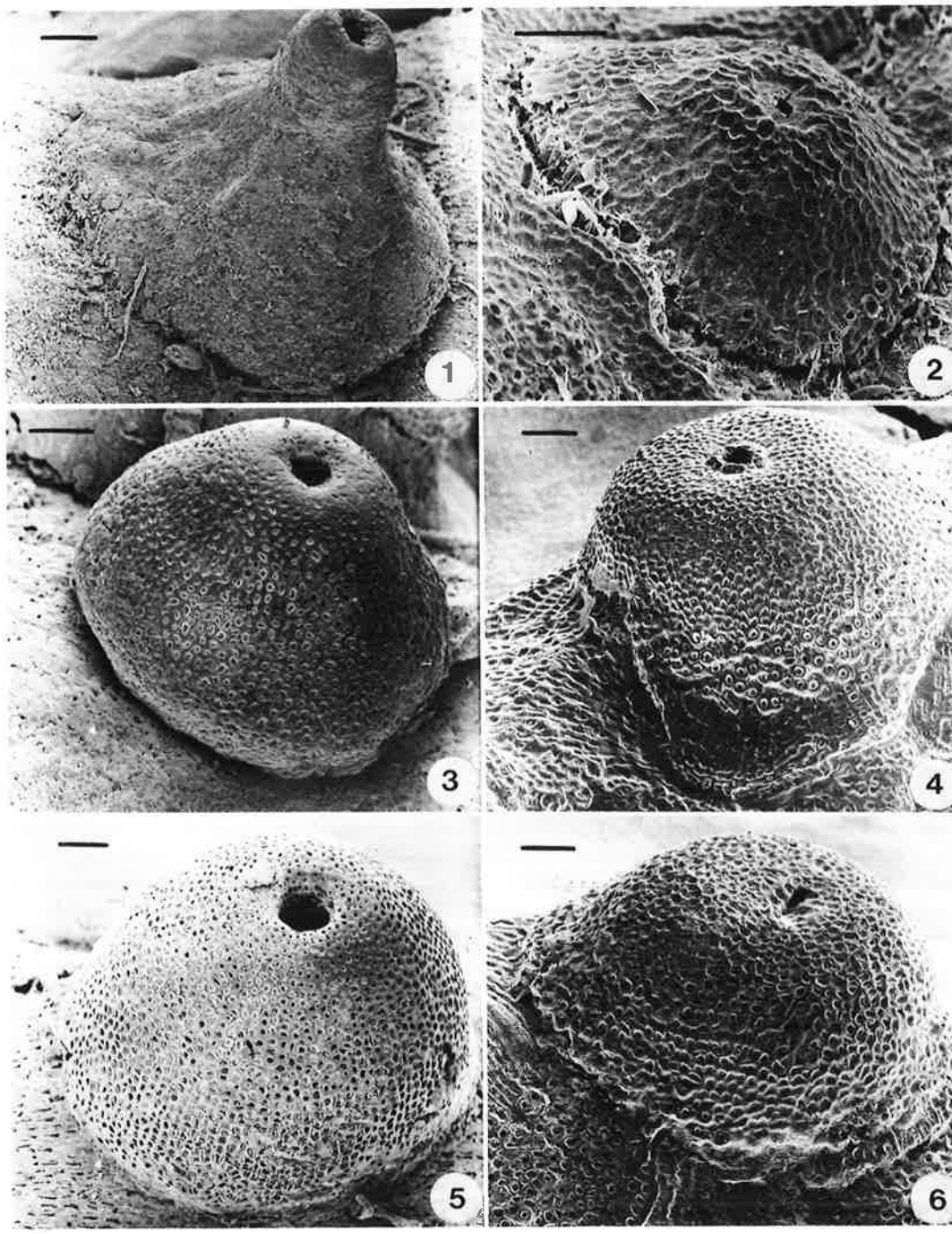
Female (Figs 3 and 4) and tetrasporangial (Figs 5 and 6) conceptacles in both species are generally domoid in shape. Pores in both female and tetrasporangial conceptacles of *M. rosea* are surrounded by a ring of twenty or more cells, and thus are similar to the pores of male conceptacles. In *L. melobesioides,* pores of female and tetrasporangial conceptacles are rarely surrounded by more than ten to twelve cells. In addition, the ring of cells immediately adjacent to the pore of most female conceptacles (Fig. 4) is raised slightly and usually forms a small rim.

Numeric data relating to conceptacles are summarized in Table 1. During this study, only two monoecious gametic plants of *M. rosea* and none of *L. melobesioides* were encountered; all other gametic plants were dioecious.

Tetrasporangial conceptacle ontogeny and anatomy

Tetrasporangial conceptacle formation in both species begins when localized groups of primary or secondary hypothallial cells undergo single periclinal divisions and give rise acropetally to a layer of cells which constitutes a new secondary meristem (Fig. 7). This meristem has an internal place of origin and is dorsal in location. At this stage the initials are situated beneath epithallial cells, and thus are intercalary in position. Concurrent with meristem formation, however, the overlying epithallial cells become detached from their hypothallial progenitor cells and may collectively form an irregular to domoid covering over the developing meristem (Fig. 8). As a result, the initials become terminal in position. The detached epithallial cells soon degenerate and the covering breaks apart and is sloughed off. Subsequent development of tetrasporangial conceptacles follows one of two patterns, neither of which conforms completely to any of the four patterns previously described (Johansen, 1976) for non-geniculate Corallinaceae.

In *L. melobesioides,* most initials undergo



Figs 1–6. Conceptacles. Scale bars = 100 μm.
Fig. 1. Male conceptacle of *Mastophora rosea* (LTB 12161).
Fig. 2. Male conceptacle of *Lithoporella melobesioides* (LTB 11811).
Fig. 3. Female conceptacle of *M. rosea* (LTB 11824).
Fig. 4. Female conceptacle of *L. melobesioides* (LTB 11821).
Fig. 5. Tetrasporangial conceptacle of *M. rosea* (LTB 11824).
Fig. 6. Tetrasporangial conceptacle of *L. melobesioides* (LTB 11821).

Table 1. Summary of numeric data relating to male (M.C.), female (F.C.) and tetrasporangial (T.C.) conceptacles

Taxon/character	M.C. (μm)	F.C. (μm)	T.C. (μm)
Mastophora rosea			
External diam.	630–880	590–800 (875)*	700–800 (860)
External ht.	375–675	(290) 380–530	490–710 (858)
Chamber diam.	450–710	220–430	525–610 (652)
Chamber ht.	100–160	(50) 150–575	360–430
Pore diam.	27–35	13–115	25–78
Pore ht.	270–425	(70) 140–200 (252)	75–216
Sporangium length	—	—	190–250
Sporangium diam.	—	—	150–210
Lithoporella melobesioides			
External diam.	380–500 (580)	525–700	525–660
External ht.	150–175 (210)	190–275	250–355 (441)
Chamber diam.	210–315	230–370	(229) 260–425
Chamber ht.	60–90 (125)	81–160	(163) 214–270
Pore diam.	50–185	19–69	55–105
Pore ht.	85–105	71–104	52–90 (106)
Sporangium length	—	—	120–220
Sporangium diam.	—	—	85–145

* Extreme values given in parentheses.

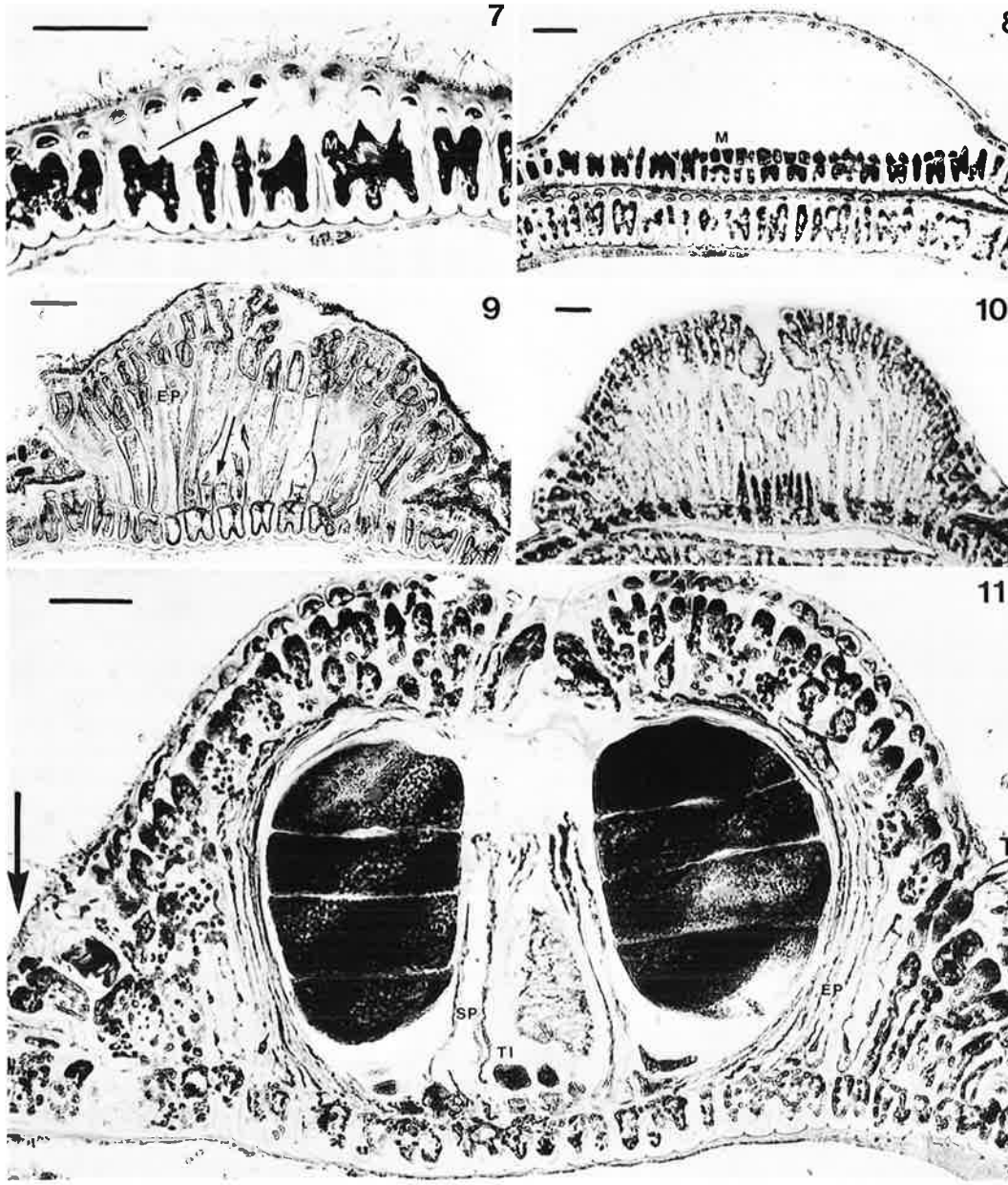
periclinal–transaxial divisions, and each usually gives rise basipetally to one to three perithallial cells (Fig. 9). These perithallial filaments remain sterile, usually grow upright or bend outwards and become part of the conceptacle roof. During roof development, the initials remain terminal in position. Eventually, however, most of the initials undergo periclinal–transaxial divisions, giving rise acropetally to a single layer of epithallial cells at the surface of the conceptacle roof (Fig. 10). Following epithallial cell formation, the initials again become intercalary. Occasionally one or more initials become transformed into trichocytes (Fig. 11), similar in structure to terminal trichocytes in vegetative portions of the plant (Turner & Woelkerling, 1982, Fig. 36). Meristematic activity usually ceases after formation of trichocytes or epithallial cells.

In tetrasporangial conceptacles of *L. melobesioides,* a few of the more centrally located filaments also may remain sterile, but do not become involved in conceptacle roof formation. Instead, the terminal meristem cells cease dividing after production of a single perithallial cell (Fig. 9). This helps to create a gap in the developing roof (Fig. 10). The gap apparently becomes the conceptacle pore through which mature sporangia escape. The abortive perithallial filaments, which are usually interspersed among the tetrasporangial initials, ultimately degenerate either partially or completely (Fig. 11). No central columella of sterile tissue develops.

A distinctive feature of tetrasporangial conceptacle development in *L. melobesioides* is that the first-formed (most basal) perithallial cells of most sterile filaments become extremely elongate, compared with other perithallial cells and meristem cells (Figs 9 and 10). Johansen (1968, 1981) refers to these as cavity cells. Greatest elongation occurs in cavity cells situated near the centre of the developing conceptacle, while cavity cells near the conceptacle margin are progressively less elongate. As the conceptacle matures, many of these cavity cells degenerate, thus creating a chamber for the developing tetrasporangia. Remains of cavity cells are often evident around the periphery of the chamber (Fig. 11).

Perithallial cells, distal to the cavity cells, are much smaller in size and in most cases do not exceed meristem cells in length. In mature conceptacles, fusions may occur between non-elongate perithallial cells of contiguous filaments, or between contiguous meristem cells after formation of epithallial cells, but fusions were not observed between epithallial cells or between contiguous cavity cells.

Tetrasporangia develop from a small group of more or less centrally situated initials which do not produce sterile tissue or become involved in



Figs 7–11. Tetrasporangial conceptacle development in *Lithoporella melobesioides*. Scale bars = 50 μm.

Fig. 7. Onset of meristem formation (M) and detatchment (arrow) of overlying epithallial cells (LTB 11811).

Fig. 8. Later stage of meristem development with uplifted, domoid epithallial layer (LTB 11811).

Fig. 9. Development of sterile roof filaments containing elongate perithallial cells (EP) and tetrasporangial initials (arrow) (LTB 11565).

Fig. 10. Conceptacle pore formation and divided tetrasporangial initials showing incipient stalk cells and tetrasporangia (LTB 11811).

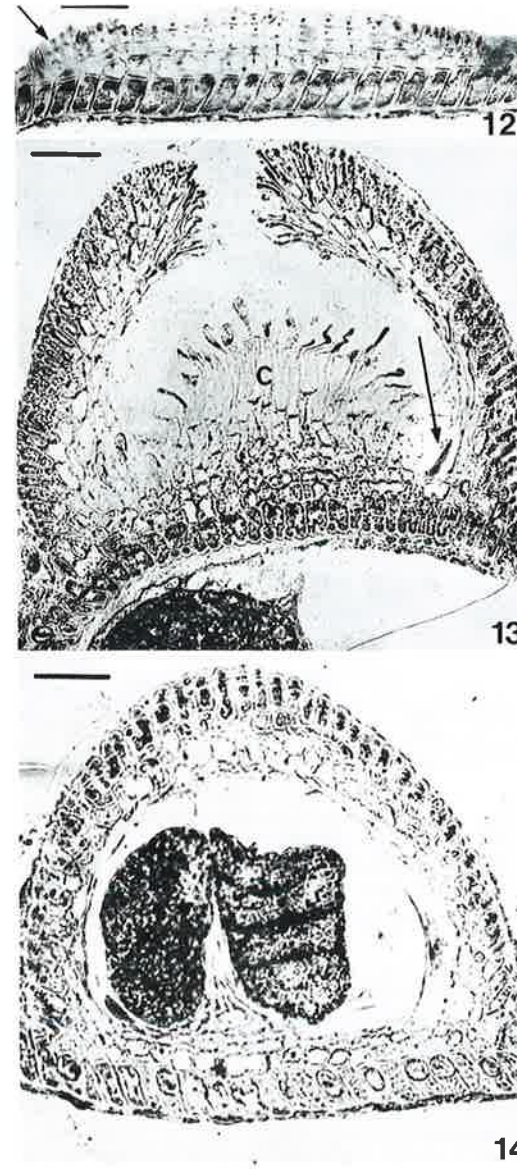
Fig. 11. Mature conceptacle. Note zonately divided contents of two tetrasporangia, several centrally situated tetrasporangial initials (TI), interspersed among several senescent perithallial filaments (SP), remains of other elongate perithallial cells (EP) at the periphery of the conceptacle chamber, trichocytes (T) in the conceptacle roof, and the onset of secondary branch formation (arrow) (LTB 11811).

conceptacle roof formation. Instead, these initials become densely cytoplasmic, and each undergoes a single periclinal–transaxial division (Fig. 10). The basal product of this division functions as a stalk and the apical product eventually develops into a tetrasporangium. As this cell enlarges, meiosis presumably occurs. At maturity each sporangium contains four zonately arranged tetraspores (Fig. 11). Spore discharge apparently occurs after the entire sporangium is released from the conceptacle; sporangial wall remains never were seen in old conceptacles. A particular initial apparently gives rise to only one tetrasporangium, and tetrasporangia seem to mature successively in groups of one to three (Fig. 11) as room becomes available in the conceptacle chamber after release of earlier formed tetrasporangia.

The secondary internal meristem from which a conceptacle develops can also give rise indirectly to secondary vegetative branches in *L. melobesioides* (Fig. 11). These branches arise from meristem cells, adjacent to the vegetative hypothallium.

Subsequent to the formation of a secondary internal meristem and the onset of perithallium production, tetrasporangial conceptacle development in *M. rosea* differs markedly from that in *L. melobesioides*. At first, several layers of perithallial cells are produced more or less uniformly beneath the entire meristem (Fig. 12). These never become extremely elongate and they do not degenerate; instead, they become a permanent part of the conceptacle floor. Cavity cells do not form.

Soon afterwards, differentiation into two distinct groups of sterile filaments occurs (Fig. 13), but only the group situated at the periphery of the meristem becomes involved in conceptacle roof formation. These peripheral filaments, which may contain eight or more perithallial cells, grow upwards and arch inward over the central portion of the incipient conceptacle to form a dome-like roof (Fig. 13). Opposing parts of the developing dome never meet and the gap left at the top of the dome superstructure by arrested meristem activity becomes the conceptacle pore (Figs 5 and 13). When periclinal–transaxial divisions of meristem cells in most peripheral filaments produce a single layer of epithallial cells, the meristem cells again become intercalary in position and meristem activity

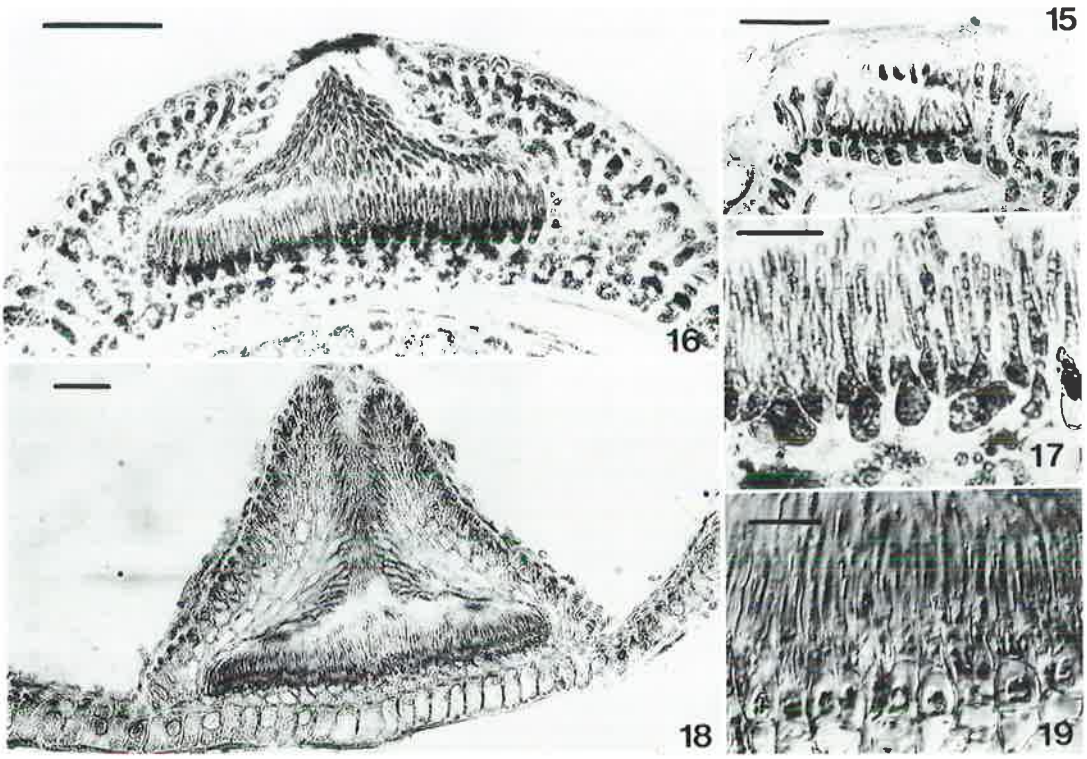


Figs 12–14. Tetrasporangial conceptacle development in *Mastophora rosea*. Scale bars = 100 μm.

Fig. 12. Early development showing terminal conceptacle meristem and several layers of subtending perithallial cells, and onset of roof filament (arrow) development (LTB 12161).

Fig. 13. Later stage of development. Note central columella (C), tetrasporangial initial (arrow) and pore (LTB 11822).

Fig. 14. Section through periphery of mature conceptacle showing tetrasporangia with zonately divided contents. Central columella not evident (LTB 12161).



Figs 15–19. Spermatangial conceptacles.
Fig. 15. Early stage of development in *Lithoporella melobesioides* (LTB 11811). Scale bar = 100 μm.
Fig. 16. Mature spermatangial conceptacles of *L. melobesioides* (LTB 11811). Scale bar = 100 μm.
Fig. 17. Spermatangia of *L. melobesioides* (LTB 11811). Scale bar = 100 μm.
Fig. 18. Mature spermatangial conceptacle of *Mastophora rosea* (LTB 12161). Scale bar = 100 μm.
Fig. 19. Spermatangia of *M. rosea* (LTB 12161). Scale bar = 25 μm.

ceases. In filaments adjacent to the roof pore, however, epithallial cells are not produced and the initials remain terminal (Fig. 13). In mature conceptacles, cell fusions occur between contiguous perithallial cells and between arrested meristem cells.

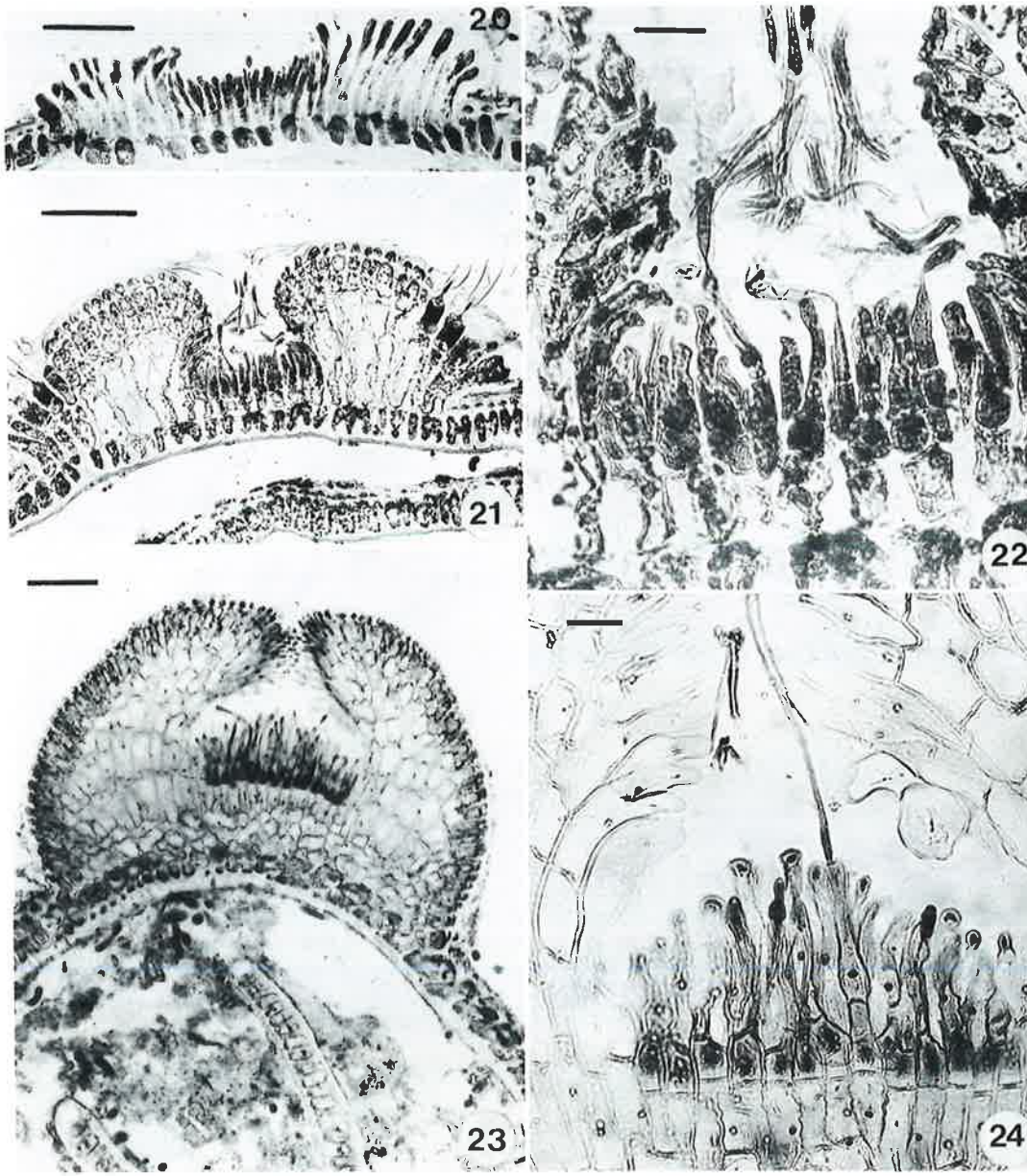
The second, centrally located group of sterile filaments (Fig. 13) never becomes involved in roof or conceptacle pore formation. Rather, it persists as a central columella. Meristem activity in columellar filaments is limited, and only a few additional perithallial cells are produced basipetally. Meristem initials always remain terminal, and epithallial cells apparently never form. As the conceptacle matures, columellar filaments may undergo varying degrees of degeneration (Figs 13 and 14).

Tetrasporangial ontogeny in *M. rosea* is similar to that in *L. melobesioides*. In *M. rosea*, however, tetrasporangial initials only develop in a ring between the central and peripheral groups of sterile filaments. As sporangia develop, the conceptacle chamber becomes larger as a result of sterile filament degeneration both in the columella and in the inner wall of the conceptacle roof. Remains of degenerate cells often are evident in mature conceptacles (Fig. 14). Other aspects of tetrasporangial formation and release appear to be the same in both taxa. Mature tetrasporangia in the *M. rosea* plants studied (including Cordero's collections from the Philippines at UC) all contained zonately divided contents; consequently the report of tetrahedral divisions (Cordero, 1977, p. 94) appears questionable.

A summary comparison of the two patterns of tetrasporangial conceptacle development described above, together with data on the other known patterns, appear in Table 2.

Gametangial conceptacle ontogeny and anatomy

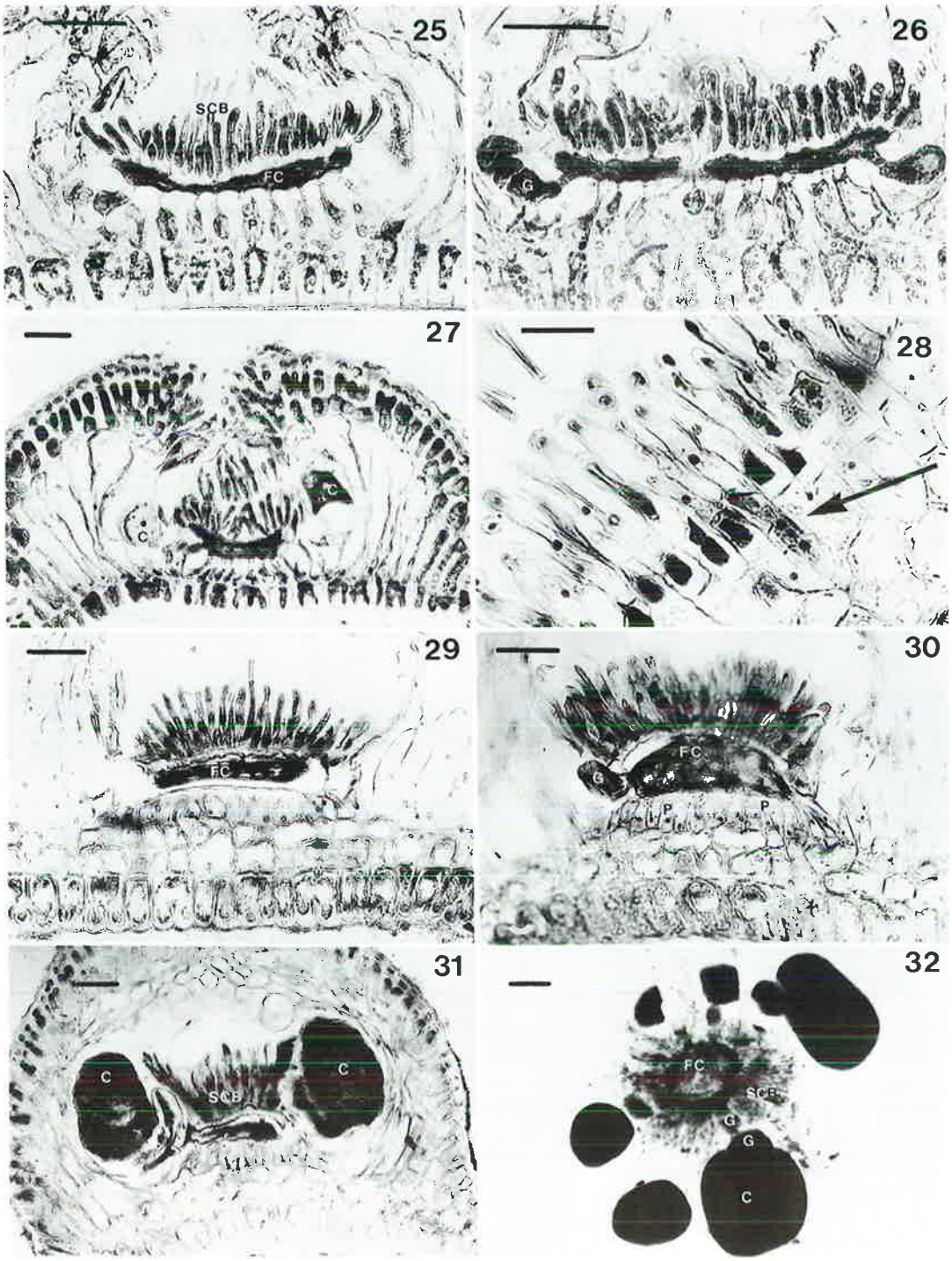
Gametangial conceptacles (Figs 15–24) in both species appear to have a number of develop-



Figs 20–24. Female conceptacles.
Fig. 20. Early stage of development in *Lithoporella melobesioides* (LTB 11811). Scale bar = 100 μm.
Fig. 21. Mature female conceptacle of *L. melobesioides* (LTB 11811). Scale bar = 100 μm.
Fig. 22. Carpogonial branches with mature carpogonia in *L. melobesioides* (LTB 11811). Scale bar = 20 μm.
Fig. 23. Mature female conceptacles of *Mastophora rosea* (LTB 12161). Scale bar = 120 μm.
Fig. 24. Carpogonial branches with mature carpogonia in *M. rosea* (LTB 12161). Scale bar = 5·0 μm.

mental features in common. Both male and female conceptacles (like tetrasporangial conceptacles) are initiated from secondary internal meristems (Figs 15 and 20). Conceptacle roofs develop from tissue produced by more peripherally situated meristem cells. These initials undergo a series of periclinal–transaxial divisions and give rise basipetally to filaments which eventually arch over, or otherwise largely enclose a central region, thus creating a chamber for developing gametangia.

Pore formation results from a gap left in the



Figs 25–32. Carposporophyte development. FC = fusion cell; SCB = senescent carpogonial branches; G = gonimoblast filament; C = carposporangium; P = perithallial cells subtending the fusion cell. Scale bars = 50 μm (Figs 25–27, 29–32), 10 μm (Fig. 28).

Fig. 25. Fusion cell of *Lithoporella melobesioides* prior to gonimoblast filament formation (LTB 11811).

Fig. 26. Gonimoblast filaments in *L. melobesioides* (LTB 11811).

developing roof. During roof development, peripherally situated meristem initials at first remain terminal in position. Eventually, however, a single layer of epithallial cells is produced acropetally at the roof surface; meristem initials become intercalary and meristematic activity stops (Figs 16, 18, 22 and 24). Meristem initials adjacent to the pore, in contrast, do not produce epithallial cells and remain terminal in position, even though meristematic activity ceases.

Gametangia in both species arise over the entire conceptacle chamber floor. Interspersed sterile filaments were not observed and a columella does not develop.

At maturity, male conceptacles of *L. melobesioides* differ in certain respects from those of *M. rosea*. Firstly, conceptacle roofs are frustoconiform (Fig. 16) rather than conoidal-rostriform (Fig. 18). As a result, the pore channels in male conceptacles of *L. melobesioides* seldom are more than 100 μm long; in *M. rosea*, pore channels are usually over 250 μm long. Secondly, the roof of *L. melobesioides* male conceptacles rarely comprise more than two to three layers of variously shaped perithallial cells, including a basal layer of extremely elongate cavity cells (Fig. 16). In *M. rosea*, the roof of male conceptacles usually comprises six or more layers of perithallial cells which do not become extremely elongate and are more regularly cylindrical in shape (Fig. 18). Thirdly, trichocytes occur occasionally in the roofs of *L. melobesioides*, but were not observed in those of *M. rosea*. While fusions between cells of contiguous roof filaments occurred in both taxa, they were far more common in *L. melobesioides*. Finally, secondary branches may develop from the base of the roof in *L. melobesioides*, but were not seen in *M. rosea*.

Spermatangial initials in both species are confined to the conceptacle chamber floor and arise directly from meristem cells, without the protective layer of tissue found in certain other nongeniculate Corallinaceae (Lebednik, 1978). Several spermatangia arise laterally or obliquely from each initial, but individual spermatangia remain unbranched. During development, spermatangia are attached to the initials by long hyaline stalks. Eventually, however, they become detached from the stalk and accumulate in considerable numbers in the pore channel and upper chamber, prior to release from the conceptacle. Spermatangia in *L. melobesioides* tend to be larger (Fig. 17) and produced in smaller numbers than in *M. rosea* (Fig. 19). In *L. melobesioides*, meristem cells which give rise to spermatangial initials do not produce any perithallial cells basipetally and thus remain in direct contact with the subtending unistratose hypothallial cells (Figs 16 and 17). In *M. rosea*, by contrast, meristem cells produce up to four layers of perithallial cells basipetally before giving rise to spermatangial initials (Figs 18 and 19).

Female conceptacles of *L. melobesioides* (Figs 20–22) differ from those of *M. rosea* (Figs 23 and 24) in two important anatomical respects. In *L. melobesioides*, roof filaments seldom are more than three to four cells long, and nearly all of the basal-most perithallial cells become markedly elongate (Fig. 21) and form cavity cells similar to those in tetrasporangial conceptacles (Fig. 11). Roof filaments in *M. rosea*, by contrast, commonly are six or more cells long and cavity cells never form (Fig. 23). Secondly, the perithallial cells, from which fertile axes arise in *L. melobesioides*, are attached directly to hypothallial cells lining the conceptacle chamber floor, whereas in *M. rosea* these perithallial cells normally are separated from the underlying hypothallial cells by three to five layers of sterile tissue. Occasionally, trichocytes occur in roofs of female conceptacles in *L. melobesioides*, but they were not observed in roofs of female conceptacles of *M. rosea*. Fusions between cells of contiguous roof filaments occur in both species.

Fertile axes in *L. melobesioides* consist of a supporting cell and one or two carpogonial branches which are one to two cells long (Fig. 22). In *M. rosea*, most fertile axes consist only of a supporting cell and the carpogonium, al-

←

Fig. 27. Mature carposporophyte in *L. melobesioides* (LTB 11811).
Fig. 28. *Mastophora rosea:* migration (arrow) of presumably diploid nuclei from carpogonium to supporting cell prior to the onset of fusion cell formation (LTB 12161).
Fig. 29. Fusion cell of *M. rosea* prior to gonimoblast filament formation (LTB 12161).
Fig. 30. Onset of gonimoblast filament production in *M. rosea* (LTB 12161).
Fig. 31. Sectional view of mature carposporophyte of *M. rosea* within an old female conceptacle (LTB 12161).
Fig. 32. Surface view of mature carposporophyte of *M. rosea* excised from the conceptacle. Note spores of different sizes and stages of maturity (LTB 12161).

though a few axes contain a third cell in between (Fig. 24). In both taxa, cells of the fertile axes are usually densely cytoplasmic (Figs 21 and 23), in comparison with subtending cells. Although most carpogonia produce trichogynes, only a few trichogynes become extremely elongate, and these are usually associated with more or less centrally located carpogonia. Plasmogamy and karyogamy have not been observed in either species.

Carposporophytes

Very early stages of carposporophyte ontogeny have not been observed in *L. melobesioides* during this study. Prior to development of gonimoblast filaments, however a large, thin, flattened or somewhat dorsally concave fusion cell forms across the conceptacle chamber floor (Fig. 25). As in *Metamastophora* (Woelkerling, 1980a), this fusion cell appears to comprise the amalgamated supporting cells of the previously formed carpogonial branches, remains of which undergo varying degrees of senescence on the dorsal surface of the fusion cell. Fusion cell anchorage to the conceptacle floor is effected ventrally by a group of perithallial cells, each of which originally bore a fertile axis.

In *L. melobesioides*, gonimoblast (carposporangial) filaments arise from the ventral surface of the fusion cell near the margin (Fig. 26). Gonimoblast filaments are two to three cells long and are terminated by cells which eventually develop into carposporangia (Fig. 27). As carposporangia enlarge, the fusion cell margins become bent upward. Sporangia may vary considerably in shape and generally do not exceed 100 μm in greatest dimension.

Following presumed fertilization in *M. rosea*, the zygotic nucleus divides, and these derivatives migrate down, through the cells of the carpogonial branch, to the supporting cell which then functions as an auxiliary cell (Fig. 28). Transfer tubes of the sort described by Lebednik (1977b; cf. Woelkerling, 1980a) do not develop. Soon, additional supporting cells become amalgamated and a flattened or dorsally convex cell develops, eventually covering most of the conceptacle chamber floor (Fig. 29). As in *L. melobesioides*, senescent carpogonial branches occur along the dorsal surface and anchorage is effected by ventrally situated perithallial cells.

Gonimoblast filaments in *M. rosea* arise only from the lateral margin of the fusion cell (Fig. 30) and not from the ventral surface. The filaments are two to three cells long and each produces a terminal, more or less, ovoid to spherical carposporangium (Fig. 31). Fusion cells normally bear six to eight gonimoblast filaments (Fig. 32) and carposporangia apparently mature at varying rates.

The patterns of procarp and carposporophyte development, reported here for *M. rosea*, are generally consistent with patterns found in most other non-geniculate Corallinaceae. None of the unusual phenomena recorded in Heydrich's (1907) account were detected during this study, and it is possible that Heydrich's observations were based either on poorly preserved or highly aberrant specimens. Both Suneson (1937, p. 64) and Lebednik (1977b, p. 382) have also questioned various reports of Heydrich.

DISCUSSION

Morphological–anatomical implications

Utilizing data from a number of earlier studies, Johansen (1972) characterized the various types of tetrasporangial conceptacle roof formation recorded up to that time for the Corallinaceae, and subsequently (Johansen, 1976) reviewed how various morphological–anatomical features of tetrasporangial conceptacles have been regarded phylogenetically and employed taxonomically. Among non-geniculate Corallinaceae in which developing tetrasporangia do not produce apical wall thickenings (sporangial plugs), Johansen (1976, p. 235) listed two modes of tetrasporangial conceptacle roof development: (1) 'COL' in which the roof is formed '. . . by growth of filaments interspersed among sporangia as well as by a centrally located tuft of sterile filaments called a columella . . .', and in which the pore is formed by a breakdown of the upper part of the columella; and (2) 'SUR' in which the roof is formed '. . . mostly by overgrowth of filaments surrounding a group of developing tetrasporangia . . .'. Precise mode of pore formation was not stated for 'SUR'. Johansen's diagrams (Johansen, 1976, Figs 59 and 60) show that in 'COL', tetrasporangia develop only around the periphery of the conceptacle chamber floor whereas in 'SUR', tetrasporangia develop across the entire conceptacle chamber floor and a columella does not occur.

Apparently it has been generally presumed that the presence of a columella or of peripheral sporangia is characteristic of 'COL' develop-

ment, while the absence of a columella or the presence of scattered sporangia is characteristic of 'SUR' development. Thus, it has been common practice to determine roof and pore formation patterns, based on observations of mature conceptacles when developmental data are lacking; many of the references cited by Johansen (1972; 1976, p. 238, Table 2), for example, contain only information on mature conceptacles.

The modes of tetrasporangial conceptacle development in *L. melobesioides* and in *M. rosea,* described in this study, clearly differ from the four patterns (Table 2) outlined by Johansen (1976). Although roof formation in *L. melobesioides,* like that in the 'COL' pattern, involves growth of filaments interspersed among developing tetrasporangia, there is no regular development of a columella. Formation of the pore results from a gap in developing roof tissue, rather than from columellar or other tissue breakdown as takes place in 'COL', and tetrasporangia usually develop near the centre of the conceptacle chamber floor or in a scattered fashion, rather than around the periphery of the chamber floor as occurs in 'COL'. In *M. rosea,* roof formation, like that in the 'SUR' pattern, involves the overgrowth of filaments surrounding a group of developing tetrasporangia. Unlike the 'SUR' pattern, however, a columella regularly occurs and developing tetrasporangia are confined to the periphery of the conceptacle chamber floor. Pore formation also results from a gap left in the top of the conceptacle roof and not from columellar or other tissue breakdown.

Thus, it appears that at least six patterns of tetrasporangial conceptacle development exist among taxa of non-geniculate Corallinaceae (Table 2), and further study may reveal additional patterns in other taxa. Among the few detailed developmental accounts published to date are those of Adey, Masaki & Akioka (1974) for *Ezo epiyessoense,* Adey *et al.* (the 'COL' pattern); Lebednik (1977a) for *Clathromorphum parcum* and *C. reclinatum* [the 'PMU' pattern]; Minder (1910) and Suneson (1937) for *Choreonema thuretii* (Bornet) Schmitz [the 'SUR' pattern]; and Suneson (1945) for *Metamastophora flabellata* (as *Mastophora lamourouxii*) (cf. Woelkerling, 1980b for nomenclatural details), which conforms to the pattern found in *M. rosea.*

At least two different systems of naming the patterns of tetrasporangial conceptacle development have been proposed. One (Johansen, 1972, p. 118) is based on use of a representative generic name (e.g. the *Lithothamnium* type); the other (Johansen, 1976, pp. 234, 235 and 237) employs acronyms derived from associated morphological characteristics (e.g. 'SUR' for the pattern of overgrowth by surrounding filaments and 'COL' for the pattern in which a columella develops). To accommodate the patterns of development found in *Lithoporella melobesioides* and in *M. rosea,* use of either system would require coining additional names. It also would necessitate modifying existing names such as 'SUR' and 'COL' which could potentially apply to more than one pattern and thus create confusion. In principle, a naming system based on morphological characteristics seems more informative. However, it also seems premature to add to or modify an existing system, especially when detailed data are available for so few taxa and further study may reveal other patterns. Thus, until additional information is published and the possible combinations of morphological characters are better known, it seems preferable to describe (Table 2) the various patterns present rather than to suggest a new or modified naming system, which may require further revision in several years time.

Conceptacle attributes as taxonomic characters

Various morphological–anatomical attributes (Table 2) associated with tetrasporangial conceptacles have been employed to delineate taxa of non-geniculate Corallinaceae ever since Heydrich (1897) first used differences in the number of pores in the conceptacle roof to distinguish genera (Johansen, 1976). Johansen (1976, p. 234) also noted that differences in mode of pore formation '. . . reflect important phylogenetic schisms . . .', and examination of his Table 2 (Johansen, 1976, p. 238) shows that only a single pattern of tetrasporangial conceptacle development is listed for any one genus. Although present knowledge of tetrasporangial conceptacle development in the Corallinaceae is far from complete, available evidence (cf. discussion above and Table 2) appears to indicate clearly that a number of defined developmental patterns occur, and that at least some differences among these patterns can provide meaningful and reliable bases upon which to delineate taxa of generic or higher rank. Accordingly, *Mastophora* and *Lithoporella* are recognized here as distinct genera, because differences in attributes asso-

Table 2. Morphological–anatomical characteristics associated with various patterns of tetrasporangial conceptacle development among nongeniculate Corallinaceae. Pattern 4 occurs in *L. melobesioides*; pattern 6 occurs in *M. rosea*

Pattern*	Mode of roof† development	Mode of pore formation	Relative no. of pores per conceptacle	Occurrence of columella	Occurrence of sporangial plugs	Position of tetrasporangia in conceptacle chamber	Johansen (1976) acronym for pattern
1	Interspersed	Sporangial plug removal	One	Absent	Present	One spore per conceptacle	'PUN'
2	Interspersed	Sporangial plug removal	Several	Absent	Present	Scattered	'PMU'
3	Interspersed	Columella breaks down	One	Present	Absent	Peripheral	'COL'
4	Interspersed	Gap due to filament abortion	One	Absent	Absent	Central to scattered	—
5	Peripheral	Not stated	One	Absent	Absent	Scattered	'SUR'
6	Peripheral	Gap due to incomplete dome formation	One	Present	Absent	Peripheral	—

* Data for patterns 1, 2, 3 and 5 are based in part on information provided by Johansen (1976).
† 'interspersed' means that filaments interspersed among developing tetrasporangia are involved in conceptacle roof formation; 'peripheral' means that only filaments at the margin of the conceptacle are involved in roof formation.

ciated with conceptacle development appear to be consistently stable in these taxa. Emended diagnoses are provided below.

Further studies are necessary to determine the extent to which some attributes associated with tetrasporangial conceptacle development can be utilized in delineating taxa of generic or higher rank. The occurrence of a columella, for example, has been used by Johansen (1969, p. 46) to help characterize the subfamily Lithophylloideae, while Desikchary & Ganesan (1963) used the same feature to help delineate two species within the genus *Hydrolithon* (subfamily Mastophoroideae). Rosenvinge (1917), however, noted presumed intraspecific variation in columellar occurrence within several species of *Heteroderma* (as *Melobesia*). Similarly, the position of tetrasporangia on the conceptacle chamber floor has been used to help characterize certain genera (Foslie, 1900; Kylin, 1956; Masaki, 1968, pp. 5–6; Setchell & Mason, 1943; Suneson, 1937, p. 85), but in other instances variation has been recorded within genera (e.g. *Heteroderma*—Mason, 1953, p. 334; *Dermatolithon*—Mason, 1953, pp. 342–343; *Hydrolithon*—Desikachary & Ganesan, 1967) and within species (e.g. *Fosliella minutula*—Ganesan, 1963, p. 39). Until confirming studies on relevant species are undertaken, and until information is published for a greater range of taxa of Corallinaceae, the use of these characters for delineation of genera or other taxa within the family seems best restricted to situations for which relatively clear-cut evidence is available, as is the case for *Mastophora* and *Lithoporella*.

The diagnostic significance of certain characters associated with conceptacle pore and roof morphology remains uncertain. Garbary & Veltkamp (1980, p. 51) suggested that certain features may have diagnostic value, but noted that more taxa need to be examined. Although a number of differences have been found in conceptacle shape and pore morphology during this study, their potential value as generic characters cannot be determined until detailed investigations of the other taxa presently assigned to these two genera are undertaken.

Carposporophyte attributes as taxonomic characters

Several attributes associated with carposporophyte morphology have been considered taxonomically significant among geniculate Corallinaceae assigned to the subfamily Corallinoideae. Johansen (1972; 1976, p. 237 and Table 3) has used differences in fusion cell shape

Table 3. Attributes used to delineate *Mastophora* and *Lithoporella* as genera and attributes useful for recognizing plants of *Mastophora rosea* and *Lithoporella melobesioides*

Attributes delineating genera	*Mastophora*	*Lithoporella*
Mode of tetrasporangial roof formation	Peripheral filaments	Interspersed filaments
Cavity cells in tetrasporangial conceptacle roof	Absent	Present
Columella in tetrasporangial conceptacles	Present	Absent
Position of tetrasporangia on conceptacle floor	Peripheral	Central
Attributes distinguishing species	***M. rosea***	***L. melobesioides***
Fusion cell shape	Compact, convex and thick	Elongate, concave and thin
Origin of gonimoblast filaments	Margin of fusion cell	Ventral surface of fusion cell
Cavity cells in gametic conceptacle roofs	Absent	Present
No. of layers in perithallium subtending fertile axes	Three to five	One
Shape of male conceptacle	Conoidal–rostriform	Frustoconiform
Perithallial tissue subtending spermatangial initials	Present	Absent
No. of cells surrounding pores in all conceptacles	Twenty or more	Twelve or less

and size to help characterize various genera. Subsequently, Johansen & Silva (1978) employed these attributes, as well as differences in the place of origin of gonimoblast filaments, to help delineate two tribes within the Corallinoideae. In the tribe Corallineae, fusion cells are thin (<12 μm), expanded (90–300 μm broad) and produce gonimoblast filaments from the margins and/or upper surfaces. In the tribe Janieae, fusion cells are thick (up to 35 μm, compact (40–130 μm broad) and produce gonimoblast filaments only from the margins.

Lebednik (1977b, Tables 3 and 4) tabulated and reviewed published data on fusion cell morphology and gonimoblast filament production in all groups of Corallinaceae. Although most taxa in various subfamilies showed particular patterns, Lebednik noted that exceptions occurred and that data for some taxa were lacking.

Results from the present study indicate that fusion cells of *L. melobesioides* tend to be elongate and thin, like those of the Corallineae, whereas fusion cells of *M. rosea* tend to be more compact and thick, like those of the Janieae. Moreover gonimoblast filaments in *L. melobesioides* emanate from the lower surface of the fusion cell (a position not reported for any other taxon of Corallinaceae), while gonimoblast filaments in *M. rosea* emanate from the margin of the fusion cell.

The taxonomic significance of these differences is difficult to assess at present, since there are no comparable data for other species presently assigned to *Lithoporella* and to *Mastophora*. Similarly, there are too few data upon which to delineate tribes within the Mastophoroideae, based on differences in carposporophyte attributes. Carposporophyte development and structure in the type species of most genera require detailed examination, and further study also is needed of other species, including those cited by Lebednik (1977b) as exceptions to the developmental patterns reported for most of the Mastophoroideae.

Generic concepts and typification

Decaisne (1842a, p. 365) established the genus *Mastophora* for taxa of Corallinaceae (1) possessing an expanded, thin, submembranaceous, cellular, unevenly branched frond with involute, obtuse or truncate apices and (2) having mammose conceptacles with vertically inserted, pyr-

iform tetraspores. Decaisne (1842a, p. 359) included only one species (*M. licheniformis* Decaisne) and listed (1842a, p. 365) only one collection from Manilla (Cuming exsiccatae No. 2232); his illustrations (Decaisne, 1842a, p. 380, pl. 17, Figs 11a and b) show the fronds to be non-geniculate and the tetrasporangial conceptacles to be uniporate.

During the next 100 years at least thirty-one taxa were referred to *Mastophora*; Setchell (1943), however, recognized only three species, reducing many others to synonymy or excluding them from the genus. Setchell (1943, pp. 128–129) also reviewed the nomenclatural history of *Mastophora* and provided an updated generic circumscription which included the following attributes:

(1) a monostromatic thallus whose layers are not normally 'superposed';
(2) strong calcification;
(3) lateral or pinnate branching or lobing;
(4) a more or less decumbent habit;
(5) attachment via adventitious, unicellular rhizoids; and
(6) the absence of a distinct thickened stipe or midrib.

Apparently no new taxa of *Mastophora* have been described since publication of Setchell's paper.

Although Decaisne (1842a) mentioned only *M. licheniformis* in the original account, he subsequently (Decaisne, 1842b, p. 126) regarded *Zonaria rosea* C. Agardh (1824, p. 264) as a synonym. Setchell (1943) apparently accepted Decaisne's taxonomic judgement without examining the relevant specimens and, recognizing the nomenclatural priority of the Agardh epithet, used *M. rosea* (C. Agardh) Setchell as the earliest correct name for the type species of the genus and listed *M. licheniformis* Decaisne as a later taxonomic synonym. During the course of the present studies, the lectotype specimen of *Z. rosea* C. Agardh (LD 50714) has been compared with three syntype specimens of *M. licheniformis* (two Cuming exsiccata 2232 specimens in BM and one comparable specimen in TCD, none of which bear institutional herbarium members). All of these type specimens have been found to be conspecific, thus confirming Decaisne's taxonomic opinion and re-affirming Setchell's nomenclatural arrangement.

The genus *Lithoporella* was established by Foslie (1909, p. 58) for Corallinaceae (1) possessing a thin, somewhat calcified, more or less broadly crustose thallus, comprising several superimposed usually twisted layers, each composed of a single tier of vertically elongate cells (except for conceptacles) without covering epithallial cells, and (2) having reproductive organs as in *Mastophora*. (Examination of unnumbered holotype material in TRH and isotype slides in L (960 218 821) has shown that epithallial cells do occur.) Foslie included five species but did not designate a type species. Later Ishijima (1954, p. 9) selected *L. melobesioides* (Foslie) Foslie as lectotype species.

Since 1909, at least twenty taxa have been assigned to *Lithoporella*. Lemoine (1974, p. 52), however, recognized only three living species (Lemoine, 1976, lists of fossil species) and concluded that *Lithoporella* and *Mastophora* as genera were anatomically concordant and differed only in the degree of calcification. Turner & Woelkerling (1982), comparing the type species found no reliable bases upon which to delineate *Mastophora* and *Lithoporella* using vegetative characters.

Results from the present study, however, have led to the conclusion that *Mastophora* and *Lithoporella* are generically distinguishable because of reproductive differences, despite Foslie's (1909, p. 58) statement to the contrary.

The following emended descriptions incorporate results and conclusions presented here and in a companion paper (Turner & Woelkerling, 1982). Table 3 summarizes data on those characteristics which delineate *Mastophora* and *Lithoporella* as genera and on other characteristics which can be used to recognize plants of *M. rosea* and *L. melobesioides*.

MASTOPHORA (Decaisne) emend.

Thallus non-geniculate, anchored ventrally by cellular adhesion and by scattered rhizoids; comprising a series of procumbent, branched, lobose and/or elongate axes which develop from primary and secondary meristems. Thallus structurally composed of a unistratose hypothallium and a unistratose epithallium and of localized non-confluent patches of several-layered perithallium confined largely to areas where secondary axes arise. Contiguous cell fusions common in hypothallium and perithallium; adjunctive cell fusions present. Secondary pit-connections absent. Reproductive structures borne in dorsally situated conceptacles. Tetrasporangial conceptacles uniporate with roof arising from filaments peripheral to developing

sporangia. Columella present; roof pore formed from a gap and not involving tissue breakdown. Tetrasporangia with zonately divided contents and without sporangial plugs; tetrasporangia confined to the periphery of the conceptacle chamber floor centripetal to the central columella.

Type species: ***Mastophora licheniformis*** Decaisne 1842a: 359, 365, pl. 17, Fig. 11. Note: *M. licheniformis* is conspecific with *M. rosea* (C. Agardh) Setchell 1943: 129 (*Basionym: Zonaria rosea* C. Agardh 1824: 264).

LITHOPORELLA (Foslie) emend.

Thallus non-geniculate, anchored ventrally by cellular adhesion and occasionally also by rhizoids; comprising a series of procumbent, branched, lobose axes which develop mostly from secondary meristems. Thallus structurally composed of a unistratose hypothallium and a unistratose epithallium and of localized non-confluent patches of several-layered perithallium confined largely to areas where secondary axes arise. Contiguous cell fusions common in hypothallium and perithallium; adjunctive cell fusions present. Secondary pit-connections absent. Reproductive structures borne in dorsally-situated conceptacles. Tetrasporangial conceptacles uniporate with roof arising from filaments interspersed among developing sporangia. Columella absent; roof pore formed from a gap and not involving tissue breakdown. Tetrasporangia with zonately divided contents and without sporangial plugs; largely confined to the centre of the conceptacle chamber floor.

Type species: ***Lithoporella melobesioides*** (Foslie) Foslie 1909: 59. *Basionym: Melobesia melobesioides* Foslie 1903: 24.

Species concepts within both genera remain poorly known and require further study. Relevant type collections, taxa recently transferred (Adey, 1970) into *Lithoporella* from *Litholepis*, and the various taxa mentioned by Lemoine (1974, 1976) and Setchell (1943, including synonyms) also must be considered. Preliminary studies (unpublished data) of southern Australian collections (including those used by Kraft & Woelkerling, 1981) and of a syntype collection (TRH) suggest that the taxon originally described is *Melobesia pacifica* Heydrich [Heydrich, 1901, p. 529; non Masaki, 1968, p. 8] is referred to correctly as *Mastophora pacifica* (Heydrich) Foslie rather than as *Lithoporella pacifica* (Heydrich) Foslie. Once the proper status and generic disposition of the various taxa are known, other aspects including the geographic distribution of each genus, can be considered properly.

Relationships to other Corallinaceae

In considering the relationships of *Mastophora* and *Lithoporella* to other genera of Corallinaceae, the classification system of Johansen (1976; Lebednik, 1977b, p. 381; 1978, addendum) has been selected again (Woelkerling, 1978, 1980b) to provide a framework for discussion. Johansen recognized three subfamilies of non-geniculate Corallinaceae:

(1) the Lithophylloideae (comprising taxa which lack tetrasporangial plugs but possess secondary pit-connections);

(2) the Mastophoroideae (comprising taxa which lack both tetrasporangial plugs and secondary pit-connections); and

(3) the Melobesioideae (comprising taxa which possess tetrasporangial plugs but lack (exceptions: *Sporolithon, Synarthrophyton*) (Woelkerling, 1980b, pp. 240 and 241) secondary pit-connections).

Both *Mastophora* and *Lithoporella* clearly belong to the Mastophoroideae.

Johansen (1976, p. 232) assigned seven other genera (*Choreonema, Fosliella, Heteroderma, Hydrolithon, Neogoniolithon, Porolithon, Pseudolithophyllum*) to the Mastophoroideae. Despite our limited understanding of these seven genera, *Mastophora* and *Lithoporella* appear to differ from all other Mastophoroideae, except *Hydrolithon,* in producing a unistratose, palisade hypothallium. In addition, *Mastophora* and *Lithoporella* appear to be distinctive among Mastophoroideae in producing branches from secondary superficial meristems and in possessing non-confluent, localized patches of perithallium which arise from localized secondary internal meristems independently of conceptacle production. None of the other seven genera is known to produce branches from secondary superficial meristems. In *Hydrolithon, Neogoniolithon, Porolithon* and *Pseudolithophyllum,* perithallial tissue apparently is confluent throughout the thallus (Johansen, 1976, p. 238). In *Choreonema, Fosliella* and *Heteroderma,* vegetative perithallial tissue, where present, is usually associated with conceptacle production.

Adjunctive cell fusions apparently have not

been reported for other genera of Mastophoroideae, but further studies are needed to determine whether presence of adjunctive cell fusions represents another distinctive attribute of *Lithoporella* and *Mastophora*.

Comparisons of *Mastophora* and *Lithoporella* with other genera of Mastophoroideae in terms of reproductive attributes must be regarded with caution since further detailed developmental studies are required for the type species of all of the other genera. According to Johansen (1976, p. 238, Table 2), the seven other genera of Mastophoroideae conform to a 'SUR' pattern of tetrasporangial conceptacle development (Table 2, pattern 5). This contrasts with both *Mastophora* (Table 2, pattern 6) and *Lithoporella* (Table 2, pattern 4). Once additional data are available for the type species of the other genera, generic and suprageneric delineations may become clearer among the non-geniculate Corallinaceae as a whole.

Information on sexual conceptacles for genera of Mastophoroideae is too fragmentary to permit thorough comparisons. Male conceptacles in *Mastophora* and *Lithoporella* differ from one another in certain respects, but are uniform with respect to the mode of origin of spermatangial initials, the (non-)occurrence of a protective layer, the mode of roof formation, and the arrangement of spermatangial progenitor cells—four features considered significant by Lebednik (1978, p. 392). Lebednik (1978, p. 392) notes variation among genera of Mastophoroideae but, except for *Fosliella*, the data are based only on single studies.

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THE GENUS *SCHMITZIELLA* BORNET ET BATTERS (RHODOPHYTA): CORALLINACEAE OR ACROCHAETIACEAE?

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Examination of a wide range of specimens of *S. endophloea* Bornet et Batters including the type, has shown that the species, the type of the genus *Schmitziella* Bornet et Batters, is similar vegetatively to members of the Acrochaetiaceae. Because it bears zonate tetrasporangia, which have not been recorded for this family, and because the presence of carposporophytes described by Batters has not been confirmed, we regard the genus as incertae sedis but close to the Acrochaetiaceae. It is suggested that further studies may show that it has a heteromorphic life history. *S. endophloea* does not possess any of the characteristic features of the Corallinaceae such as cells with calcified walls, secondary pits or cell fusions, multiaxial thallus construction or tetraspores produced by simultaneous division.

The description of the only other species, *S. cladophorae* V. J. Chapman, is shown, in our opinion, to have been based on a misidentification of *Melobesia membranacea* (Esper) Lamour.

Bornet & Batters (in Batters, 1892a) established the genus *Schmitziella* and the species *S. endophloea* Bornet et Batters for an endophyte growing between the outer layers of the cell wall of *Cladophora pellucida* Kuetzing. The diagnosis was published jointly but the rest of the account was prepared by Batters and based on specimens in hand from several localities in the British Isles together with information obtained from Bornet and from Schmitz on presumably conspecific specimens from the northern shores of France. Batters (1892a, p. 193, last paragraph) apparently never actually examined Bornet's plants, and no Bornet specimens of *S. endophloea* are now present in the Batters herbarium in BM.

Among the distinctive features of *S. endophloea* enumerated by Batters (1892a) and generally evident in the illustrations are the following:

(1) The thallus is noncalcareous, endophytic, and contains two types of filaments—those composed of long cylindrical cells and those composed of very irregularly shaped cells;
(2) The reproductive structures are borne in "nemathecial sori" in which the roof is formed largely by the locally uplifted outermost cell wall layer of the host *Cladophora*.

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Batters described what he considered to be sporangial and cystocarpic sori. In the British specimens, the "sporangial sori" contained bisporangia, but Bornet (see Batters, 1892a, p. 191, legend for fig. 11) reported tetrasporangia with zonately divided contents in French specimens and sent Batters a sketch (Batters, 1892a, fig. 11). The presumed "cystocarpic sori" contained undivided sporangia which Batters interpreted as carposporangia. Batters (1892a, p. 191) noted that the two types of sori were similar and sometimes difficult to tell apart. Even though it appeared to be well separated from other genera in the family, Batters (1892a, p. 193) was nevertheless firmly convinced that *Schmitziella* belonged to the Corallinaceae. Subsequently, Foslie (1903, p. 25) placed *Schmitziella* in its own "group" of Corallinaceae and later Svedelius (1911) established Foslie's "group" as a distinct tribe. More recently Johansen (1969, 1981) elevated *Schmitziella* to its own subfamily within the Corallinaceae.

Suneson (1944), recognizing the incompleteness of the account of carposporophyte development provided by Batters, undertook a further detailed study of *S. endophloea* but failed to find any sexual material and recorded only bisporangial sori. He provided some additional drawings of the vegetative thallus and of sori and noted the absence of epithallial cells. Suneson, like Batters, referred *Schmitziella* to the Corallinaceae.

Prior to 1946, *Schmitziella endophloea* was recorded only from western Europe and northern Africa. Then Chapman (1946, p. 111, footnote) reported the species (as *Smitziella*) from New Zealand. Later, however, he (Chapman, 1951) described the New Zealand material as a distinct species, *S. cladophorae*. He provided few details in his protologue and did not compare *S. cladophorae* and *S. endophloea* except to state that *S. cladophorae* appeared to be restricted to *Cladophora feredayi* Harvey while *S. endophloea* appeared to occur only in *C. pellucida*. No further species of *Schmitziella* have been described, nor have detailed or comparative morphological/anatomical accounts of the two species been published.

Since 1968, the taxonomic affinities of *Schmitziella* have become shrouded with uncertainty. Some authors (e.g. Ardré, 1970; Bressan, 1974; Cabioch, 1972; Dixon & Irvine in Parke & Dixon, 1976; Guiry, 1978a; Johansen, 1981; Lebednik, 1977; Lemoine, 1970) have retained *Schmitziella* within the Corallinaceae (Order Cryptonemiales). Denizot (1968, pp. 205, 206) also retained *Schmitziella* within the Corallinaceae but quoted J. Feldmann's unpublished suggestions that the genus may not be corallinaceous and that it more closely resembled some taxa previously ascribed to the Squamariaceae (Order Cryptonemiales); subsequently, Chapman & Parkinson (1974) transferred *Schmitziella* to the Squamariaceae. [Denizot (1968, p. 308) showed that this name is illegitimate; the family was redefined and named Peyssonneliaceae by him.] Other authors (e.g. Adey & Johansen, 1972; Chamberlain, 1978; Johansen, 1972, 1976) have also felt that *Schmitziella* may not belong to the Corallinaceae, but none has suggested any other family to which the genus could be assigned. Indeed, Johansen (1976, pp. 225, 232) excluded *Schmitziella* from detailed consideration in his review paper on generic concepts in the Corallinaceae, but referred it to a group of poorly known or unclearly understood genera. A list of general references to the taxonomy of *Schmitziella* is included in Table II.

The present study was initiated while the first author was examining collec-

tions of Corallinaceae at the British Museum (Natural History), London, in May 1980. Preliminary inspections of Batters's original material of *S. endophloea* (the type species of *Schmitziella*) and of specimens collected more recently by the second author resulted in establishing the hypothesis that *S. endophloea*, and thus *Schmitziella*, belongs to the Acrochaetiaceae (Order Nemaliales) rather than to the Corallinaceae (Order Cryptonemiales). The investigation has since been extended to embrace a study of both described species of *Schmitziella*. Specific objectives included (1) ascertaining whether attributes of the vegetative thallus agree more closely with those of taxa in the Acrochaetiaceae or with those of taxa in the Corallinaceae; (2) examining critically the reproductive morphology and anatomy, especially with respect to the so-called "conceptacles" and "nemathecia" and "sexual" structures; and (3) assessing the taxonomic status and affinities of *Schmitziella* and its included species.

MATERIALS AND METHODS

Data were obtained from the type specimens and other collections gathered originally in England, France, and New Zealand which currently are housed at AKU, BM, CHR, LTB or PC (Table I). Microtechnique procedures follow Woelkerling (1980) and a representative set of permanent slides from all collections examined has been retained at LTB. Measurements quoted include the cell walls as in most cases the protoplasts of dried specimens were distorted. Liquid preservation procedures for recently collected material follow Parsons (1980). Scanning electron microscopy procedures are outlined by Woelkerling (1978) and herbarium abbreviations are taken from Holmgren & Keuken (1974, 1977).

TABLE I. Specimens of *S. endophloea* and *S. cladophorae* examined during this study

Schmitziella endophloea	
BRITISH ISLES:	
Devon:	Plymouth, xii. 1980, Boalch (LTB 12162) Torbay, no date (BM, M. Wyatt, Algae Danmonienses, No. 193); Torquay, viii. 1883, Boning (BM); viii. 1885, Batters (BM, 1 lectotype and 2 isotypes)
Dorset:	Kimmeridge, 26.ii.1981, Farnham (LTB 12163)
Gwynedd:	Bangor, ix. 1895, Phillips (BM, Holmes, Algae Britannicae Rariores Exsiccatae, Fasc. VIII, No. 192); Puffin Island, vi. 1890, Batters (BM); vi. 1890, Murray (BM)
Isle of Man:	Isle of Man, iii. 1865, Mrs R. (BM)
Co. Wexford:	Kilmore Quay, viii. 1969, D. Irvine (BM)
Co. Down:	Ardkeen, ix. 1975, O. Morton (BM; BEL F 957)
FRANCE:	Cherbourg, 29. iii. 1854, Bornet (PC); 13.x.1856, Bornet (PC); undated, Bornet (BM: Schmitz slides)
Schmitziella cladophorae	
NEW ZEALAND:	Stewart Island (Ringa Ringa), 1.i.1946, Lindauer (AKU 6858); 9.i.1946, Lindauer (AKU 6951); 11.i.1946, Lindauer (AKU 6981); 15.i.1946, Lindauer (AKU 7047, neotype). All specimens presently are filed under the host species, *Cladophora feredayi*

OBSERVATIONS AND DISCUSSION

Schmitziella endophloea

TYPIFICATION; DISTRIBUTION

Bornet & Batters in Batters (1892a) based the protologue primarily on plants collected from Torquay and Puffin Island but did not specify a holotype. Un-

numbered host plants from both localities are preserved at **BM** and in 1972 the material in one of the four Torquay host specimens, representing a number of individuals of *S. endophloea*, was chosen as lectotype (Fig. 1) by the second author. In addition to the dried material, eight permanent slides (**BM** 10252–**BM** 10259) of Torquay material prepared by Batters also exist and these are considered to constitute part of the lectotype.

S. endophloea has been recorded in the literature from various localities in western Europe and northern Africa (Table II). The New Zealand report (Chapman, 1946) really refers to *S. cladophorae*. The record of *S. endophloea* from the Gulf of Naples (Funk, 1927, p. 428) was considered dubious by Suneson (1944, p. 240), but subsequently Funk (1955, p. 96) stated that re-examination of the relevant specimens was not possible. Consequently, Funk's records have not been included in Table II. Most accounts mention *Cladophora pellucida* as the only host, but Hamel & Lemoine (1953) also list *Cladophora rupestris* Kuetzing and *Bornetia secundiflora* (J. Agardh) Thuret as hosts. Gillham (1954, p. 221) states that *Schmitziella endophloea* also occurs on *Chaetomorpha*, *Ahnfeltia*, *Laurencia* and other algae, but these records are probably based on misidentification of the epiphyte(s) present.

THE PROSTRATE SYSTEM

The general morphological features described and illustrated by Batters (1892a) and by Suneson (1944) are evident in the type collections and in the other specimens examined, but a number of new observations and interpretations have emerged during the present study, leading to the conclusions that *S. endophloea* plants are heterotrichous and that data on vegetative tissues published by Batters (1892a) and by Suneson (1944) pertain largely to the prostrate system.

The prostrate system comprises most of the vegetative thallus and consists of axes and laterals. Axes [referred to as primary filaments by Batters (1892a) and Suneson (1944)] usually are composed of elongate, more or less cylindrical cells 14–110 μm long and 4–14 μm in diameter (Figs 2–6). Sometimes, however, cells become more irregular in shape (Figs 2, 6). All axial cells measured were at least 2·5 diameters long and most were 5–16 diameters long. Axes are readily recognizable even under conditions of extreme crowding because of their elongate cells and their obviously filamentous appearance.

Two types of branch systems can develop from axes. In one, the filaments possess a morphology identical to that of the parent axis and generally are indistinguishable from it. Accordingly, these filaments also are considered as axes. Once such filaments arise, they may grow parallel to and appressed to the parent axis (Figs 3, 5), resulting in two to five or more axes [Suneson (1944) reports up to 15] developing in laterally conjoined series. In other cases, new axes diverge from the parent axis (Fig. 4) and either join with other parallel series of axes or remain solitary. The end result of such branching is a more or less reticulate system of clearly filamentous axes developing between cell wall layers of the host plant.

The second type of branch system involves production of divaricate laterals [referred to as secondary filaments by Batters (1892a) and Suneson (1944)]

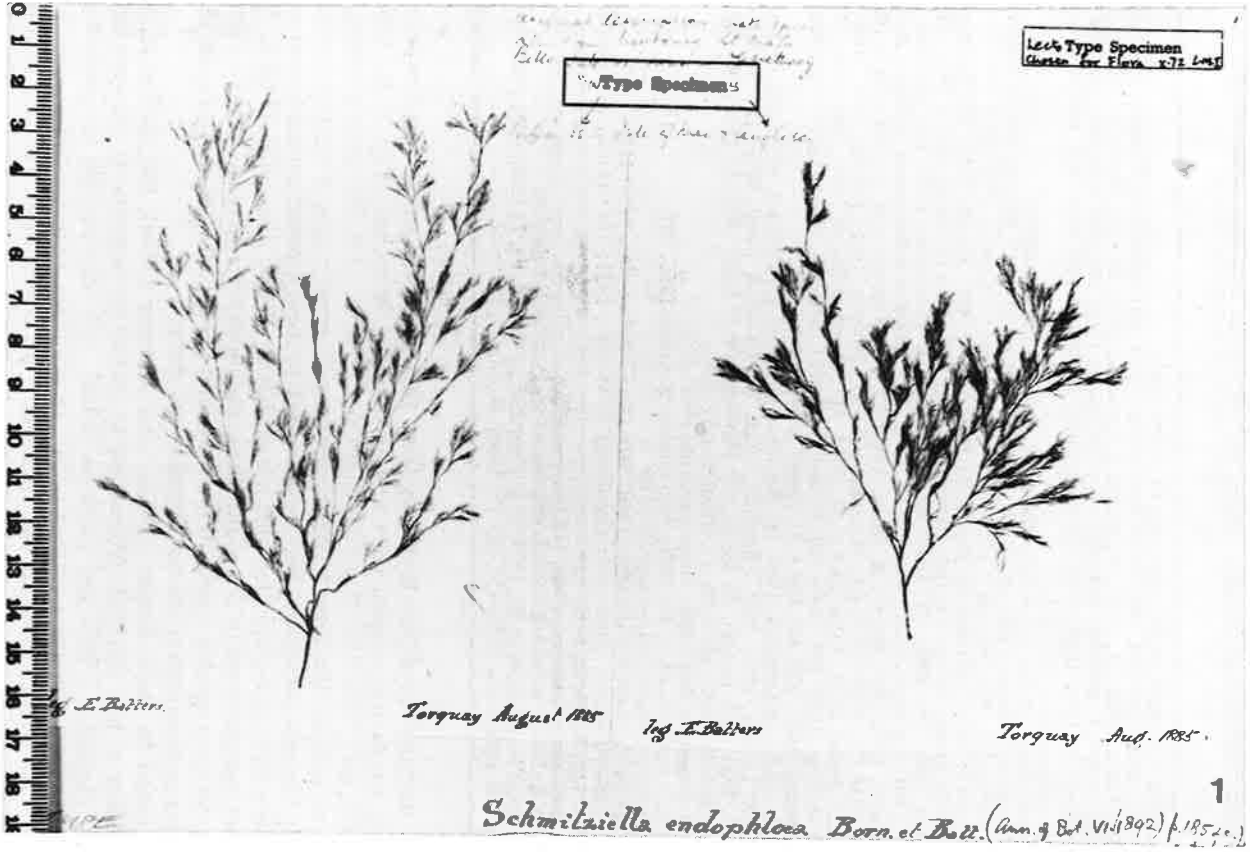


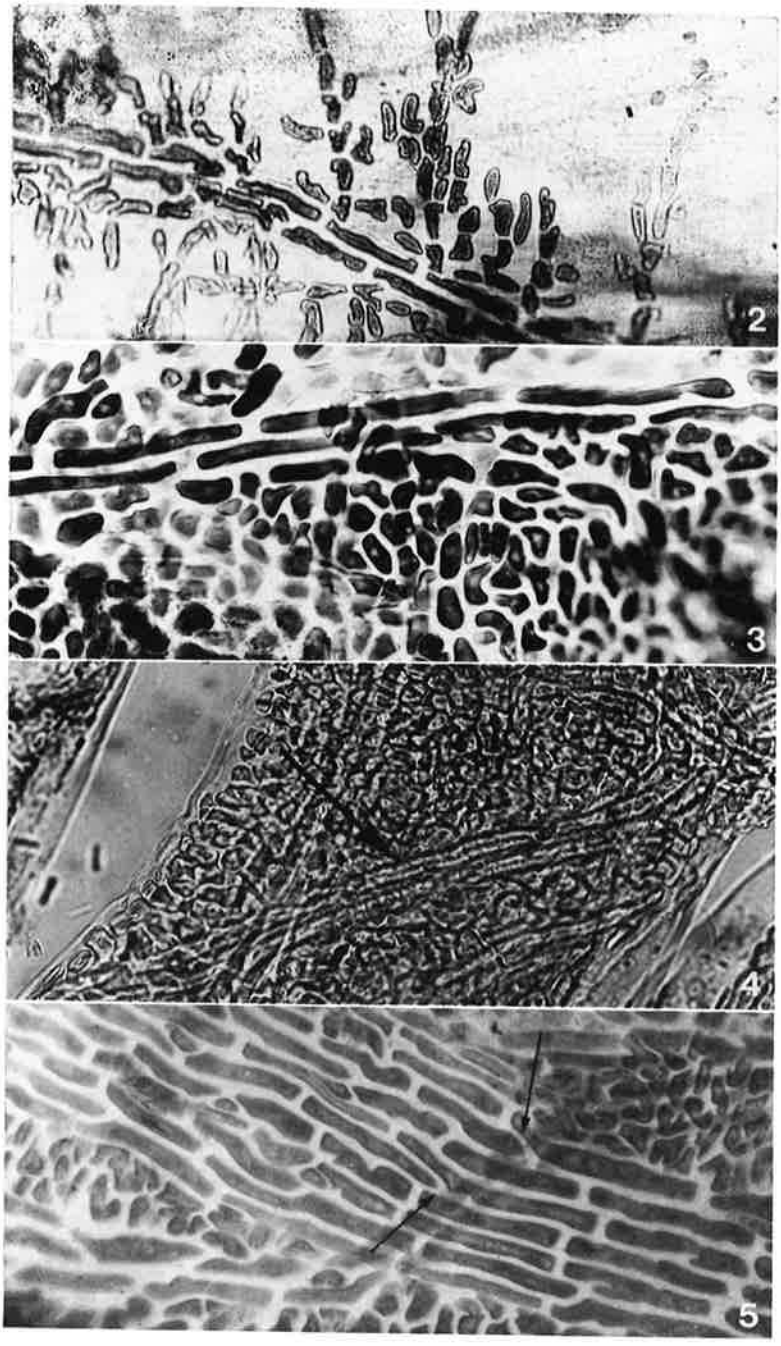
FIG. 1. Lectotype (right) and isotype specimens of *Schmitziella endophloea* Bornet & Batters on host at BM ×0·56.

TABLE II. Summary of general references on *Schmitziella* and of published records for the geographic distribution of included species. Not all records have been confirmed and some (e.g. Gillham 1954) probably represent misidentifications

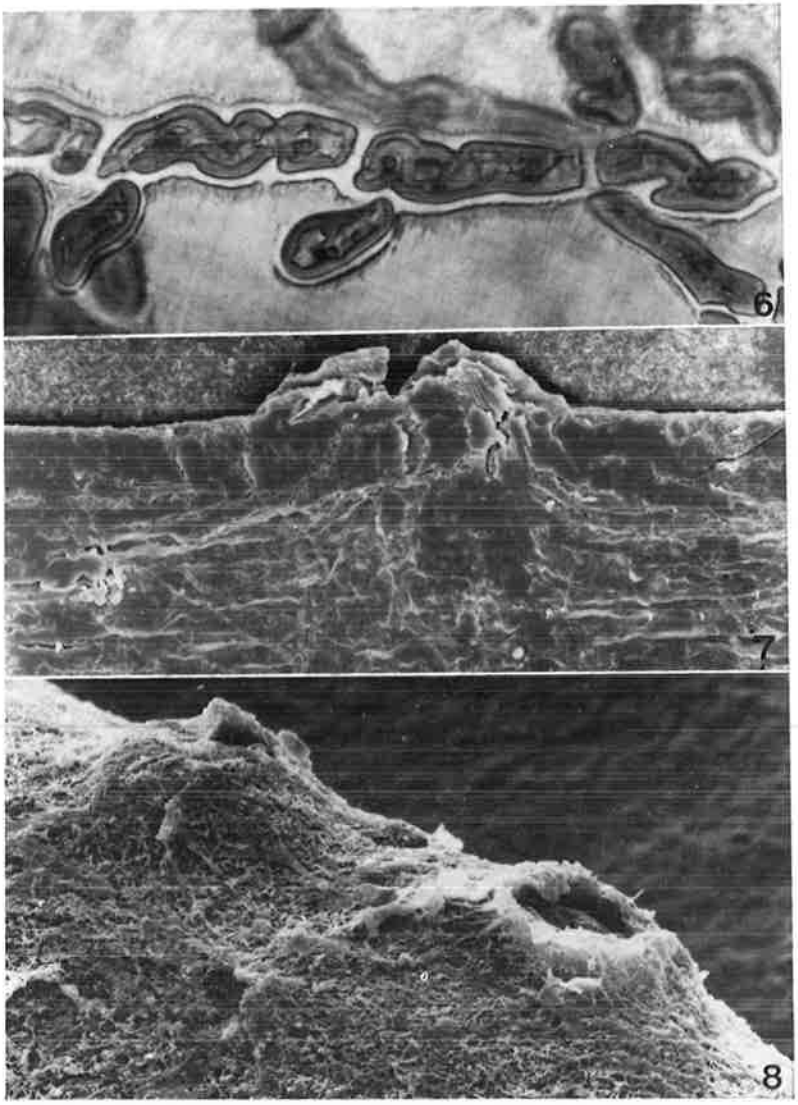
(A) General references on the taxonomy of *Schmitziella*
Cabioch, 1972: 243–245, 264, 268; Chamberlain, 1977: 68; 1978: 232; Denizot, 1968: 39, 205, 206; Foslie, 1903: 25; 1904: 10; Hamel & Lemoine, 1953: 28, 116; Heydrich, 1900: 313; Johansen, 1969: 43, 46; 1976: 225, 232; 1981: 11; Kylin, 1956: 204, 209; Lebednik, 1977: 381; Mazza, 1916–22: 1075, 1080; 1917: 79, 84; Schmitz & Hauptfleisch, 1897: 539, 541; Suneson, 1944; Svedelius, 1911: 264, 265.
(B) *S. endophloea*: published records relating to geographic distribution
BRITISH ISLES—Adams, 1908: 52; Anon., 1894: 63; Anon., 1952: 45; Batters, 1892a: 185–193, pl. 10; 1892b: 22; 1902: 96; 1907: 110; Burrows, 1963: 246; Chapman, 1934: 233; 1937: 248; Cotton, 1912: 101; Cullinane, 1973: 36, 97; Davey, 1953: 420; Dixon, 1959: 68; (Gillham, 1954: 221?); Guiry, 1978b: 34, 164; Harvey–Gibson, 1891: 116, 127 (nom. nud.); 1913: 141; Herdman, 1891: 26; 1896: 52; 1897: 427; Herdman & Thompson, 1903: 164; Holmes & Batters, 1891: 101 (nom. nud.); Irvine et al., 1972: 134; Johnson & Hensman, 1899: 25; Jones & Williams, 1966: 319; Knight & Parke, 1931: 52, 102; Lemoine, 1912: LIII; 1913: 142; Mazza, 1916–22: 1080; 1917: 84; Morton, 1974: 35; Newton, 1931: 298, fig. 185; Norton, 1970: 265; Parke, 1935: Table after p. 32; 1953: 511; Parke & Dixon, 1964: 508; 1968: 790; 1976: 534; Rees, 1929: 282; 1935: 129; Russell, 1968: 581; Scannell, 1969: 197; Sinclair, 1949: 173; Suneson, 1944: 239–245, figs 1–2; Tittley & Price, 1978: 511.
FRANCE—Adey & Lebednik, 1967: 36; Belsher et al., 1976: 57; Cabioch, 1972: 155; Chalon, 1905: 203; Debray, 1899: 162; Feldmann, 1954: 79; Hamel & Lami, 1931: 32; Hamel & Lemoine, 1953: 116, text-fig. 82–83, pl. 23; Lemoine, 1912: LIII; 1921: 9; 1931: 206, 207; Mazza, 1916–22: 1080; 1917: 79, 84; Mouret, 1911: 106.
ITALY—Giaccone, 1969: 505; Giaccone et al., 1972: 223.
PORTUGAL—Ardré, 1970: 91; 1971: 561; Ginsburg–Ardré, 1966: 357.
MADEIRA ARCHIPELAGO—Levring, 1974: 68.
ALGERIA—Feldmann & Feldmann, 1940: 460; Hamel & Lemoine, 1953: 116.
MOROCCO—Dangeard, 1949: 153; Gattefosse & Werner, 1935: 101; Hamel & Lemoine, 1953: 116; Raphelis, 1929: 729.
NEW ZEALAND—Chapman, 1946: 111 (as *Smitziella*).
(C) *S. cladophorae*: published records relating to geographic distribution
NEW ZEALAND—Adams et al., 1974: 218; Chapman, 1951: 84, fig. 1; 1956: 477; 1961: 351; Chapman & Parkinson, 1974; 157, fig. 47; South & Adams, 1976: 42.

whose morphology differs markedly from that of axes. Laterals are composed of very irregularly shaped cells and usually are branched (Figs 3–5). Cells generally vary from 6 to 25 μm in length and from 6 to 12(–16) μm in diameter; nearly all cells are less than 2·5 diameters long. Normally cells of various laterals quickly become contiguous with one another to form a pseudoparenchymatous layer in which individual filaments are no longer clearly discernible (Figs 3, 5). In more mature areas of the plant, these pseudoparenchymatous regions completely fill the available spaces in the reticulum produced by major axes and the prostrate system appears to be a continuous sheet.

As noted by both Batters (1892a) and Suneson (1944), the thallus of *S. endophloea* is not calcified. Moreover, as noted by Schmitz & Hauptfleisch (1897), Heydrich (1900) and Suneson (1944), cells comparable to epithallial cells of the Corallinaceae do not occur. In addition, cells are linked only by primary pit connections. Neither secondary pit-connections nor cell fusions could be found, a further contrast to the Corallinaceae in nearly all taxa of which one or both occur consistently. Two further points require emphasis. Thallus growth is uniaxial with most cell divisions occurring either within apical cells or in association with branch initiation (Fig. 2). There is no indication of multiaxial development or of the presence of multicellular meristems typical of the



FIGS 2–5. Prostrate system morphology. Fig. 2. Young plant showing axes and laterals. LTB 12162 ×375. Fig. 3. Older plant in which laterals have become pseudoparenchymatous. LTB 12162 ×363. Fig. 4. Prostrate system of lectotype specimens. Note axes (arrow). BM Slide 10252 ×363. Fig. 5. Branching of filaments (arrows) in a conjoining series of axes. LTB 12162 ×400.



FIGS 6–8. Chloroplasts and host wall morphology. Fig. 6. Chloroplasts in prostrate system cells. LTB 12162 ×570. Fig. 7. Scanning electron micrograph of wall rupture in *Cladophora* host cell of the lectotype specimen. BM ×500. Fig. 8. Scanning electron micrograph of wall rupture in recently collected host material. LTB 12162 ×475.

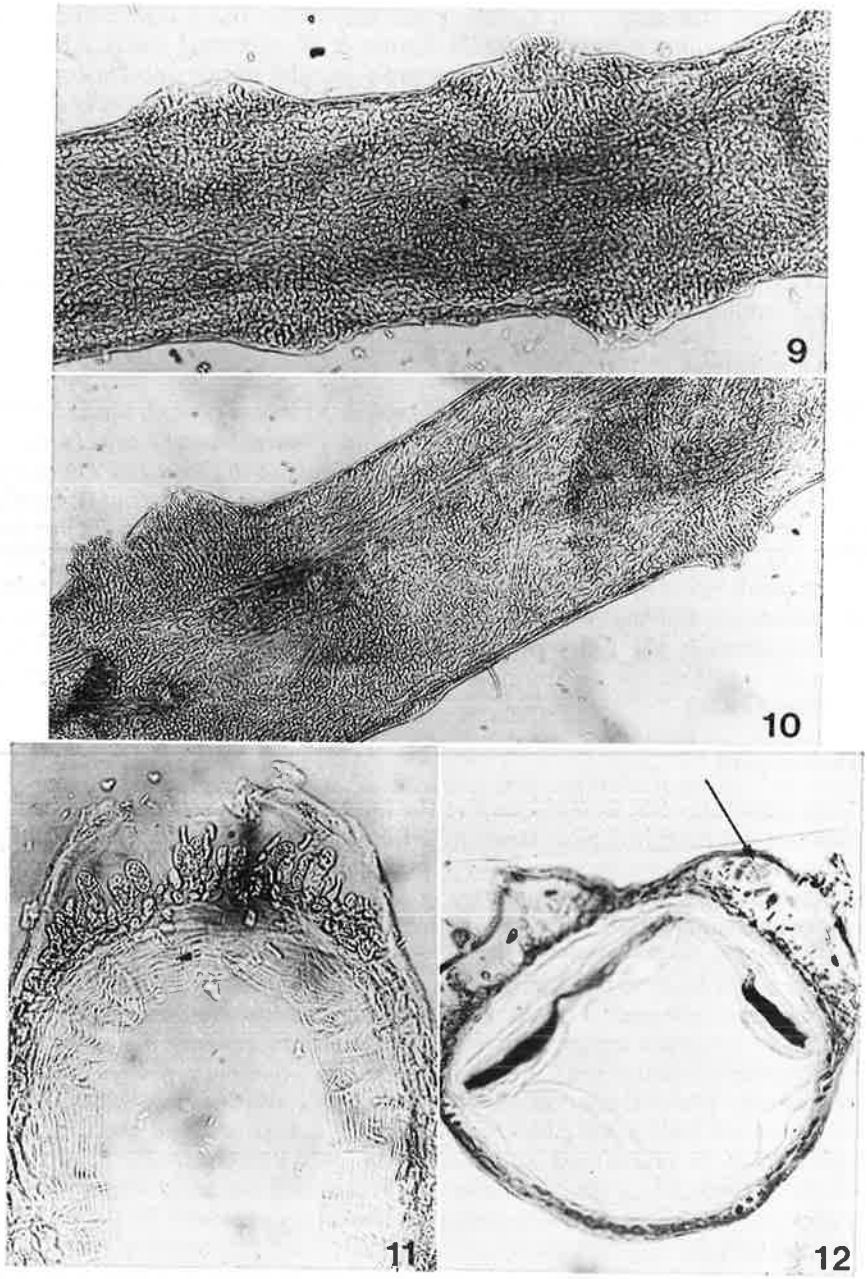
Corallinaceae (for details on Corallinaceae meristems and a discussion of the genus *Schmitziella* see Cabioch, 1972; Turner & Woelkerling, 1982). Although major axes in *S. endophloea* plants may grow parallel to one another for short distances, no definable multicellular meristem occurs and axes generally diverge from one another or become parallel to one another in a completely irregular manner. Finally, cells of *S. endophloea* filaments each contain a single, parietal, lamelliform, irregularly lobate chloroplast which rarely may become fragmented into several parts and which apparently lacks pyrenoids (Fig. 6). In irregularly-shaped cells, the chloroplast appears to line nearly the entire periphery of the cell cavity (Fig. 3). Chloroplasts of this type apparently have not been reported for the Corallinaceae.

THE ERECT SYSTEM

Filaments of the erect system of *S. endophloea* seldom exceed 60 μm in length, almost always are unbranched and rarely contain more than five cells (Figs 11, 14, 15). Most cells are more or less cylindrical to ovoid in shape but sometimes can be more irregular. Terminal cells in some cases become attenuate distally (Fig. 15). Most cells are 1–4 diameters long with cell lengths of 5–22 μm and cell widths of 3–8 μm. Protoplasts of successive cells within a filament are joined by very small primary pit connections. Each cell contains a single chloroplast with a structure like that found in each cell of the prostrate system. When erect filaments develop, the cell wall of the host *Cladophora* becomes uplifted and eventually ruptures, usually during the course of spore production by the endophyte (see below).

REPRODUCTION

Most accounts of *S. endophloea* give the impression that reproduction occurs within distinct morphological structures. Results obtained in the present study, however, have led to the conclusion that conceptacles, nemathecia etc., of distinctive and consistent morphology do not occur. Instead, the sporangia are borne on filaments which are part of the erect system of the heterotrichous thallus. Erect filaments develop only in localized patches and, wherever such development occurs, it leads to the uplifting and eventual rupture of the outer layer of the *Cladophora* cell wall. Usually the uplifted wall forms an irregularly frusto-conoidal to domoidal bulge (Figs 7–10) sometimes resembling the conceptacle roofs in some nongeniculate Corallinaceae (e.g. see Chamberlain, 1978; Garbary & Veltkamp, 1980; Turner & Woelkerling, 1982; Woelkerling, 1980). These *Cladophora* cell wall bulges, however, form as a consequence of erect filament production in *S. endophloea* and thus occur only coincidentally in areas of potential *S. endophloea* spore production. Protruding conceptacle roofs in the Corallinaceae, in contrast, are multicellular structures produced by the coralline plant, and they develop specifically as an integral part of the reproductive process. Furthermore, the localized uplifted wall portions of infected *Cladophora* cells eventually rupture in a haphazard fashion (Figs 7, 8, 10) whereas conceptacles of Corallinaceae normally do not rupture to release spores because they possess pores which form in a consistent, defined manner. Batters (1892a, p. 192, pl. 10, figs 12–13) described what he considered to be carpogonial branches and mature

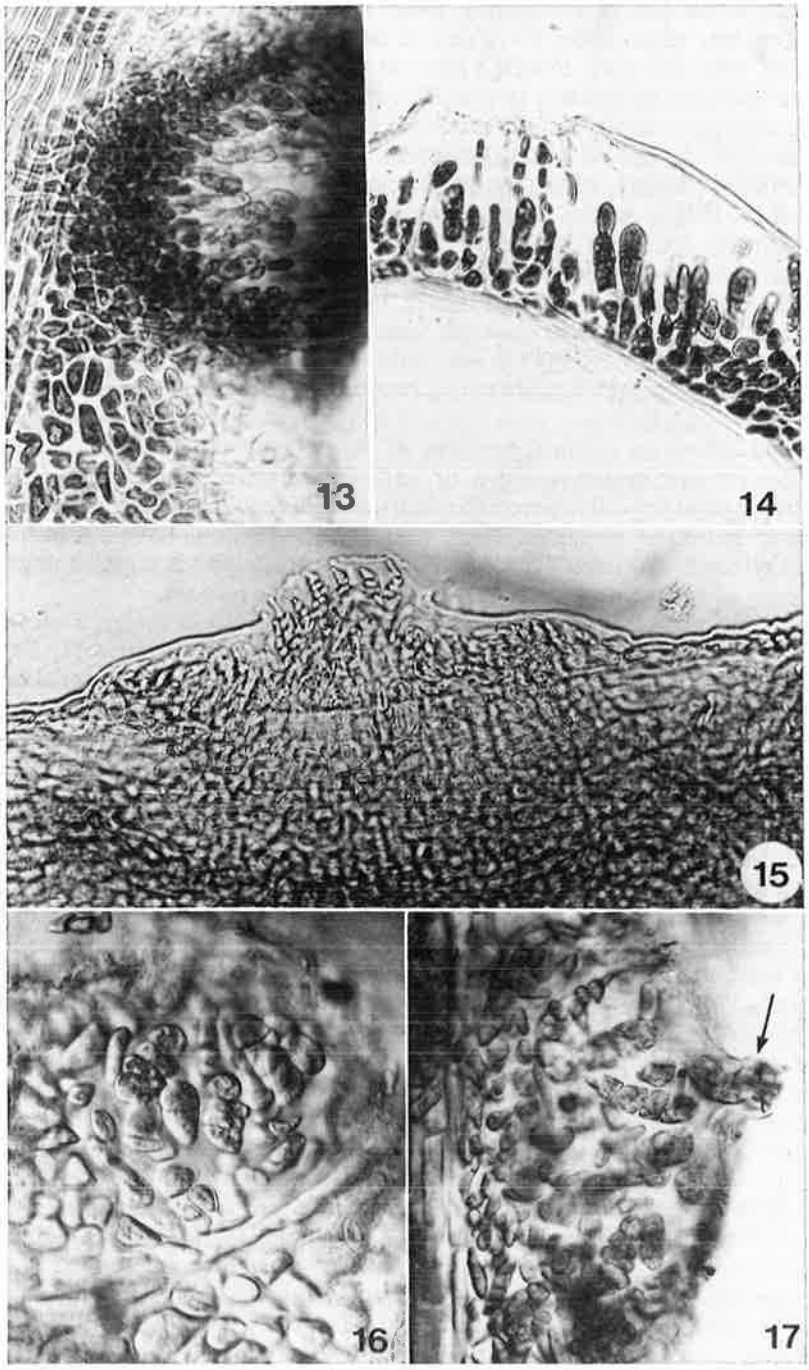


FIGS 9–12. Erect system. Figs 9–10. Wall protuberances of various shapes and erect filaments in the lectotype element of *S. endophloea*. BM Slide 10252 ×90. Fig. 11. Transverse section of host showing erect filaments and bisporangia beneath ruptured host wall of lectotype. BM slide 10257 ×240. Fig. 12. Transverse section of Bornet specimen of host showing bisporangium (arrow) and erect filament cells. PC ×180.

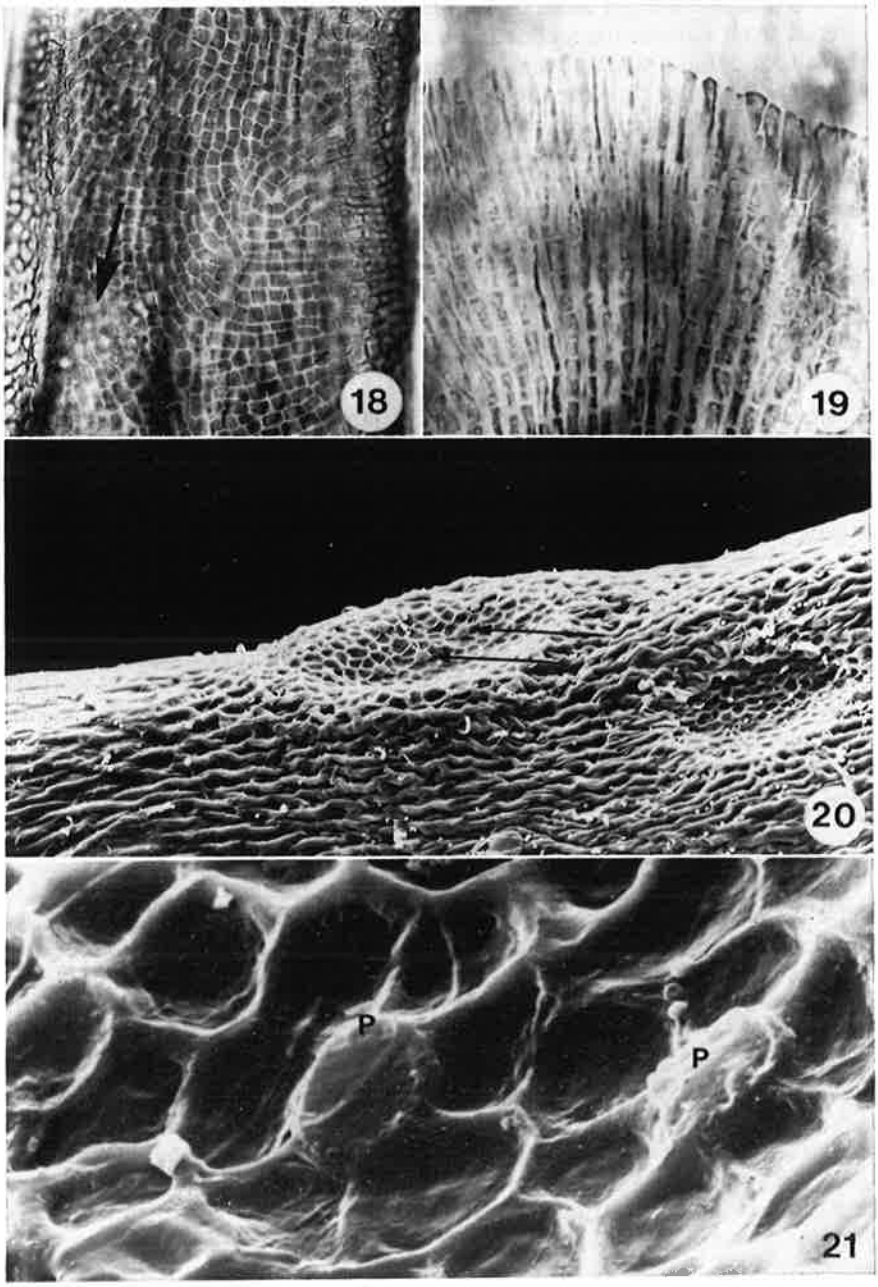
cystocarps. Structures resembling those illustrated by Batters could not be found on any of his slides or in any of the other material examined. Suneson (1944, p. 240), regarded Batters's account as unsatisfactory in this respect, and we consider it to be rather questionable for several reasons. Firstly, Batters may have misinterpreted the distally attenuate terminal cells commonly seen on erect filaments as carpogonia with trichogynes. He illustrated such cells in both his bisporangial (Batters, 1892a, fig. 9) and presumed carpogonial (fig. 12) sori and himself (p. 191) expressed concern over the difficulty of making such a distinction. Similar cells (fig. 15) occurred in one otherwise sterile group of erect filaments on one of Batters's slides. Secondly, fig. 13 showed what he considered to be a nearly mature carposporophyte, but he provided no developmental details. Structures of this sort were not seen in this study. A letter dated 4 August 1891 from Bornet to Batters (in **BM**) indicates that Bornet had rejected several earlier drawings sent by Batters to him because they did not show the distinguishing features with sufficient precision and it is clear that they found it difficult to reach agreement on the interpretation of the structures they saw. It is possible that Batters saw monosporangia or undivided tetra or bisporangia on some aberrantly enlarged cells of erect filaments, but this could not be confirmed from a reexamination of his slides. Thus, Batters's observations have not been confirmed either by Suneson (1944) or during this study and it remains uncertain what sort of sexual structures, if any, occur in *S. endophloea*.

The reproductive structures most commonly observed in the type specimens and in other collections of *S. endophloea* were bisporangia (Figs 11, 12, 14). These sporangia either occurred directly on cells of prostrate filaments or terminated one to three celled erect filaments and were (14–)16–25(–33) μm long and 8–11(–14) μm in diameter. Not all groups of erect filaments contained bisporangia; when they did, sporangia occurred in a scattered fashion within each erect filament group. Both Batters (1892a, p. 191) and Suneson (1944, p. 242) mention a central group of sterile filaments (which they term paraphyses) surrounded by a number of fertile ones. Such an arrangement was not found in type collection plants (Fig. 11) or in other specimens (Figs 12–14) examined and, indeed, one of Suneson's illustrations (1944, p. 243, fig. 2B) shows typical scattered sporangia. Thus, the distinction between fertile filaments and paraphyses seems misleading and is not used here.

Batters (1892a, p. 191, fig. 11) also reported the occurrence of zonately arranged tetraspores in Bornet's specimens from Cherbourg. Apparently Batters never saw Bornet's plants but based his record on a sketch sent by Bornet (Batters 1892a, p. 194, legend to fig. 11). The Bornet-Thuret herbarium in **PC** contains two Cherbourg collections identified as *S. endophloea* (see Lemoine, 1911, p. LIII). Mica mounted fragments apparently prepared by Bornet from both collections have been examined and several additional dried fragments from both collections have been embedded and sectioned during this study. Although plants of *S. endophloea* are abundant in these samples and a number of patches of erect filaments enclosed by *Cladophora* wall protuberances were seen, tetrasporangia (zonate or otherwise) were not found. A few bisporangia (Fig. 12) were observed, however, and several *Cladophora* wall protuberances also contained some detached unicellular spores. Whether these latter were monospores or separated bispores remains uncertain.



FIGS 13–17. Erect system and sporangia of *Schmitziella endophloea*. Fig. 13. Surface view of a patch of erect filaments producing bisporangia. LTB 12162 ×275. Fig. 14. Transverse section of host showing erect filaments and bisporangia. LTB 12162 ×275. Fig. 15. A sterile group of erect filaments with attenuate terminal cells in lectotype plants. BM, Batters slide 10252 ×250. Fig. 16. Surface view of a mixed group of bisporangia and tetrasporangia in Cherbourg material prepared by Schmitz. BM, Schmitz slide 332 E ×325. Fig. 17. A group of erect filaments containing all tetrasporangia from the same plant shown in Fig. 16. Note sporangium near point of host wall rupture (arrow). BM, Schmitz slide 332 E ×375.



FIGS 18–21. "*Schmitziella cladophorae*", Figs 18–19. Prostrate system in neotype plants of "*Schmitziella cladophorae*". Fig. 18. Parallel rows of vegetative filaments. Note cell fusion (arrow). AKU 7047 ×325. Fig. 19. Tips of vegetative filaments forming a multiaxial meristem. AKU 7047 ×350. Figs 20–21. Reproduction in neotype specimen of "*Schmitziella cladophorae*". Fig. 20. Tetrasporangial conceptacles. Note position of pores (arrows). AKU 7047 ×295. Fig. 21. Two pores in roof of tetrasporangial conceptacle with tetrasporangial plugs (P) still blocking the ostioles. AKU 7047 ×2980.

In addition to the Bornet specimens in PC however, the Schmitz slide collection in BM contains eight slides of *S. endophloea* prepared (in 1891) from Bornet's material from Cherbourg (collection date not specified). Several fragments on these slides contain a number of regularly or obliquely zonate tetrasporangia (Figs 16–17) similar to those illustrated by Batters (1892a, fig. 11). Some of the tetrasporangia (length 25–40 μm; diameter 11–19 μm) appear to be associated with groups of erect filaments of *Schmitziella* within the *Cladophora* cell wall bulges, although none could be seen to be definitely attached to the *Schmitziella* filaments. In several cases bisporangia occurred in the same erect filament group as the tetrasporangia (Fig. 16), suggesting that the divisions are sequential rather than simultaneous as in the Corallinaceae (see Guiry, 1978a, p. 121). Batters (1892a, p. 193) made no mention of the Schmitz slides, which appear to contain the only extant tetrasporangial material collected prior to that time. Tetrasporangia were also reported by Feldmann & Feldmann (1940) from Algeria, but this record has not been confirmed.

Denizot (1968, p. 206) noted that one illustration (Newton, 1931, p. 298, fig. 185c) showed a sporangium with seemingly cruciately divided contents. Such sporangia were not seen in any of the specimens examined during the present study; since Newton provided no further information in the text and did not indicate the source of her illustration, this record must be considered questionable. The only specimens known to us from the British Isles with tetrasporangia were collected in Co. Wexford (Kilmore Quay, 29.viii.1969, D. Irvine) and Co. Down (Ardkeen, 27.ix.1975, O. Morton).

The tetrasporangia are borne on the erect filaments, are similar in shape to those seen in the Schmitz slides but slightly smaller (17–23 $\times$ 8–11 μm), and typical bisporangia are associated with them. This suggests that the so-called bisporangia could be incompletely divided tetrasporangia. It is possible that the second division is usually followed immediately by spore release, so that the four-spore stage is rarely seen.

TAXONOMIC IMPLICATIONS

The results of this study of the type and other collections of *S. endophloea* provide a basis for reassessing the taxonomic affinities of this species and the status of *Schmitziella* as a genus. The doubts expressed by several previous investigators (e.g. Adey & Johansen, 1972; Chamberlain, 1978; Johansen, 1972, 1976) concerning the assignment of *S. endophloea* to the Corallinaceae have been substantiated and most evidence seems to indicate that *S. endophloea* has affinities with the Acrochaetiaceae as shown by a comparative analysis (Table III) of some salient morphological and anatomical characteristics of the two families and of *S. endophloea*. Although the presumed carposporophytes described by Batters (1892a) bear no resemblance to those of either the Corallinaceae or the Acrochaetiaceae, their occurrence has not been confirmed during this study and thus has not been taken into account in considering the affinities of *S. endophloea*. (It should be noted that sexual stages of most Acrochaetiaceae, however, also remain unknown, see Woelkerling, 1971.)

The occurrence of tetrasporangia with zonately divided contents in *S. endophloea* presents a more difficult problem. Such tetrasporangia are unknown

TABLE III. Characteristics of the Corallinaceae, the Acrochaetiaceae and *Schmitziella endophloea*, type species of *Schmitziella*

Character	Corallinaceae	Acrochaetiaceae	*Schmitziella endophloea*
Thallus calcification	Present	Absent	Absent
Type of thallus growth	Multiaxial	Uniaxial	Uniaxial
Epithallial cells	Present	Absent	Absent
Secondary pit connections	Present in some species	Absent	Absent
Cell fusions	Present in some species	Recorded for only 2 species*	Absent
Chloroplasts	1–many, irregularly shaped	1–many, of various shapes	1 parietal laminate chloroplast which may fragment
Conceptacles	Present	Absent	Absent
Fusion Cells	Present	Absent	Unknown

*See West (1970), Irvine et al. (1975).

in the Acrochaetiaceae and Papenfuss (1961) and Guiry (1978a, pp. 122–3) have questioned whether taxa (i.e. the monogeneric Wurdemanniaceae) with plants bearing such sporangia should be included in the Nemaliales, to which the Acrochaetiaceae usually is assigned. Moreover, although there are at least six families (Guiry, 1978a, table 1) in which both zonate and cruciate tetrasporangia occur, among which are certain genera (e.g. *Contarinia*—see Denizot, 1968; *Hildenbrandia*—see Denizot, 1968; *Schizymenia*—see Abbott & Hollenberg, 1976; *Sporolithon*—see Johansen, 1981) containing some species with cruciate and others with zonate tetrasporangia, these families are in the Cryptonemiales and Gigartinales. This situation led us to consider other taxa to which *S. endophloea* might be related with respect to both reproductive and vegetative features.

Genera combining a non-calcified, prostrate habit and zonate tetrasporangia include members of the Blinksiaceae, Cruoriaceae, Hildenbrandiaceae and Rhizophyllidaceae (see Abbott & Hollenberg, 1976; Denizot, 1968; Kylin, 1956) as well as some of uncertain systematic position (see Denizot, 1968). Most of these are encrusting algae for which gametangial phases were unknown for many years, although more recently several have been implicated in the life histories of larger erect algae (see Ardré, 1977). Nearly all these form distinct, compact crusts with a basal layer(s) of radiating filaments, and lack bisporangia; the totally different vegetative thallus shows no close affinity with that described for *Schmitziella*. The same is true for species of *Rhodophysema* (Cabioch, 1975; Fletcher, 1975, 1977) which have been referred to the Palmariales by De Cew (1981) and DeCew & West (1982) also reinterpreted reports of bisporangia.

Dixon (1973, p. 194) discussed various genera and species for which the products of germination of a carpospore are prostrate branch systems of varying degrees of aggregation and for which the term "*Hymenoclonium*-phase" has been used. *Schmitziella* has some morphological features in common with these entities, such as the divaricate nature of the lateral branching, but until recently none was known which produced zonate tetrasporangia or bisporangia. Thus, *Schmitziella* did not appear to be closely related to these taxa either, even though

it too may represent a phase in the life history of another genus. Guiry & Maggs (1982) have, however, reported zonate tetrasporangia in the *Hymenoclonium*-phase of *Meredithia* (*Kallymenia*) *microphylla* (J. Ag.) J. Ag. (Kallymeniaceae, Cryptonemiales).

At present, however, *S. endophloea* and thus the genus *Schmitziella* are taxa of uncertain affinity in which the vegetative system is like that of taxa assigned to the Acrochaetiaceae. Another feature common to both *Schmitziella* and at least some taxa of the Acrochaetiaceae is the occurrence of presumed bisporangia (see Guiry, 1978a; Woelkerling, 1971). Although the presence of zonate tetrasporangia precludes unequivocal assignment of *Schmitziella* to the Acrochaetiaceae, we suggest that for pragmatic reasons *Schmitziella* be listed as a genus incertae sedis next to that family. The ultimate taxonomic disposition of *Schmitziella* must await further studies, particularly those involving attempts to elucidate the life history in laboratory culture.

Schmitziella cladophorae

Chapman (1951) originally described *Schmitziella cladophorae* as "forming an expanded flattened plate one cell thick composed of radiating rows of cells within the wall of the host; non-calcareous; branching of cell rows dichotomous". He did not designate a type specimen, state a type locality or list the specimens he examined. Searches at **AKU**, **CHR** and **WELT**, moreover, have failed to disclose any material which Chapman identified as *S. cladophorae* or any collections of the host (*Cladophora feredayi*) which were annotated by Chapman as containing *S. cladophorae*. Consequently, verification of the original material upon which the protologue of *S. cladophorae* is based cannot be made with absolute certainty.

Chapman first mentioned the occurrence of *Schmitziella* in New Zealand in a footnote in the paper published in December 1946. The only New Zealand specimens of the stated host, *Cladophora feredayi* (Chapman, 1951), presently housed at **AKU** (where Chapman worked) which would have been available to him prior to December 1946 and which contain material that he could have interpreted as a species of *Schmitziella* are a series of four sheets in the Victor Lindauer collections (**AKU** 6858, 6851, 6981, 7047) from Stewart Island dated January 1946. Examination of all four sheets, however, has shown that the red alga present is *Melobesia membranacea* (Esper) Lamouroux.

Several features of these *Melobesia* specimens agree with the limited information provided by Chapman (1951) in the protologue of *Schmitziella cladophorae*. The vegetative parts of the thallus form an expanded flattened plate which appears to be one cell thick and composed of more or less radiating filaments of cells (Fig. 16). At the thallus margins, the filaments are terminated by a series of contiguous apical cells (Fig. 17) which resemble those present in protologue illustrations (Chapman, 1951, figs. 1a, b, d). Finally, the vegetative portions are not obviously calcified and the cell dimensions fall within the range of those calculated from protologue drawings.

Chapman (1951) and Chapman & Parkinson (1974) described *Schmitziella cladophorae* plants as parasitic within the cell walls of the host. In the Stewart Island specimens, however, the *Melobesia* plants definitely are pigmented and therefore presumably are not parasitic. Moreover, the *Melobesia* plants are

epiphytic and not endophytic, but, since most vegetative parts of the *Melobesia* specimens are less than 6 μm thick, careful examination is required to determine this.

Protologue information on reproduction is scant and the illustration is largely uninterpretable. Chapman (1951, p. 84) simply states: "reproductive bodies forming nemathecia within swollen protuberances". The Stewart Island *Melobesia* collections contain both cystocarpic and tetrasporangial plants (Figs 18–21). In unstained whole mounts the conceptacles are inconspicuous and vaguely resemble one of Chapman's illustrations (1951, fig. 1e); the conceptacle pores are not observed readily and thus easily could have been overlooked. In scanning electron micrographs, in contrast, the pores are more apparent (Figs 18–21).

Considering all of the above information, either of two different courses of action with respect to the taxonomic disposition of *Schmitziella cladophorae* seems possible. One would be to consider *S. cladophorae* as a species inquirenda. This course of action would result in continued recognition of *S. cladophorae* as a member of the New Zealand flora. The alternative would be to conclude that Chapman mistook plants of the common Corallinaceous epiphyte *Melobesia membranacea* for a species of *Schmitziella,* in which case material on one of the Stewart Island host specimens could then be designated as neotype of *Schmitziella cladophorae.* This course of action would result in removing *Schmitziella cladophorae* from consideration as an independent taxon and as a dubious name in the algal literature. This second course of action appears preferable. The choice of the Stewart Island material seems justified since it was readily accessible to Chapman when the protologue was written and the plants present show most of the features mentioned. The apparent discrepancies between the protologue information and the designated neotype material are probably due to the superficiality of the original investigation, as evidenced by the paucity of protologue data. The specimens on AKU 7047 are therefore chosen as neotype of *Schmitziella cladophorae* Chapman and *S. cladophorae* is regarded here as a heterotypic synonym of *Melobesia membranacea* (Esper) Lamouroux.

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Short Communication

AVICENNIA CANOPY EFFECTS ON MANGROVE ALGAL COMMUNITIES IN SPENCER GULF, SOUTH AUSTRALIA

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ABSTRACT

Beanland, W.R. and Woelkerling, Wm.J., 1983. *Avicennia* canopy effects on mangrove algal communities in Spencer Gulf, South Australia. *Aquat. Bot.*, 17: 309—313.

Studies of mangrove algal communities at eight localities in Spencer Gulf, South Australia, provide evidence that the presence or absence of an *Avicennia* tree canopy may influence the frequency distribution of algal species on pneumatophores. Certain algae occurred with significantly higher frequencies on pneumatophores beneath the canopy, while other species were significantly more frequent on pneumatophores beyond the canopy. The distribution of total algal cover, total algal biomass, and total species diversity, however, does not appear to be correlated with the presence or absence of a tree canopy.

INTRODUCTION

Based on studies of *Rhizophora mangle* L. dominated mangrove algal communities in Puerto Rico, Almodovar and Pagan (1971) concluded that algal diversity was greatest in shaded regions and that species of the red algal genera *Bostrychia*, *Caloglossa*, and *Catenella* were absent from sun-exposed regions of the community. The possibility that similar sun—shade effects occurred in *Avicennia marina* (Forsk.) Vierhapper dominated mangrove algal communities in Spencer Gulf, South Australia, became evident during the course of floristic studies in this region (Beanland and Woelkerling, 1982), and the hypothesis that the presence or absence of a tree canopy over the *Avicennia* pneumatophores influences the nature of the algal communities seemed worthy of further investigation. Thus, while collecting floristic information on Spencer Gulf mangrove algae, some additional data were obtained from eight localities (Fig. 1) to determine whether marked differences occurred in the species frequency, cover, biomass and/or total diversity in algal communities on pneumatophores situated underneath the *Avicennia* canopy as opposed to pneumatophores situated beyond the canopy along the seaward margin of each mangrove community.

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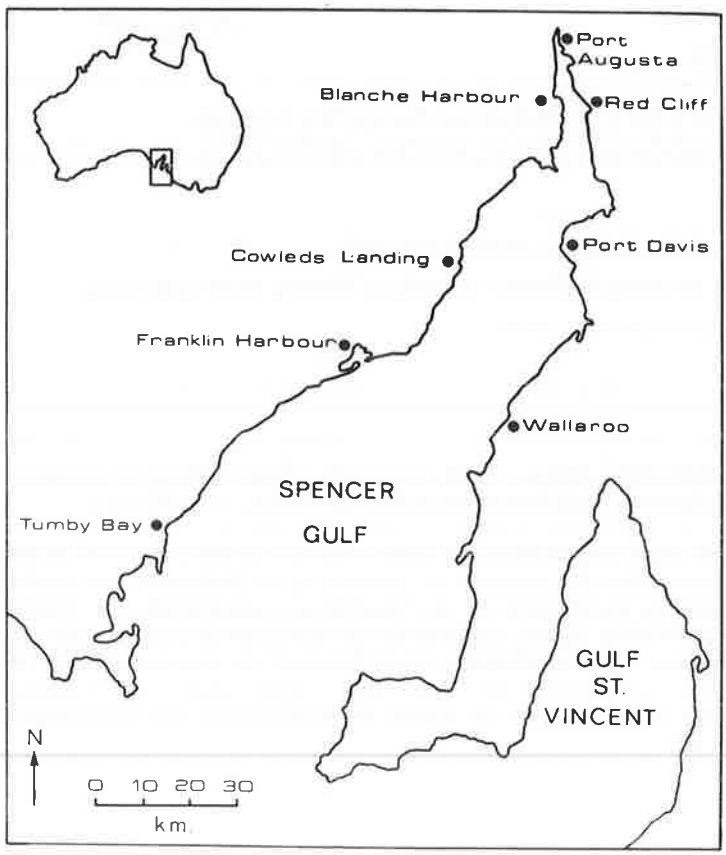

Fig. 1. Map showing localities sampled in Spencer Gulf, South Australia.

METHODS

Using random, paired co-ordinates, 25 pairs of pneumatophores were collected from each of three 10 m wide, 50 m long contoured belt transects located along the seaward margin of the mangrove canopy; one of each pair of pneumatophores came from beneath the tree canopy while the other came from the more sun-exposed region beyond the canopy. A total of 600 pairs of pneumatophores (75 pairs for each of the 8 localities) were sampled. Species frequency, cover, biomass and total algal diversity data were determined for the canopy-covered and the exposed pneumatophores in each transect. Cover data represent the length of pneumatophores occupied by algae as a percentage of the total pneumatophore length sampled at each locality. Dry weight biomass was obtained by carefully scraping the algae into aluminium 'boats', removing any flecks of bark, and drying to constant weight at 70°C; biomass data have been expressed as algal mass per total length of pneumatophore in mg cm^{-1}.

RESULTS AND DISCUSSION

Data on species frequency for the 15 most commonly occurring algae are summarized in Table I. Based on *T*-distribution analyses ($P = 0.01$) of mean frequency values for canopy-covered versus exposed pneumatophores from all localities, six species [*Bostrychia moritziana* (Sonder in Kützing) J. Agardh, *B. radicans* (Montagne) Montagne, *Caloglossa lepreurii* (Montagne) J. Agardh, *Gelidiella nigrescens* (Feldmann) Feldmann and Hamel, *G. tenuissima* Feldmann and Hamel, and *Wittrockiella salina* Chapman] occurred with significantly greater frequencies on pneumatophores

TABLE I

Summary of frequency data for the 15 most common algae on sun-exposed and canopy-covered pneumatophores

		Blanche Harbour	Cowleds Landing	Franklin Harbour	Port Augusta	Port Davis	Red Cliff	Tumby Bay	Wallaroo	*
CHLOROPHYTA										
Cladophora sp.	A	0.33	0.03	0.35	0.36		0.05	0.04	0.24	*Sun
	B	0.20	0.01	0.05	0.05		—	0.04	0.28	
Enteromorpha sp.	A	0.39	0.01	0.39	0.71	0.90		0.27		*Sun
	B	0.13	0.03	0.05	0.43	0.20		0.32		
Percursaria	A	0.39		0.03			0.20	0.08	0.19	
percursa	B	0.19		0.01			0.08	0.21	0.47	
Rhizoclonium	A	0.04	—	0.45	0.48	0.98	0.25	0.03	0.13	
riparum	B	0.05	0.11	0.43	0.26	0.70	0.26	0.04	0.12	
Ulva lactuca	A			0.35	0.03	0.04			0.03	
	B			0.12	0.01	—			0.25	
Wittrockiella	A	0.01	0.59	0.12	0.11		0.01	0.03	0.24	*Shade
salina	B	0.03	0.88	0.21	0.01		0.01	0.32	0.71	
CYANOPHYTA										
Rivularia atra	A	0.12	0.79	0.47	0.63		0.32	0.05	0.60	*Sun
	B	0.05	0.29	0.21	0.35		0.07	0.05	0.39	
R. polyotis	A	0.13	0.49	0.04			0.44			*Sun
	B	0.08	0.05	—			—			
RHODOPHYTA										
Bostrychia	A	—	0.01	0.12		0.12	0.03		—	*Shade
moritziana	B	0.21	0.31	0.39		0.80	0.36		0.17	
B. radicans	A	—	0.01	—		0.10	—	—	0.05	*Shade
	B	0.03	0.52	0.21		0.89	0.61	0.85	0.67	
Caloglossa	A	0.07	0.23	0.68	0.55	0.54	0.21		0.05	*Shade
leprieurii	B	0.41	0.68	0.44	0.65	1.00	0.94		0.11	
Centroceras	A			0.07			0.12	0.31	—	*Sun
clavulatum	B			—			—	0.12	0.12	
Gelidiella	A								0.08	*Shade
nigrescens	B								0.64	
G. tenuissima	A		0.01		0.01		—		0.29	*Shade
	B		0.12		—		0.05		0.72	
Spyridia	A	0.01	0.01	0.11			0.30	0.33	0.21	*Sun
filamentosa	B	0.03	—	0.01			0.04	0.12	0.27	

*Significance ($P = 0.01$) for comparisons of sun-exposed (A) and canopy covered frequencies (B)

situated underneath the canopy. Six other taxa [*Centroceras clavulatum* (C. Agardh) Montagne, *Cladophora* sp., *Enteromorpha* sp., *Rivularia atra* Roth, *R. polyotis* (J. Agardh) Bornet & Flahault, and *Spyridia filamentosa* (Wulfen) Harvey] occurred with significantly greater frequencies on pneumatophores situated in the more sun-exposed region beyond the canopy. Significant differences did not occur for *Percursaria percursa* (C. Agardh) Rosenvinge, *Rhizoclonium riparium* (Roth) Harvey or *Ulva lactuca* L.

Data on algal cover and biomass and on species diversity are summarized in Table II. Based on comparisons of canopy-covered and exposed pneumatophores using Mann-Whitney U tests ($P = 0.05$), both cover and biomass were significantly higher on canopy-covered pneumatophores at four localities (Blanch Harbour; Red Cliff; Tumby Bay, Wallaroo). At Port Davis, however, both cover and biomass were significantly higher on sun-exposed pneumatophores. At Cowleds Landing, moreover, cover, but not biomass, was significantly higher under the canopy, while at Port Augusta biomass but not cover was significantly higher beyond the canopy. The levels of mean cover and biomass present at the eight localities (Table II) varied greatly and this, in part, was due to the types of algae present. At Wallaroo, for example, the comparatively high levels of biomass present reflect the occurrence of the fucoid brown alga *Hormosira banksii* (Turner) Decaisne

TABLE II

Summary of data on algal cover, biomass and species diversity. Values for cover and biomass represent means of 75 measurements (S.D. given in parentheses)

	Algal cover (%)		Algal biomass (mg algae cm^{-1} pneumatophore)		Total species diversity	
Habitat	A	B	A	B	A	B
Blanche Harbour	13.8 (20.4)	28.5* (33.2)	0.63 (0.42)	1.29* (0.70)	10	13
Cowleds Landing	53.8 (33.3)	77.5* (27.4)	3.13 (3.04)	3.55 (0.72)	16	17
Franklin Harbour	50.4 (32.8)	48.6 (36.4)	2.40 (1.36)	2.55 (0.77)	19	14
Port Augusta	53.0 (38.1)	50.8 (36.9)	1.56 (0.41)	0.90 (0.47)	13	8
Port Davis	94.1 (8.7)	83.9* (18.1)	6.29 (1.47)	4.35* (0.66)	7	5
Red Cliff	35.5 (30.1)	80.3* (26.0)	1.37 (1.09)	5.09* (1.67)	14	11
Tumby Bay	11.3 (18.7)	61.8* (36.9)	0.30 (0.16)	4.07* (0.98)	14	14
Wallaroo	26.8 (23.5)	67.1* (30.5)	6.70 (11.89)	20.37* (11.70)	21	23

A = sun exposed; B = canopy-covered; * = significance ($P = 0.05$).

on some pneumatophores. Attached plants of this species did not occur in samples from other localities.

At most localities, total algal diversity (Table II) was similar on canopy covered and on more sun-exposed pneumatophores, although at most localities, some of the rare species (frequencies of 0.05 or less) were recorded only from one of the two habitats. Only at Port Augusta did a marked difference in total diversity occur between canopy-covered and more sun-exposed pneumatophores, but since seven of the thirteen species at Port Augusta occurred with overall frequencies of 0.05 or less (see Beanland and Woelkerling, 1982: Table 4), this difference may be of little consequence.

Several conclusions emerge from results obtained during this study. Firstly, the data provide evidence that the presence or absence of a tree canopy may influence the frequency distribution of algal species on pneumatophores along the seaward margin of a mangrove community. Some species occurred far more frequently beneath the canopy while others occurred far more frequently beyond the canopy. Although species of *Bostrychia* and *Caloglossa* had significantly higher frequencies beneath the canopy, they were not totally absent in more sun-exposed regions as was the case in Puerto Rico (Almodovar and Pagan, 1971). Secondly, the presence or absence of a tree canopy does not appear to be correlated with the distribution of algal cover or biomass. Thirdly, total algal diversity was not markedly different beneath and beyond the canopy, in contrast to the situation reported by Almodovar and Pagan (1971).

To date few ecological data are available for macroscopic algal communities of mangroves in Australia (Davey and Woelkerling, 1980; King, 1981a, b) or elsewhere (Chapman, 1976, 1977). Results from the present investigation, however, suggest that more detailed ecological studies of mangrove algal communities are warranted, especially if extended to include the entire mangrove fringe.

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SEASONAL VARIATION IN STANDING CROP, DENSITY AND LEAF GROWTH RATE OF THE SEAGRASS, *HETEROZOSTERA TASMANICA*, IN WESTERN PORT AND PORT PHILLIP BAY, VICTORIA, AUSTRALIA

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ABSTRACT

Bulthuis, D.A. and Woelkerling, Wm. J., 1983. Seasonal variation in standing crop, density and leaf growth rate of the seagrass, *Heterozostera tasmanica* in Western Port and Port Phillip Bay, Victoria, Australia. *Aquat. Bot.*, 16: 111—136.

Standing crop, density and leaf growth rate of *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog along with light, temperature, nutrient and sediment characteristics were determined monthly for fifteen months at three study sites in Western Port and one site in Port Phillip Bay, Victoria, Australia. Erect vegetative stems of *H. tasmanica* were frequently branched, were present throughout the year and accounted for 25—60% of the above-sediment biomass, with the stem proportion higher during winter than summer. At three of the four sites there was a unimodal seasonal pattern in which minimum leaf standing crop (27—61 g dry wt. m^{-2}), density (600—2000 leaf clusters m^{-2}) and leaf productivity (0.34—0.77 g dry wt. m^{-2} day^{-1}) generally occurred during winter (June—August) and maximum leaf standing crop (105—173 g dry wt. m^{-2}), density (2700—5000 leaf clusters m^{-2}) and leaf productivity (2.6—4.2 g dry wt. m^{-2} day^{-1}) occurred during summer (December—February). A bimodal seasonal pattern with minimum standing crop and density during midsummer occurred at one site. This anomalous seasonal pattern may be due to exposure and desiccation stress during spring low tides. At the site receiving the lowest irradiance, standing crop, density and annual leaf production also were lowest, but length and width of leaves, shoot height and leaf growth rate per leaf cluster were the highest of the four study sites. On average, each leaf cluster at any one of the study sites produced 30—31 leaves per year with mean leaf turnover rates of 1.3—1.7% day^{-1}. Annual leaf production of *H. tasmanica* ranged from 410 to 640 g dry wt. m^{-2} at the four sites.

INTRODUCTION

The seasonal patterns of standing crop, density and leaf growth rate of temperate seagrasses have been the subject of a number of recent inves-

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tigations. Studies on *Zostera marina* L., for example, indicate that minimum standing crop (0—140 g dry wt. m^{-2}), density (0—900 shoots m^{-2}), and leaf growth rate (<0.06—1 g dry wt. m^{-2} day^{-1}) occur during the winter months (Sand-Jensen, 1975; Thayer et al., 1975; Penhale, 1977; Jacobs, 1979; Nienhuis and de Bree, 1980). During spring, leaf growth rate, standing crop and density of *Z. marina* increase markedly, and maxima generally occur during mid-summer and may be as high as 1500 g dry wt. m^{-2} for leaf standing crop, 4500 shoots m^{-2} for density, and 13 g dry wt. m^{-2} day^{-1} for leaf growth rate (McRoy, 1970; Nienhuis and de Bree, 1980; see also reviews by McRoy and McMillan, 1977 and Zieman and Wetzel, 1980). Penhale (1977), however, reported a *Z. marina* community in North Carolina which had maximum standing crop during early spring (March) and which decreased during the remainder of the year, although productivity (1.8 g C m^{-2} day^{-1}) was at a maximum during late summer and autumn. For *Posidonia australis* Hook *f.* in Botany Bay, Jervis Bay and Port Hacking, New South Wales, Australia, West and Larkum (1979) and Kirkman and Reid (1979) reported very little seasonal change in leaf biomass, but leaf growth rate was markedly seasonal with a summer maximum (November—February) and a winter minimum (July—August). Similarly, for *Z. capricorni* Aschers. in Port Hacking, relative leaf growth rate was at a maximum in late summer and a minimum in winter (Kirkman et al., 1982).

There have been no reports on the seasonal patterns of growth and standing crop of *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog. *Heterozostera tasmanica* differs from *Z. marina* and *P. australis* in possessing lignified stems which represent a major proportion of the standing crop. Den Hartog (1970), Aston (1973), Tomlinson (1974), Cambridge (1975), and Jacobs and Williams (1980) state that these stems are shed during autumn and replaced by winter foliage, thus indicating a seasonal fluctuation in stem standing crop.

The objectives of the present study have been (1) to investigate the seasonal patterns of leaf and stem standing crop, erect shoot and leaf cluster density and leaf growth rate of *H. tasmanica* at four study sites in Western Port and Port Phillip Bay, Victoria, Australia, (2) to relate these patterns to the physical and chemical characteristics of these sites, and (3) to compare the general seasonal pattern of growth and leaf production of *H. tasmanica* to other temperate seagrasses.

STUDY SITES

At three study sites in Western Port and one in Port Phillip Bay (Fig. 1) the standing crop, density and leaf growth rate of *H. tasmanica* were determined monthly for fifteen months. These four sites were selected from among 50 potential sites to represent the diverse light, nutrient and depth conditions in which *H. tasmanica* grows. At all four sites *H. tasmanica* covered an area of at least 50 × 100 m. The Charing Cross site (38° 15′

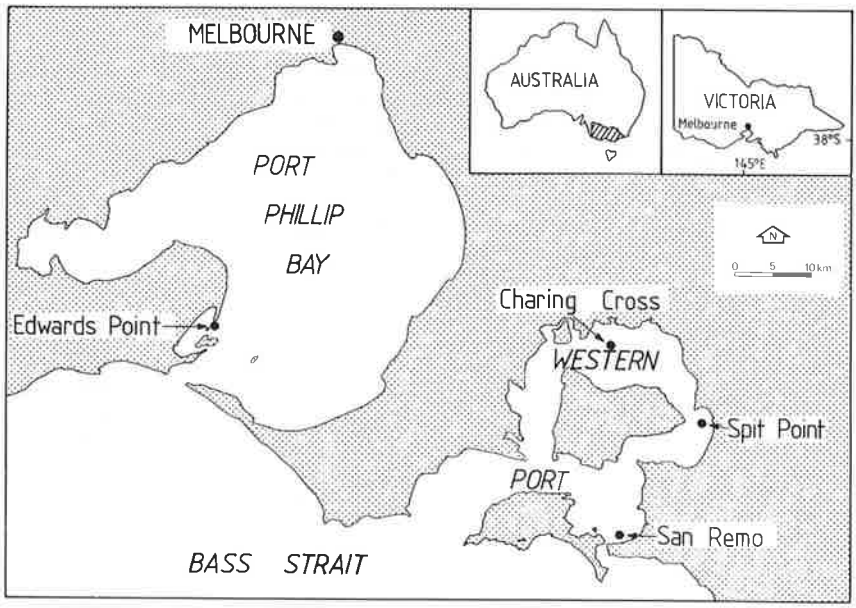

Fig. 1. Location of study sites in Western Port and Port Phillip Bay at which growth and standing crop of *H. tasmanica* were determined.

30″ S, 145° 21′ 55″ E) was located within extensive intertidal banks covered with *H. tasmanica* in the Upper North Arm, the section of Western Port which has the greatest area and highest standing crop of *H. tasmanica* (Bulthuis, 1981). Earlier investigations at this site had indicated that nitrogen limits the leaf growth rate of *H. tasmanica* during spring and early summer (Bulthuis and Woelkerling, 1981). The San Remo site (38° 13′ 30″ S, 145° 23′ 50″ E) is subtidal. The Spit Point site (38° 21′ 15″ S, 145° 31′ 15″ E) received less light than the other intertidal sites because of the more turbid overlying water. The Edwards Point site (38° 13′ 20″ S, 144° 41′ 45″ E) in Port Phillip Bay, had the highest levels of phosphorus in the water of any site and was the only intertidal site with a perceptible bottom gradient (approximately 40 cm over the 50 m width of the site) which facilitated water runoff during low tide. The sediments next to the Edwards Point site on the shallower side were either bare or were covered with *Zostera muelleri* Irmisch ex Aschers.; those on the lower side of the site were covered with *H. tasmanica*. In Western Port, *H. tasmanica* surrounded each of the three sites for at least 500 m in all directions.

The physical and chemical characteristics of the four sites are summarised in Tables I—III. Sediments at all sites were anaerobic muds beginning less than 1 cm below the surface and organic carbon ranging from 0.7% at San Remo to 6.5% at Charing Cross (Table I). The presence of lignified stems to a depth of 30—45 cm at the three Western Port sites implies that *H. tasmanica* had been growing at the sites for several years at least.

TABLE I

Depth (below mean water), tidal amplitude (of spring tides), organic carbon of surface (upper 5 cm) sediments (mean ± s.e. of 10 samples), depth of anaerobic mud and stems and rhizomes (mean of 2 one-metre cores) and bottom slope of four study sites in Western Port and Port Phillip Bay at which growth and standing crop of *H. tasmanica* were determined

	Charing Cross	Spit Point	San Remo	Edwards Point
Depth (m)	1.0 Intertidal	1.0 Intertidal	3.6 Subtidal	0.6 Intertidal
Tidal amplitude (m)	3.1	3.1	3.0	1.1
Surface sediment type	Anaerobic mud	Anaerobic mud	Anaerobic mud	Anaerobic mud
Organic carbon (% of dry wt.)	6.5	2.5	0.7	4.9
Depth of anaerobic muds (cm)	60	30	>90	*
Depth of old stems and rhizomes of *H. tasmanica* (cm)	45	30	45	*
Bottom slope	<10 cm × 100 m^{-1}	< 10 cm × 100 m^{-1}	<10 cm × 100 m^{-1}	40 cm × 50 m^{-1}

*No data.

TABLE II

Nutrient concentrations and salinity of water at four study sites in Western Port and Port Phillip Bay at which growth and standing crop of *H. tasmanica* were determined. Mean and range of monthly samples from March 1978 to May 1979

	Charing Cross	Spit Point	San Remo	Edwards Point
Nitrogen (μg at N l^{-1})				
NH_4^+	0.34	0.32	0.26	0.41
	< 0.1 — 0.9	< 0.1 — 1.2	0.1 — 0.9	< 0.1 — 1.3
NO_3^-	0.23	0.73	0.38	0.24
	0.1 — 1.24	0.1 — 6.4	0.1 — 2.3	0.1 — 0.6
NO_2^-	0.06	0.09	0.06	0.06
	< 0.01— 0.28	< 0.01— 0.50	0.01— 0.30	< 0.01— 0.20
Phosphorus (μg at P l^{-1})				
PO_4^{3-}	0.08	0.18	0.10	0.81
	0.02— 0.23	0.05— 0.58	0.03— 0.20	0.30— 1.80
Total P	0.32	0.78	0.37	1.27
	0.20— 0.58	0.32— 2.67	0.18— 0.94	0.58— 2.71
Silica (μg at Si l^{-1})				
SiO_3	4.0	10.6	3.2	3.6
	1.8 — 9.8	1.6 —28.3	0.8 —10.9	1.0 — 9.8
Salinity (‰)				
Salinity	34.59	33.39	34.77	34.81
	31.61—37.13	28.01—37.51	32.71—36.26	32.36—36.03

Salinity and nutrients in the water varied widely between months, but there were no seasonal trends at any of the sites; mean and range of values encountered during the fifteen months of study are indicated in Table II. Salinity was generally similar to oceanic levels; none of the sites received large freshwater inputs. The lowest salinities were recorded at Spit Point, which according to the circulation pattern proposed by Harris et al. (1979) would be due to the streams and small rivers that enter Western Port in the north-east corner. This probably also accounts for the higher reactive silicate, nitrate and phosphorus observed at Spit Point compared to the other two sites in Western Port. Edwards Point, in Port Phillip Bay, had mean reactive phosphorus and total phosphorus levels in the water 2—10 times higher than the Western Port sites (Table II).

The three intertidal sites (Charing Cross, Spit Point, and Edwards Point) had similar maximum and minimum water temperatures each month (note standard errors in Fig. 2) so the data were combined (Fig. 2). The plants at the subtidal site experienced less extremes in temperature than did those at the intertidal sites, particularly during the summer months when maximum intertidal temperatures averaged 30° C compared with 24° C at San Remo.

Light penetration through the water at all sites varied greatly between sampling visits as indicated by the wide range of extinction coefficients

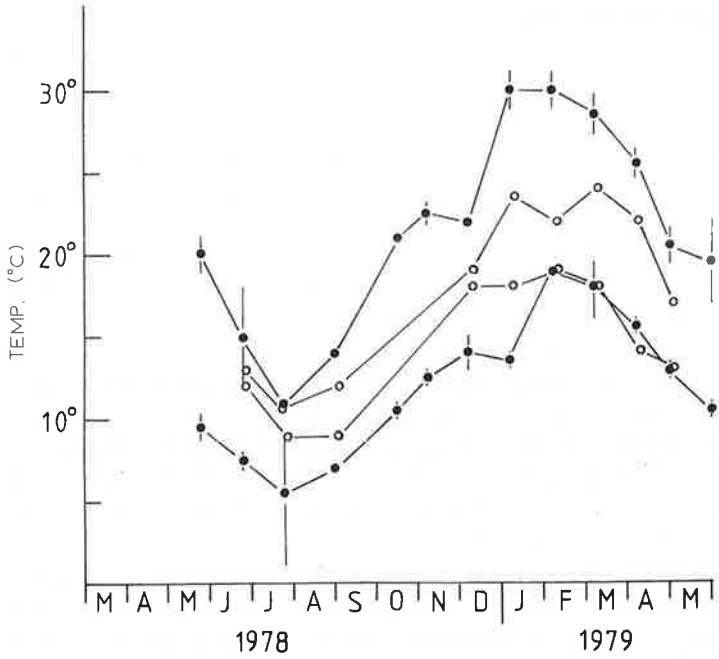

Fig. 2. Monthly maximum and minimum temperatures of surface waters at three intertidal (closed circles, mean ± 1 s.e.) study sites in Western Port and Port Phillip Bay and at one subtidal (open circles) site in Western Port.

TABLE III

Extinction coefficients (mean and range of K, determined monthly from March 1978 to May 1979) of water and irradiance to *H. tasmanica* community (assuming mean depth and mean K) at four study sites in Western Port and Port Phillip Bay

	Charing Cross	Spit Point	San Remo	Edwards Point
K (per m)	0.66	1.24	0.58	0.75
	0.12—1.66	0.48—2.83	0.33—1.03	0.45—1.32
Mean depth (m)	1.0	1.0	3.6	0.6
Irradiance (% of surface)	52	29	12	64

at each site (Table III). There was no seasonal trend in the fluctuations and the mean of all values at each site indicates the overall relative light conditions. The mean depths and extinction coefficients were used to estimate the percent of surface irradiance reaching the *H. tasmanica* community at each station. Charing Cross and Edwards Point were similar and received the greatest amount of light, while seagrasses at Spit Point received about half as much and plants from San Remo (subtidal) received the least amount of light (Table III).

METHODS

At the four study sites the standing crop, density and leaf growth rate of *H. tasmanica* as well as the physical—chemical characteristics of each site were determined monthly for fifteen months. An area 100 × 100 m at each site (50 × 100 m at Edwards Point) was marked at one corner with a permanent marker (10 cm diameter, 7 m long steel pole) ensuring that the same area was sampled each time and serving as a reference point for determining the location of random samples. Monthly samples for all parameters at the three intertidal sites were taken during low tide. Damage to the site was minimised by moving to and around the site and sampling from fibreglassed, styrene foam floats (1.5× 2.5× 0.2 m) which floated on the 2—10 cm of water that usually remained on the mudflats during low tide. At the subtidal site, San Remo, all sampling and leaf marking was completed underwater with the aid of SCUBA.

The sediment characteristics of the sites also were determined. In August 1978, three, one-metre-deep cores of the sediment were taken at each site for examination of depth of anaerobic muds as indicated by black colour. Ten samples of the upper 5 cm of sediment were randomly taken at each site and organic carbon determined by the wet digestion method (Jackson, 1958). At each site a shaded maximum—minimum thermometer

was placed at the sediment surface in a position that kept the thermometer submerged at all times. Temperature was read and the thermometer was reset monthly.

Salinity, total phosphorus, reactive phosphorus, ammonium, nitrate and nitrite were determined in samples of the overlying water taken twice each month, once at mid-ebb tide and once (at intertidal sites) just before the return of the flood tide. Salinity was determined on a 601-MIII Autolab salinometer. Nutrient concentrations were determined with a Technicon Autoanalyzer II; reactive phosphorus, nitrate, nitrite and ammonia by the methods described by Strickland and Parsons (1972); total phosphorus by persulphate digestion followed by analysis of reactive phosphate; and reactive silicate by the method of Koroleff (1972).

Light penetration in the overlying water was determined monthly as downwelling irradiance with a Lambda LI-192S quantum sensor (400—700 nm). Extinction coefficients (K) of the water were calculated from eqn. (1) which is based on Lambert's law

$$I_z = I_0 e^{-Kz} \tag{1}$$

where I_z = light quanta at depth z; I_0 = light quanta just below the water surface; e = base of the natural logarithms; z = depth in metres; K = extinction coefficient.

Ten samples for standing crop and density were taken each month at each site. The location of each of the ten samples was determined with a random numbers table and a map of the 100 × 100 m area divided into 160000 potential 0.25 × 0.25 m quadrats. Samples were located in the field by measuring the indicated distance from the permanent marker. A metal frame was set over a 0.0625 m^2 quadrat [this size had the lowest ratio of variance to mean for leaf standing crop of quadrats ranging from 0.00391 to 0.25 m^2 (Kershaw, 1973)] and was used to cut the sides of the turf. The turf, including all plants, rhizomes, and about 10 cm of sediment, was then removed and placed in plastic boxes of the same size, covered, transported to the laboratory and kept cool (5°C) until sorting, which was usually within 3 days and always within 7 days of sampling.

In the laboratory, all stemmed erect shoots were removed from each standing crop-density sample; shoot length was measured from the insertion of the first root to the top of the longest leaf; and the number of leaf clusters and adventitious shoots was recorded. The shoot was rinsed free of mud and divided into stems and leaves (stems included some persistent fibrous sheaths, leaves were wiped by hand to remove macro-epiphytes, but leaf dry weight included the tightly-adhering diatom crust and associated micro-epiphytes) and dried at 80°C to constant weight (usually within 48 h). The number of stemless shoots was recorded separately. Percent ash-free dry weight, i.e., organic weight (Westlake, 1963) was determined in two randomly selected 1-g subsamples each month

from each site. Subsamples were ashed in pre-heated aluminium foil boats at 550° C to constant weight (usually within 3 h).

Leaf growth was measured each month at three sample stations randomly selected within each of the four 100 × 100 m sampling sites. Vegetative shoots of *H. tasmanica* may be unbranched or branched (contrary to description by den Hartog, 1970), with a cluster of leaves [analogous in *Z. marina* to 'turion' in Sand-Jensen (1975), and to 'leaf bundle' in Nienhuis and de Bree (1980)] at the apex of each branch. Within each cluster the youngest leaf is in the centre with successively older leaves outside of the centre. New leaves emerge in the centre of the cluster. The time interval between the initiation of two successive leaves in a leaf cluster is the plastochrone interval (Patriquin, 1973; Jacobs, 1979). Leaf growth within each cluster is limited to the three youngest (centremost) leaves, similar to the pattern described by Mukai et al. (1979) and Jacobs (1979) for *Z. marina*. Sixteen leaf clusters at each of the three stations had a prelabelled cable-tie attached between two leaf nodes on the lignified stem below the leaf cluster. Care was taken to prevent damage to the stems and to ensure that the tag could not slip past either node. The tag allowed each leaf in the cluster to be uniquely identified relative to the tag. The length of the three youngest leaves in each leaf cluster was recorded, care being taken not to crack the brittle lignified stems or disturb their attachment to the rhizome. Tagged plants were left for one month and the surviving plants were harvested and returned to the laboratory where the original 3 youngest leaves were re-measured, any new leaves noted and measured, and the total number of leaves in the cluster noted. Leaf growth rate was calculated as the sum of the growth of all leaves (old and new) within each leaf cluster. Leaf dry weight and organic weight per unit length of leaf was determined on young leaves without epiphytes, as described above for organic weight analysis of standing crop.

RESULTS AND DISCUSSION

Standing crop

The above-sediment biomass (standing crop) of *H. tasmanica* was about 50% stem and 50% leaf (Table IV). The leaf proportion of the standing crop increased during spring (September—November) and summer (December—February) to about 60% at Charing Cross, Spit Point and San Remo, and up to 75% at Edwards Point. During autumn (March—May) the leaf proportion decreased to about 40% at Charing Cross, Spit Point and San Remo. Edwards Point averaged a somewhat higher proportion of leaves (mean: 64%) compared with the other three sites (mean: 50%).

Organic weight as a percentage of dry weight of leaves and stems remained relatively constant throughout the year. Mean values ranged from 75 to 81% for both leaves and stems from all four sites (Table V).

TABLE IV

Standing crop of leaves and stems of *H. tasmanica* at four sites in Western Port and Port Phillip Bay from March 1978 to May 1979
Mean (g dry wt. m^{-2}) ± 1 s.e.; n = 10, n.a. = not available

Month	Leaf				Stem				Total above ground			
	Charing Cross	Spit Point	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edwards Point
March	85±12	54± 7	31±10	81±27	133±16	105±15	49±35	80±22	218±26	158±20	83±52	161±49
April	88± 8	69±11	49± 5	139± 9	121±17	69±12	56± 6	147±15	209±24	138±22	105±10	286±23
May	79± 7	54±10	43± 4	87±15	107±10	59±12	55± 9	87±24	186±15	113±21	99±13	174±38
June	67± 6	63± 9	48± 4	80± 5	90± 9	59± 9	46± 4	36± 3	157±14	122±19	94± 7	116± 7
July	65±11	63± 3	32± 5	n.a.	80±15	63± 5	31± 8	n.a.	145±25	126± 7	63±13	n.a.
August	73± 9	41± 6	28± 6	120±13	76±14	30± 6	29± 7	39± 6	148±22	71±12	56±13	159±18
September	92± 8	114±12	33± 6	128±17	103±19	77± 9	26± 6	48± 9	196±27	191±20	59±11	176±25
October	61±14	114± 7	58± 7	100± 9	47±10	77± 8	45± 5	44± 5	107±23	191±14	103±13	144±14
November	103± 8	120± 8	105±11	94±11	94±13	70± 6	79±13	44± 6	197±20	190±14	184±24	138±17
December	116±16	96± 6	72±10	88± 9	94±14	66± 6	71±12	33± 5	209±29	162±11	143±21	121±13
January	96±10	173±11	87± 9	59±12	75±10	113±13	139± 7	39± 7	171±18	279±21	226±25	99±19
February	83±13	130±12	55± 7	89±10	89±16	111±11	103±16	52± 6	172±29	241±22	157±22	141±15
March	80±12	72±11	28± 4	103±14	109±16	85±15	50± 6	74± 9	189±26	157± 8	78±10	177±20
April	84± 9	44±11	27± 4	121±14	111±13	50± 7	36± 7	80±10	195±20	94±16	63±11	200±24
May	79±10	39± 7	47±10	63±12	85±13	43± 5	53±10	42±11	163±22	82±12	102±20	105±22

TABLE V

Organic weight as percentage of total dry weight of leaves and stems of erect shoots of *H. tasmanica* at four study sites in Western Port and Port Phillip Bay (Mean ± s.e.; n = 15 monthly means from March 1978 to May 1979)

	Charing Cross	Spit Point	San Remo	Edwards Point
Leaves	79.4 ± 0.58	73.9 ± 1.11	76.6 ± 1.15	79.9 ± 0.69
Stems	79.7 ± 0.71	75.6 ± 0.76	81.1 ± 0.89	78.1 ± 0.74

The standing crop of leaves increased from two- to four-fold between winter (June—August) and summer (December—February) (Table IV). At Charing Cross, Spit Point and San Remo, winter minima were 65, 40 and 30 g m^{-2} and increased to summer maxima of 115, 170 and 105, respectively. Seasonal fluctuations at Charing Cross were less marked than at Spit Point or San Remo. At Edwards Point the seasonal pattern was markedly different from the other three sites. There were two peaks of standing crop, one in early spring (September: 130 g m^{-2}) and a second in autumn (April: 120 g m^{-2}). Minima occurred in winter (May—June: 80 and 65 g m^{-2}) and in mid-summer (January: 60 g m^{-2}). The mid-summer minimum was particularly striking as it occurred when *H. tasmanica* leaf standing crop was at or near its maximum at the other three sites (Table IV).

The differences observed at Edwards Point appear to be related to temperature and exposure stresses. Edwards Point was the only site at which there was a perceptible slope (Table I) and phosphorus in the water was higher than at the other sites (Table II). However, light and temperature, the abiotic factors usually suggested as the causative agents of seasonal fluctuations, and the other nutrients were similar at Edwards Point to the two other intertidal sites (Tables II and III, Fig. 2). During low-water spring tides, which are about 0.2 m lower during summer (November—January) than during winter in Port Phillip Bay, the water drains down the slope at the Edwards Point site leaving *H. tasmanica* exposed. At the two other intertidal sites there is less slope (Table I) and natural levees at the channel edge retard water flow from the mudflats into the channels; hence, there is always some water on the mudflat surface. Therefore, *H. tasmanica* at the Edwards Point site may be exposed to greater desiccation stress during the low water spring-tides of summer than at the other sites and consequently dies back. In an unpublished report, D.A. Bulthuis and P. Ruppin indicated that *H. tasmanica* leaves blackened and died after more than 1 h of exposure at temperatures of 25°C or higher. In addition

to the potential desiccation stress, plants which are exposed to the air may be stressed by high temperatures when air temperature is higher than water temperature. Biebl and McRoy (1971) reported that photosynthesis of *Z. marina* from Alaska declined sharply above 30°C and that leaves died after 12 h exposure at 34°C. Similarly, *H. tasmanica* photosynthesis declined sharply between 30 and 35°C, with an irrevocable loss of net photosynthetic capacity after 5 min exposure to 40°C (Bulthuis, 1983a). Maximum water temperature at Edwards Point during the present study was 35°C in December and air temperatures in Melbourne occasionally exceeded 40°C during the summer. When such days coincide with spring low tides, exposed *H. tasmanica*, even with a thin film of water, will be severely stressed. Penhale (1977) reports the only other study in which the maximum standing crop of a temperate seagrass occurred at any season other than summer. In that study, *Z. marina* in North Carolina had a maximum biomass in March (early spring) and declined during the remainder of the year. Like the present study, Penhale suggested that high temperature and exposure stress may have been responsible for the unusual seasonal pattern and the decline during summer.

The standing crop of *Z. marina*, the most widely studied temperate seagrass, fluctuates seasonally with maxima generally during the summer and minima during the winter (Conover, 1958; McRoy, 1966; Phillips, 1972; Riggs and Fralick, 1975; Sand-Jensen, 1975; Thayer et al., 1975; Jacobs, 1979; Nienhuis and de Bree, 1980). In the present study, *H. tasmanica* at the three Western Port sites had a unimodal seasonal pattern of standing crop similar to that observed in *Z. marina* populations. The monthly means for standing crop of *H. tasmanica* are within the ranges reported for *Z. marina* in the reviews by McRoy and McMillan (1977) and Zieman and Wetzel (1980), but maximum standing crop, 286 g dry wt. m^{-2}, is considerably lower than the maximum reported for *Z. marina*, >1000 g dry wt. m^{-2}.

Density

The seasonal trend of shoot density and leaf-cluster density was similar to that observed for leaf standing crop (Table VI). Charing Cross, Spit Point and San Remo had winter minima of about 1400, 1200 and 400 and summer maxima of 4200, 3200 and 2700 leaf clusters m^{-2}, respectively. Edwards Point, as with leaf standing crop, had minima in winter and summer and maxima in spring and autumn (Table VI). This anomolous seasonal pattern of density is probably the result of exposure and temperature stress as has been postulated for the seasonal fluctuations in standing crop.

At the subtidal site, San Remo, almost all shoots were terminated with a single leaf cluster. Only in November to January did 10—30% of the shoots develop more than one leaf cluster, and this was reduced by February

TABLE VI

Density of *H. tasmanica* at four sites in Western Port and Port Phillip Bay from March 1978 to May 1979
(Mean (no.m^{-2}) ± 1 s.e.; n = 10; n.a. = not available)

Month	Erect shoots				Leaf clusters				Adventitious shoots			
	Charing Cross	Spit Point	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edwards Point
March	1920±280	1330± 94	576±160	2290±570	2800±358	1420±107	640±186	3070±1020	n.a.	n.a.	n.a.	n.a.
April	1700±195	1620±277	938±101	3070±448	2800±302	1730±283	992±112	4580± 558	162± 30	78±38	56±19	355±187
May	1620±128	1230±210	880± 88	1730±267	2480±197	1380±248	960±126	2240± 419	275± 79	48±28	34±12	314± 82
June	1410±142	1180±179	976± 62	1980±154	2080±200	1340±194	1010± 61	2210± 173	366± 72	10± 5	32±12	41± 19
July	1500±210	1340± 58	960±131	n.a.	1970±286	1500± 74	960±134	n.a.	525±155	16± 6	18±10	n.a.
August	1680±130	1170±126	672±110	2420±194	2060±147	1200±129	736±131	3010± 162	277± 71	n.a.	n.a.	86± 46
September	1900±106	1760±182	832± 99	3010±294	2610±173	2220±227	864±107	3660± 434	272± 73	42±12	6± 3	67± 17
October	1820±264	1950±160	1180±115	2210±224	2740±475	2990±237	1360±142	2960± 240	141± 32	37±10	10± 5	50± 19
November	2370±208	1790±149	2050±285	2180±240	4050±344	2660±230	2740±390	3280± 384	134± 34	99±50	37±14	40± 8
December	2420±389	1890±130	1780±229	2430±213	4210±662	2560±117	2000±267	2670± 278	99± 19	59±16	32± 9	42± 21
January	1660±203	2450±171	2370±203	1900±184	3630±350	3230±275	2670±227	2460± 357	45± 13	34± 8	35±11	91± 48
February	1940±235	1980±150	1920±226	3010±298	3460±510	2940±234	2020±253	3840± 454	106± 25	46±23	18± 7	10± 9
March	1540±198	1410±264	736± 82	3410±454	3730±405	2260±459	784± 88	4980± 638	139± 36	16± 7	13± 5	5± 3
April	1410± 91	980±174	544± 85	3440±189	3550±282	1410±278	592± 85	4610± 379	178± 43	5± 3	16± 8	37± 16
May	1570±184	750± 98	960±158	1420±250	2880±336	1040±157	1020±178	1920± 344	173± 58	2± 2	30±10	91± 21

to less than 5% of the population. Leaf cluster density and shoot density were thus similar (Table VI). At Charing Cross, in contrast, leaf-cluster density was at least 25% higher than shoot density, increased during the spring growth period, and was more than double the shoot density in January (Table VI). At Spit Point the number of shoots with more than one leaf cluster increased markedly from August to October and then slowly decreased (Table VI). Data in Table VI indicate that there was very little seasonal change in the percentage of shoots having more than one leaf cluster at Edwards Point.

Adventitious shoots were most numerous at Charing Cross and had a seasonal minimum in January (summer) and a maximum in July (winter, Table VI). At the other three sites densities were much lower than at Charing Cross and there was no apparent seasonal pattern (Table VI).

At the San Remo site, the shoot and leaf-cluster density and leaf standing crop of *H. tasmanica* were lower than for the other three sites (Tables IV and VI). San Remo was the only subtidal site, and irradiance at the top of the seagrass canopy was lowest at this site (Table III). The lower density and standing crop at San Remo probably resulted from these lower light levels. Numerous workers have suggested that decreased density of seagrasses with depth is due to decreased light levels (Ostenfeld, 1905; Tutin, 1942; Burkholder and Doheny, 1968; Phillips, 1974; Jacobs, 1979; Nienhuis and de Bree, 1980). Backman and Barilotti (1976) reported experimental evidence that decreased irradiance caused decreased density in *Z. marina.* In *H. tasmanica,* density decreased and leaf length increased when experimental screens reduced irradiance (Bulthuis, 1983b). It is suggested from these studies that the lower density and leaf standing crop of *H. tasmanica* at San Remo compared with the other three sites was due to the lower light level at San Remo.

The density of *Z. marina* fluctuates seasonally with maxima during the summer and minima during the winter (McRoy, 1966; Phillips, 1972; Sand-Jensen, 1975; Jacobs, 1979; Nienhuis and de Bree, 1980) similar to *H. tasmanica* at the three Western Port sites in the present study (Table VI). Although maximum standing crops for *H. tasmanica* were considerably lower than for *Z. marina* (286 compared to 1000 g dry wt. m^{-2}), maximum densities for *H. tasmanica* (3200—5000 leaf clusters m^{-2}) are at the top end of the range (150—4600 shoots m^{-2}) reported for *Z. marina* by McRoy and McMillan (1977). *Heterozostera tasmanica* has shorter and thinner leaves than *Z. marina* (den Hartog, 1970) so similar densities of leaf clusters in the two species do not have similar standing crops.

Shoot height

The histograms of shoot height (Figs. 3—6) indicate that small shoots (<20 cm tall) were present throughout the year. The shoots <20 cm tall were considered to be a single size-class during counting but, for compara-

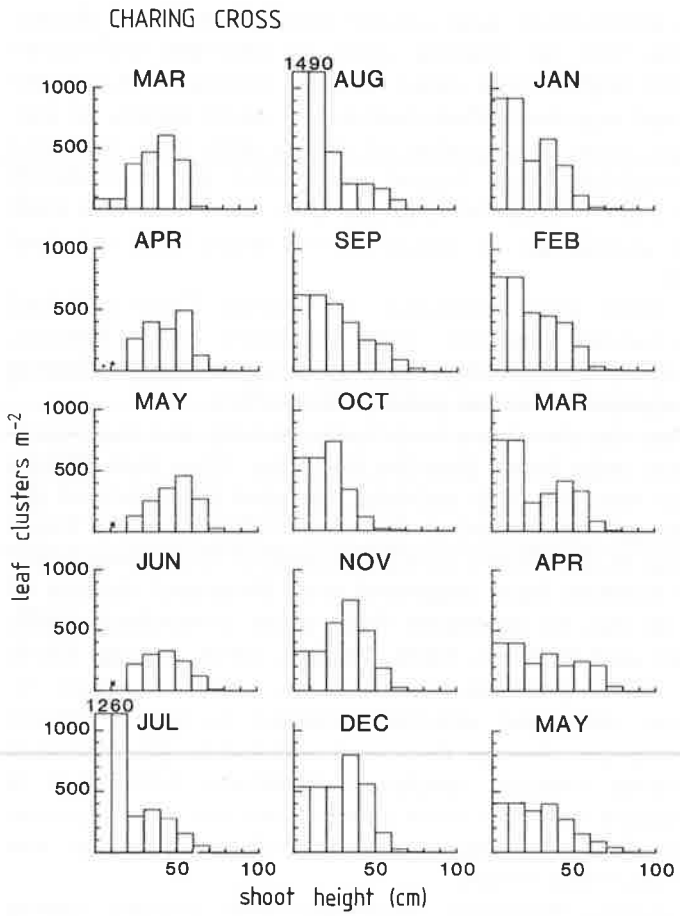

Fig. 3. Height of *H. tasmanica* shoots in 10 size classes for 15 months from March 1978 to May 1979 at Charing Cross, Western Port. *Indicates no data available for those size classes.

tive purposes in the histograms, have been equally divided into the 0—10 cm height class and the 10—20 cm height class. Maximum numbers in the <20 size-classes were recorded in winter (August: Charing Cross and Spit Point) and spring (November: San Remo and Edwards Point), but similar peaks in abundance were apparent also in summer (January—February: Edwards Point) and autumn (March: Spit Point, April: San Remo). Because erect stems of *H. tasmanica* become taller with age, the presence of small (<20 cm) erect shoots during all months of the year at all sites indicates that new shoots are produced throughout the year and not only during spring as implied in earlier descriptions of *H. tasmanica* (den Hartog, 1970; Aston, 1973; Cambridge, 1975; Jacobs and Williams, 1980). These authors also reported that erect stems were completely shed in autumn

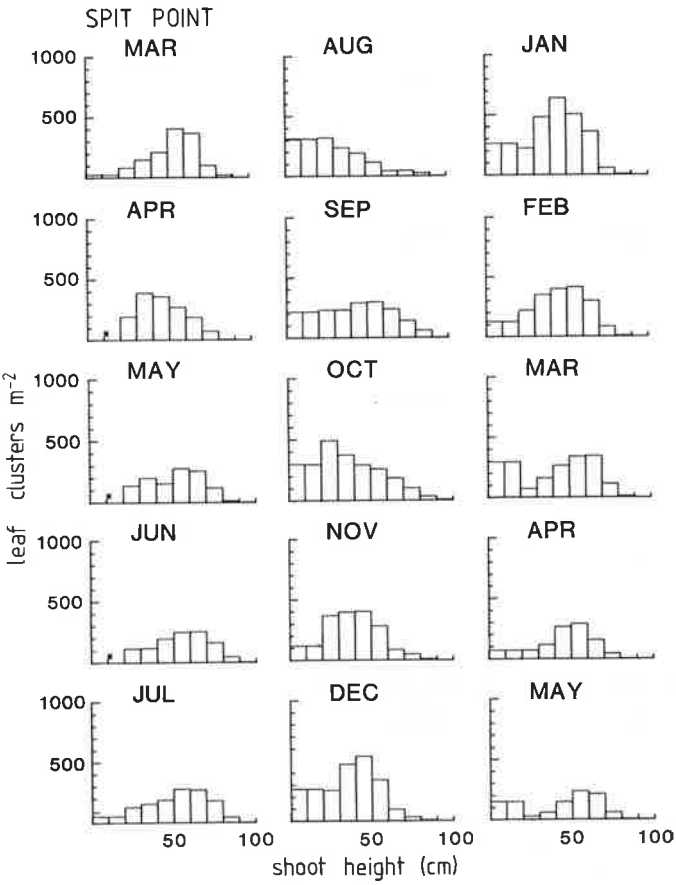

Fig. 4. Height of *H. tasmanica* shoots in 10 size classes for 15 months from March 1978 to May 1979 at Spit Point, Western Port. *Indicates no data available for those size classes.

and replaced with "winter foliage". In the present study, the density of erect stems decreased during autumn but throughout the winter months tall erect shoots were present (Tables IV and VI, Figs. 3–6). A distinct "winter foliage" was not observed at any of the four study sites. The description of "winter foliage" in these reports is similar to young erect shoots observed in the present study. It is possible that in some areas all stemmed erect shoots of *H. tasmanica* may be shed and that the presence of numerous young shoots may be responsible for the "winter foliage" descriptions.

The histograms of shoot height for Spit Point (Fig. 4) indicate that shorter (20–40 cm, presumably younger) shoots were numerous during early spring (August–October). As these shoots became taller during late spring and summer (November–March), the number of shoots in the taller size-classes (40–70 cm) increased while the number in the shorter size-

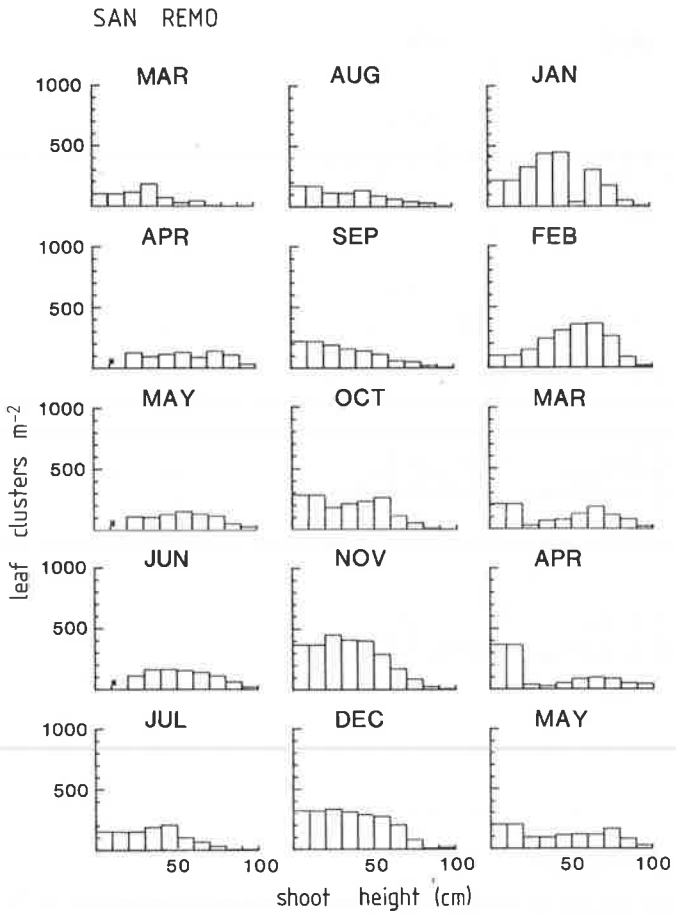

Fig. 5. Height of *H. tasmanica* shoots in 10 size classes for 15 months from March 1978 to May 1979 at San Remo, Western Port. *Indicates no data available for those size classes.

classes (20—40 cm) decreased (Fig. 4). Apart from the <20 cm shoots, the most numerous size classes at Spit Point were 45 cm in January, 55 cm in February and 65 cm in March. During autumn (March–May) shoot density decreased in all size-classes at Spit Point (Fig. 4). A similar seasonal pattern was evident at Charing Cross (Fig. 3) and San Remo (Fig. 5). However, at Edwards Point the taller shoots (>40 cm) declined from September to November and were virtually absent from December to February (Fig. 6). This pattern may be due to temperature and exposure stress during the low spring-tides of summer. It is these taller shoots which most likely would be exposed at low tide and, thus, suffer desiccation stress.

Average shoot height was greater at Spit Point (47 cm) and San Remo (47 cm) than at Charing Cross (35 cm) and Edwards Point (32 cm). This

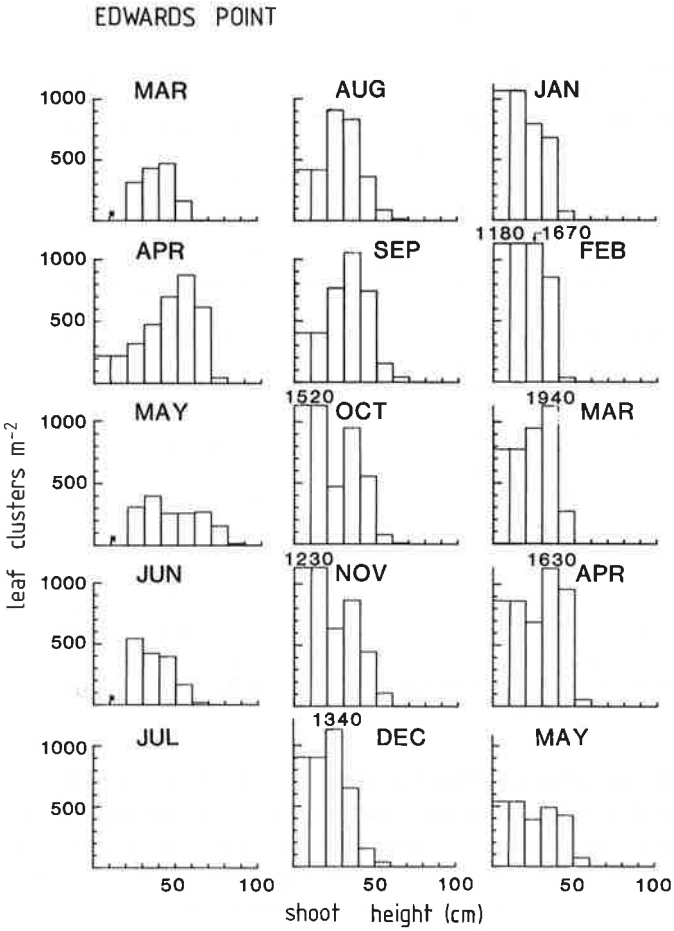

Fig. 6. Height of *H. tasmanica* shoots in 10 size classes for 15 months from March 1978 to May 1979 at Edwards Point, Port Phillip Bay. *Indicates no data available for those size classes.

is probably the result of lower light intensity at Spit Point and San Remo compared to the other two sites (Table III). Edwards Point had the lowest average shoot height which, like the summer minima in standing crop and shoot density, may be due to exposure during the low spring-tides of summer.

Leaf growth and productivity

Leaf growth rates at all sites were at a minimum in winter, about 6.5 mm (leaf cluster)$^{-1}$ day^{-1} at the three intertidal sites and about 2 times greater at the subtidal site, San Remo (Table VII). Rates increased 2—4 times during spring and were at a maximum during the summer months.

TABLE VII

Leaf growth rate and productivity of *H. tasmanica* at four study sites in Western Port and Port Phillip Bay from April 1978 to May 1979
(Mean ± 1 s.e. of leaf growth rate; n = 3 stations at which 5—16 plants were measured)

Month	Leaf growth rate (mm leaf cluster^{-1} day^{-1})				Leaf productivity (g dry wt. m^{-2} day^{-1})			
	Charing Cross	Spit Point	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edwards Point
April	10.4±1.8	17.1±1.6	23.5±3.4	14.1±0.5	1.26	1.26	1.29	2.61
May	12.4±0.3	9.2±2.0	22.4±4.3	11.3±1.2	1.34	0.55	0.95	1.02
June	6.5±0.3	6.3±1.5	13.8±2.2	6.8±0.5	0.58	0.37	0.62	0.77
July	6.2±1.6	9.1±1.6	13.7±1.1	n.a.	0.52	0.60	0.57	
August	6.5±0.4	12.3±1.2	18.4±1.4	10.5±0.6	0.58	0.64	0.60	1.27
September	5.6	11.4±0.4	15.0±0.8	9.2±2.0	0.38	1.11	0.57	1.36
October	10.0±0.9	16.4±5.1	18.2±0.1	12.4±2.2	1.18	2.13	0.89	1.48
November	15.2±1.8	31.2	14.0±2.3	13.8	2.65	3.62	2.04	1.53
December	19.7±1.6	29.2±3.1	14.3±0.7	19.4±3.2	3.58	3.24	1.27	2.09
January	18.3±1.5	26.1±2.6	22.2±3.8	19.1±0.8	2.41	3.67	2.63	1.91
February	15.6±1.0	19.6±2.7	28.2±2.0	22.7±0.7	2.32	2.51	2.52	3.52
March	19.1±1.0	20.8±2.0	18.9±3.8	20.8±3.1	3.07	2.04	0.65	4.19
April	5.2±0.6	9.1±5.4	13.2±2.6	7.6±1.4	0.80	0.56	0.34	1.41
May	6.8±0.8	14.0±1.8	24.1±1.8	11.9±2.2	0.85	0.64	1.10	0.92

Maximum rates varied from 19.7 at Charing Cross to 31.2 at Spit Point. At Edwards Point the leaf growth rate per leaf cluster was similar to the other three sites. This was in contrast to the seasonal pattern of standing crop and density in which Edwards Point differed markedly from the other three sites. This implies that the factor(s) which caused the decrease of standing crop and density during summer at Edwards Point did not also cause a decrease in growth rate of the surviving leaf clusters. The data are thus consistent with the hypothesis that density and standing crop at Edwards Point decreased during summer due to desiccation during spring low tides. Shoots, especially shorter shoots, which survived the low tides would be expected to have normal leaf growth rates per (surviving) leaf cluster.

Leaf dry weight per cm of leaf length was consistent throughout the study and the means at all sites were similar, from 40.4 to 44.4 μg cm^{-1}; so this parameter appears to be a relatively constant value for *H. tasmanica* in Western Port and Port Phillip Bay.

The leaf dry weight (g cm^{-1}) was multiplied by the leaf growth rate (cm leaf cluster^{-1} day^{-1}) and the leaf cluster density (no. m^{-2}) in order to estimate the mean productivity of leaf dry weight each month. At all sites there was a pronounced seasonal trend (Table VII). Minimum rates (0.38, 0.37, 0.34 and 0.77 g m^{-2} day^{-1} at Charing Cross, Spit Point, San

Remo and Edwards Point, respectively) occurred during the autumn and winter months (April—July). Rates increased 5—10 times to summer maxima of 3.6, 3.7, 2.6 and 4.2 g m^{-2} day^{-1}. At Charing Cross, Spit Point and San Remo, rates increased rapidly in spring and by November were at least 5 times the winter minima (Table VII). These rates were maintained throughout the summer months. However, at Edwards Point, decreasing density during summer and increasing growth rates per leaf cluster caused peak productivity to occur during February and March (Tables VI and VII). This was followed by a rapid decline during late autumn (April—May) as both density and leaf growth rate declined.

Maximum leaf productivity measured in other seagrasses was 6—14 g dry wt. m^{-2} day^{-1} for *Thalassia testudinum* Banks ex König (Patriquin, 1973; Zieman, 1975; Greenway, 1976; Thorhaug and Roessler, 1977), 5.5 g m^{-2} day^{-1} for *Posidonia australis* (West and Larkum, 1979), and 7.0, 3.0 and 12.0 in the three studies of *Z. marina* (Sand-Jensen, 1975; Jacobs, 1979; Nienhuis and de Bree, 1980). In the present study, the maximum monthly mean for *H. tasmanica* (4.2 g m^{-2} day^{-1}) is within the range of maxima reported for *Z. marina*, but considerably less than the 12.0 reported by Nienhuis and de Bree (1980). The seasonal pattern of leaf growth rate of *H. tasmanica*, a unimodal curve with the maximum in summer and minimum in winter (Table VII) was also similar to that reported for *Z. marina* and *P. australis* (Sand-Jensen, 1975; Jacobs, 1979; Nienhuis and de Bree, 1980; West and Larkum, 1979). This curve reflects seasonal curves for total insolation and it has been suggested for *Z. marina*, therefore, that light controls the seasonal pattern of leaf production (Sand-Jensen, 1975; Jacobs, 1979). Although light may be an important factor in determining seasonal leaf production of *H. tasmanica*, other factors also appear to be important. This is particularly evident in autumn when leaf productivity during April was less than one-third the productivity during March at the three intertidal sites (Table VII). This reflected decreases in density (Table VI) and leaf growth rate (Table VII) that were much greater than the reduction in total insolation.

The seasonal pattern of leaf productivity is a function of both leaf growth rate and leaf cluster density. Because both of these parameters were highest during summer in the present study, a high proportion of the annual production of *H. tasmanica* occurred from October to March (78% at Charing Cross, 81% at Spit Point, 90% at San Remo, and 68% at Edwards Point). However, even during the winter months, there was considerable leaf productivity, 0.4—0.7 g dry wt. m^{-2} day^{-1}.

Annual leaf production at each site was estimated for the period from June 1978 to May 1979 by multiplying the daily productivity times the number of days for each month and summing the monthly totals (Table VIII). This was similar to the method used by Sand-Jensen (1975) and Jacobs (1979). Annual leaf production was similar at the three intertidal sites (568—645 g dry wt. m^{-2} $year^{-1}$). The lower leaf production at San

Remo is probably the result of the lower total insolation at this subtidal site. Despite minima of density and leaf dry weight during mid-summer at Edwards Point, annual leaf production was similar to the other intertidal sites. At Edwards Point, relatively lower leaf productivity during summer was compensated by relatively higher leaf productivity during winter.

TABLE VIII

Annual leaf production of *H. tasmanica* at four study sites in Western Port and Port Phillip Bay from June 1978 to May 1979

Site	Production	
	Dry weight ($g\ m^{-2}\ year^{-1}$)	Organic weight ($g\ m^{-2}\ year^{-1}$)
Charing Cross	568	431
Spit Point	634	477
San Remo	414	333
Edwards Point	645	508

TABLE IX

Annual leaf production of three extra-tropical seagrass species in g dry wt. m^{-2}

Species	Annual leaf production	Location	Source
Zostera marina	856	Denmark — Vellerup Vig — subtidal	Sand-Jensen, 1975
	788	France — Roscoff — intertidal	Jacobs, 1979
	407	The Netherlands — Lake Grevelingen — not tidal	Nienhuis and de Bree, 1980
Posidonia australis	582	New South Wales — Botany Bay — subtidal	West and Larkum, 1979
	1170	New South Wales — Jervis Bay — subtidal	West and Larkum, 1979
Heterozostera tasmanica	616	Victoria — Western Port and Port Phillip Bay — intertidal sites	This study
	414	Victoria — Western Port — subtidal site	This study

The annual leaf production of *H. tasmanica* is within the range reported for *Z. marina* and *P. australis* (Table IX). Leaf production was an estimated 69—88% of total production (including roots and rhizomes) in *Z. marina* (Sand-Jensen, 1975; Jacobs, 1979; Nienhuis and de Bree, 1980). If leaf production of *H. tasmanica* is a similar proportion of total production, then *H. tasmanica* has an annual productivity of about 725 g dry wt. m^{-2}, 560 g ash-free dry weight m^{-2} (Table V) or 220—260 g carbon m^{-2} (using 0.39—0.46 g carbon (g ash-free dry wt.)$^{-1}$, Westlake, 1965; Nienhuis and de Bree, 1980).

Leaf characteristics

Length and width of leaves of *H. tasmanica* at each of the four sites did not change seasonally during the 15 months of the present study. Leaves from Charing Cross were shorter and narrower than leaves from the other three sites and leaves from San Remo were longer and wider (Table X). Mean leaf area per leaf generally increased between the four sites as ambient light decreased (Tables III and X). The mean length and width data were combined with the mean number of leaves per leaf cluster and the leaf-cluster density to estimate leaf area index (m^2 of leaf area per m^2 of bottom surface area). The leaf area index (LAI) fluctuated seasonally, primarily reflecting changes in leaf-cluster density. The minimum LAIs (1.0—1.8) occurred during winter and the maximum LAIs (5.1—5.9) occurred during summer (Table X).

Leaf area index reported for various species of seagrasses ranges from 0.8 to 21 (Gessner and Hammer, 1960; Gessner, 1971; Drew and Jupp, 1976; McRoy and McMillan, 1977; West and Larkum, 1979). For *Z. marina*, Phillips (1972) reported values of 1—4 in Puget Sound, Jacobs (1979) reported an annual range of 4—9.5 in Roscoff, France, and Dennison and

TABLE X

Length and width of leaves of *H. tasmanica* at four study sites in Western Port and Port Phillip Bay collected throughout the year. Means in mm ± 1 s.e.; n = 10 monthly means from August 1978 to May 1979. Each monthly site-mean is based on 4—7 plants. Means not significantly ($P > 0.01$) different from each other by the Student—Newman—Keuls multiple comparison test have the same superscript letter. The range for leaf area index (LAI; m^2 leaf m^{-2} bottom surface) is based on annual minimum and maximum density of *H. tasmanica* leaf clusters at each site

Site	Length (mm)	Width (mm)	LAI range
Charing Cross	115^{a} ± 3.2	1.45^{a} ± 0.015	1.7—5.1
Edwards Point	143^{b} ± 4.4	$1.50^{a,b}$ ± 0.023	1.2—5.9
Spit Point	170^{c} ± 5.1	1.54^{b} ± 0.018	1.0—5.4
San Remo	176^{c} ± 5.0	1.81^{c} ± 0.024	1.8—5.2

McRoy (1980) reported a range of 2—17 along a depth transect in Alaska. *Heterozostera tasmanica* ranged from 1.0 to 5.9 at the four study sites in the present study. Kain et al. (1975) suggested that LAI (or Frond Area Index) for *Laminaria hyperborea* (Gunnerus) Foslie would decrease logarithmically with depth and presented preliminary evidence to support this. Similarly, Dennison and McRoy (1980) reported changes to LAI with depth for *Z. marina*, maximum LAI occurring at "intermediate depths". In the present study, LAI was similar at all sites (Table X) even though the San Remo site was 2.5—3.0 m deeper than the other sites (Table I) and light intensity was 0.2—0.5 times the level at the other sites (Table III). Drew and Jupp (1976) also found no correlation between LAI and depth for *Posidonia oceanica* (L.) Delile from 5 to 35 m.

Each leaf cluster produced a new leaf at intervals (plastochrone intervals) ranging from 7.4—33 days (Table XI). At all sites the plastochrone intervals were highest during autumn and winter with maximum values of 23, 33, 20 and 20 days at Charing Cross, Spit Point, San Remo and Edwards Point, respectively. Minimum plastochrone intervals at the four sites during summer were all between 7.4 to 7.7 days. The seasonal pattern was similar at all sites although at San Remo the pattern was less pronounced than at the other sites (Table XI). During the twelve months from June 1978 to May 1979 an average leaf cluster at any one of the sites produced 30—31 leaves. *Zostera marina*, the only other temperate seagrass for which similar data are available, had plastochrone intervals of 8—14 days during summer with winter maxima of 28 days (Sand-Jensen, 1975; Jacobs, 1979; Mukai et al., 1979; Nienhuis and de Bree, 1980).

The number of leaves in each leaf cluster was similar at all sites. Means during spring and summer (September—February: 5.7—6.9 leaves per leaf cluster) were significantly ($P<0.05$) higher than during autumn and winter (March—August: 3.9—5.3 leaves per leaf cluster). The average number of leaves per leaf cluster each month was multiplied by the rate of new leaves produced per cluster (plastochrone interval) each month to estimate the "leaf life-span", i.e., the average number of days between emergence of a new leaf and its being shed by abscission at the junction with the leaf sheath (Table XI). The greater plastochrone interval during winter was offset by the generally lower number of leaves in each leaf cluster during winter so that calculated leaf life-span did not exhibit as pronounced seasonal trends as did the plastochrone interval. Minimum leaf life-spans generally occurred during summer and varied from 40 to 54 days at the four sites. Maximum leaf life-spans during autumn and winter varied from 95 to 144 days. Annual mean leaf life-spans were 77, 79, 72 and 65 days at Charing Cross, Spit Point, San Remo and Edwards Point, respectively. In a review of leaf morphology and anatomy in seagrasses Tomlinson (1980) stated "A consideration of mechanisms of leaf loss brings up the topic of leaf age, which is so important in productivity studies. However, apart from the pioneering work of Patriquin (1973) and Zieman (1975), which

TABLE XI

Plastochrone interval, leaf life span and leaf turnover of *H. tasmanica* at four sites in Western Port and Port Phillip Bay from April 1978 to May 1979.
Mean ± 1 s.e. of plastochrone interval (n = 3 stations at which 5—16 plants were measured)

Month	Plastochrone interval (days)				Leaf life span (days)				Leaf turnover (percent. day^{-1})			
	Charing Cross	Spit Point	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edwards Point
April	15±1.4	14± 0.6	12±1.3	15±1.6	53	54	61	71	1.9	1.9	1.6	1.4
May	15±1.9	22± 5.6	12±1.5	16±0.8	65	99	67	68	1.5	1.0	1.5	1.5
June	20±0.2	28± 5.1	18±0.9	20±1.1	105	144	98	86	1.0	0.7	1.0	1.2
July	20±2.2	18± 1.8	16±0.2	n.a.	104	94	92		1.0	1.1	1.1	
August	17±1.6	16± 0.2	14±1.1	16±0.6	103	94	81	68	1.0	1.1	1.2	1.5
September	16	15± 1.6	15±1.5	16±4.9	96	102	90	64	1.0	1.0	1.1	1.6
October	10±0.7	10± 0.2	10±1.6	14±3.6	62	64	56	95	1.6	1.6	1.8	1.1
November	9±0.8	7	12±1.2	12	66	60	66	65	1.5	1.7	1.5	1.5
December	8±0.7	8± 0.3	10±0.3	8±0.4	60	67	64	49	1.7	1.5	1.6	2.0
January	8±0.4	8± 0.3	8±0.5	8±0.6	52	55	52	40	1.9	1.8	1.9	2.5
February	9±0.9	10± 1.2	8±0.8	8±0.4	53	67	50	53	1.9	1.5	2.0	1.9
March	8±0.2	10± 1.2	10±0.9	9±0.5	48	65	60	44	2.1	1.5	1.7	2.3
April	22±2.4	33±13	17±2.4	17±0.7	77	126	91	83	1.3	0.8	1.1	1.2
May	23±1.0	17± 1.0	10±0.8	17±1.4	98	74	58	73	1.0	1.4	1.7	1.4

suggests an average life span of thirty to forty days for *Thalassia* leaves, there are too few data to permit generalisation". In addition to the work on *T. testudinum* mentioned above, leaf life-span of *Z. marina* has been estimated as 68, 44 and 56 days by Jacobs (1979), Mukai et al. (1979) and Sand-Jensen (1975), respectively. Based on these limited data, *H. tasmanica* appears to have a longer leaf life-span (annual means: 65—79 days) than the tropical seagrass *T. testudinum* (30—40 days) and similar to the temperate seagrass *Z. marina* ("growing season" means: 44—56 days, annual mean: 68 days).

Leaf turnover was calculated as the reciprocal of leaf life-span and expressed as percentage change in leaf biomass per day (Table XI). Leaf turnover was at a minimum during winter; for example, at Charing Cross it took more than 4 months from June to September to replace one crop of leaves. During November to March, it took about 2 months to replace a crop of leaves. The patterns were similar at Spit Point and San Remo. At Edwards Point the low leaf standing crop during summer coincided with high leaf productivity, resulting in high turnover rates during summer. Mean leaf turnover rates of *H. tasmanica* were 1.4, 1.3, 1.5 and 1.7% day^{-1} (i.e., 5.1, 4.7, 5.5 and 6.2 crops of leaves produced per year) at Charing Cross, Spit Point, San Remo and Edwards Point, respectively. Similar turnover rates have been reported for *Z. marina* by Jacobs (1979) (monthly range: 1.2—1.8% day^{-1}, mean: 1.5% day^{-1}) and Sand-Jensen (1975) (mean: 1.8% day^{-1}) while lower turnover rates were reported for *P. australis* by West and Larkum (1979) (means: 0.8—1.1% day^{-1}).

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BIOMASS ACCUMULATION AND SHADING EFFECTS OF EPIPHYTES ON LEAVES OF THE SEAGRASS, *HETEROZOSTERA TASMANICA*, IN VICTORIA, AUSTRALIA

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ABSTRACT

Bulthuis, D.A. and Woelkerling, Wm. J., 1983. Biomass accumulation and shading effects of epiphytes on leaves of the seagrass, *Heterozostera tasmanica*, in Victoria, Australia. *Aquat. Bot.*, 16: 137—148.

A method is described for estimating the rate of accumulation of epiphyte biomass on leaves of the seagrass, *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog and for estimating the effect of epiphyte biomass on photosynthesis of the seagrass. Epiphyte biomass was determined by comparison of the weight per unit area of epiphyte-covered and epiphyte-free leaf blades. Epiphyte weight increased as age of the seagrass leaves increased. Linear regression of epiphyte biomass vs. leaf age estimated the rate of biomass accumulation. Rates varied from 5.7 to 104 μg epiphyte dry weight per cm^2 of leaf surface per day at three sites in Western Port and Port Phillip Bay, Victoria. Rates of accumulation of epiphyte biomass were generally higher during December through March (summer) than in May (autumn), August (winter) or October (spring). Light attenuation by epiphytes increased linearly with biomass. The rate of biomass accumulation of epiphytes was compared with leaf growth rate, ambient photon flux density in *H. tasmanica* beds and the photosynthesis—photon flux density curve of *H. tasmanica*. This comparison demonstrated that epiphyte biomass can accumulate fast enough to shade *H. tasmanica* leaves and significantly reduce the time (to less than one half of the leaf life span) in which positive net photosynthesis of the leaf blade is possible.

INTRODUCTION

A number of studies on the epiphytes of seagrasses have identified and enumerated the plant and animal species present. Diatoms have been recorded on *Zostera marina* L. (Sieburth and Thomas, 1973; Main and McIntyre, 1974; Jacobs and Noten, 1980), *Thalassia testudinum* Banks ex König (Reyes-Vasquez, 1970; de Felice and Lynts, 1978; Sullivan, 1979), *Syringodium filiforme* Kütz. (reported as *Cymodocea filiforme* (Kütz.) Correll) and

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Halodule beaudettei (den Hartog) den Hartog (Sullivan, 1979). Other types of algal epiphytes have been reported on *Thalassia testudinum* (Humm, 1964) and *Zostera marina* (Brauner, 1975). In Australia, plant and animal epiphytes have been enumerated for *Amphibolis antarctica* (Labill.) Sonder et Aschers. (Ducker et al., 1977), *Ruppia maritima* L. sensu lato (Wood, 1959), *Posidonia australis* Hook *f.*, *Zostera capricorni* Aschers. and *Z. muelleri* Irmisch ex Aschers. (Womersley, 1956; Wood, 1959; May et al., 1978) and *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog (May et al., 1978, reported as *Zostera tasmanica*). Elsewhere, nitrogen, phosphorus and carbon fluxes between *Zostera marina* and its epiphytes have been investigated in a number of studies (Harlin, 1973; McRoy and Goering, 1974; Penhale and Smith, 1977; Sand-Jensen, 1977; Wetzel and Penhale, 1979; Penhale and Thayer, 1980; Smith and Penhale, 1980) and recent reviews by Harlin (1975, 1980) have summarised the plant and animal species reported to be epiphytic on seagrasses and what is known of the functional relationships between seagrasses and their epiphytes.

It has been suggested that rapid growth and biomass accumulation of epiphytes has resulted in the decline of seagrasses and of freshwater angiosperms in nutrient-rich waters, and that the major cause for the decline is shading of the leaf surface by the epiphytes (Sand-Jensen, 1977; Phillips et al., 1978; Cambridge, 1979; Johnstone, 1979). Sand-Jensen (1977) demonstrated that epiphytes reduced photosynthesis of *Z. marina* leaves by shading and Borum and Wium-Andersen (1980) reported a direct relationship between epiphyte biomass and light absorption of epiphytes in suspension. A higher biomass of epiphytes has been reported on older leaves than on younger leaves of *Z. marina* (van den Ende and Haage, 1963; Borum and Wium-Andersen, 1980; Harlin, 1980), *Posidonia oceanica* (L.) Delile (van der Ben, 1969) and *Enhalus acoroides* (L. *f.*) Royle (Johnstone, 1979). This increased biomass on older leaves would be expected to increase shading of the leaf surface and thus decrease leaf photosynthesis. However, the importance of shading by epiphytes can be evaluated objectively only when data are available to compare the rate of epiphyte biomass accumulation with the growth rate of the seagrass leaves.

Epiphyte biomass on leaves of *Z. marina* has been reported by Penhale (1977) and Borum and Wium-Andersen (1980). The pattern of accumulation of epiphytes on *Z. marina* leaves has been described qualitatively (Sieburth and Thomas, 1973). However, there apparently are no published quantitative data on the rate of biomass accumulation of epiphytes on seagrass leaves. Estimates of this rate cannot be based on biomass increment between average biomass for two sample dates because the loss of old epiphyte-covered leaves and production of new unepiphytised leaves are usually not measured. The objectives of the present study have been to develop a method for quantifying the rate of biomass accumulation of epiphytes on leaves of the seagrass, *H. tasmanica*, to determine the relationship between epiphyte biomass and shading of the leaf and to investigate the importance of

this shading on photosynthesis of *H. tasmanica* in Western Port and Port Phillip Bay, Victoria.

METHODS

Epiphyte biomass on leaves of *Heterozostera tasmanica* was estimated by comparison of the weight per unit area of epiphyte-covered and epiphyte-free leaf blades from a single leaf cluster. All leaf blades with the attached epiphytes were removed from a leaf cluster, the position relative to the youngest leaf blade was noted, and leaf length and width measured. The leaf blades and attached epiphytes were rinsed carefully (< 0.5% of the epiphyte dry weight was lost during this procedure) in formic acid isotonic with seawater to remove inorganic salts which would otherwise contribute to the dry weight, dried to constant weight at 80°C, and muffled at 550°C to constant weight for ash-free dry weight (organic weight, Westlake, 1963). In each leaf cluster, the weight per unit area was determined for the youngest leaf blade (or second youngest when the youngest leaf blade was very small, < 50 mm long). These leaf blades had no epiphytes visible on the leaf surface (by light microscopy) other than widely scattered diatoms near the leaf tip. The $\mu g\ mm^{-2}$ (specific weight) of this reference leaf was subtracted from the specific weight of older leaf blades (with attached epiphytes) from the same cluster. The difference was an estimate of the weight of epiphyte biomass on the older leaf blades. This calculation assumes that the specific weight of the leaf blade does not change significantly with age. This assumption was tested by scraping the epiphytes from the leaf blades of eight leaf clusters collected at Charing Cross, Western Port on 29 August, 1979. There was no significant ($P > 0.05$) change in specific leaf weight with age (Table I), thus substantiating the assumption used in calculating epiphyte dry weight.

TABLE I

Dry weight of leaves of *Heterozostera tasmanica* which are free of epiphytes (nos. 1 and 2) or from which epiphytes have been removed (nos. 3 to 8). Leaves were collected 29 August 1979 at Charing Cross, Western Port. One-way ANOVA indicates no significant ($P > 0.05$) differences between leaves

Leaf no.	Dry weight ($mg\ cm^{-2}$)		
	Mean	s.e.	*n*
1 (youngest)	2.434	0.126	3
2	2.720	0.074	8
3	2.486	0.245	2
4	2.748	0.170	6
5	2.706	0.195	3
6	2.536	0.087	6
7	2.482	0.135	6
8 (oldest)	2.429	0.228	3

The rate of biomass accumulation of epiphytes was estimated by combining epiphyte biomass measurements with measurements of leaf age (days since leaf emergence). Leaf age was estimated from measurement of the plastochrone interval (the time interval between the initiation of two successive leaves in one leaf cluster) as described by Bulthuis and Woelkerling (1983). The least squares linear regression of epiphyte dry weight vs. leaf age was used to estimate the rate of biomass accumulation of epiphytes in μg per cm^2 of leaf surface per day.

The rate of biomass accumulation was estimated at three sites, Charing Cross and San Remo in Western Port which contains extensive beds of *H. tasmanica* (Bulthuis, 1981) and Edwards Point in Port Phillip Bay, Victoria. The physical and chemical conditions and the seasonal pattern of seagrass growth at these sites have been described in Bulthuis and Woelkerling (1981, 1983). Six leaf clusters were randomly sampled at each site during October through March (spring and summer), the season when earlier investigations had indicated epiphyte productivity was at a maximum (Penhale, 1977; Borum and Wium-Andersen, 1980). For comparison with other seasons, samples also were taken during May and August (late autumn and winter).

Light absorption by epiphytes on leaf blades of *H. tasmanica* was determined by measuring light transmission through scraped and unscraped sections of leaves with a Zeiss photomicroscope combined with a Zeiss microscope photometer. The light source was a Zeiss 60 W, 12 V tungsten illuminator. Light absorption was measured at 12—22 evenly spaced locations along the length of each leaf blade with epiphyte-free (scraped) sections of the same leaf as reference. The mean epiphyte absorption for each leaf was divided by two to estimate light absorption by a layer of epiphytes on only one side of a leaf.

RESULTS

The general nature of the early epiphytic community on *Heterozostera tasmanica* was similar qualitatively to that described by Sieburth and Thomas (1973) for *Z. marina.* Pennate diatoms were the first epiphytes present (visible by light microscopy) and these developed into a unialgal mat covering the whole of the leaf blade. Diatom frustules and detritus later formed an amorphous crust on which filamentous green algae and encrusting coralline red algae developed. The coralline algae were more prominent at the subtidal site, San Remo, than at the intertidal sites. Filamentous green algae generally accounted for about 20—60% of the biomass on older leaves, but contributed almost all of the biomass on older leaves during 'bloom' periods. Organic and inorganic detritus was present on most leaves, but generally appeared to account for less than 20% of the accumulated biomass. No attempt was made to separate the abiotic component from the living and dead epiphytes because all three contributed to light absorption.

As leaf age (measured in number of plastochrone intervals since emergence) increased, the dry weight of the epiphytes on the leaf blade also increased. This general pattern was evident at all sites on all sampling dates with data for March 1979 given as an example (Fig. 1). In March, 1979, the rate of biomass accumulation (and the maximum biomass observed on the oldest leaves) was lower at Charing Cross than at either of the other two sites (Fig. 1). At Charing Cross and San Remo the rate of accumulation was constant during the preceding 6 plastochrone intervals, resulting in an approximately linear relationship between epiphyte dry weight and plastochrone interval. At Edwards Point biomass accumulation occurred at two rates, one on the three youngest leaves, and a faster rate on the fourth through sixth oldest leaves (Fig. 1). The effect of a 'bloom' of epiphytes on the rate of biomass accumulation is illustrated by the November through January data for the San Remo site (Fig. 2). In November, the rate of accumulation was uniformly low, resulting in 1.15 mg cm^{-2} after eight plastochrone intervals. One month later (equivalent to three plastochrone intervals), there had been an increase in the rate of biomass accumulation with 4.35 mg cm^{-2} after eight plastochrone intervals. During the following month, this rate again decreased so that in January the bloom of the previous month was evident only on the seventh oldest leaf (Fig. 2).

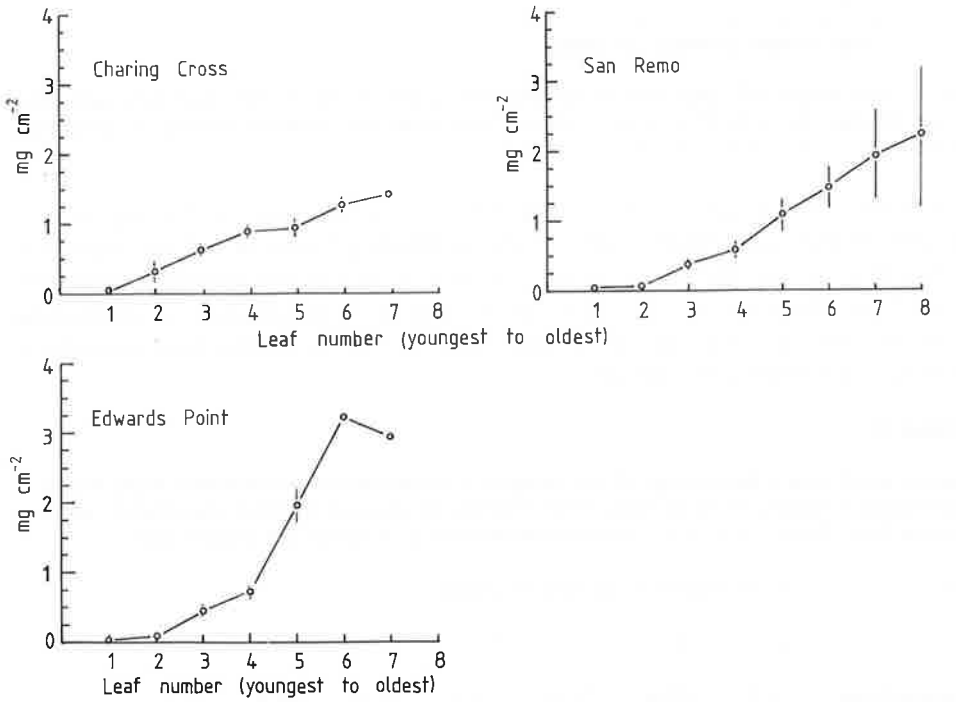

Fig. 1. Dry weight of epiphytes on successively older leaves of *Heterozostera tasmanica* at three sites in Western Port and Port Phillip Bay in March, 1979. mg epiphyte dry weight per cm^2 per leaf area, mean ± 1 s.e., n = 3—6 leaves.

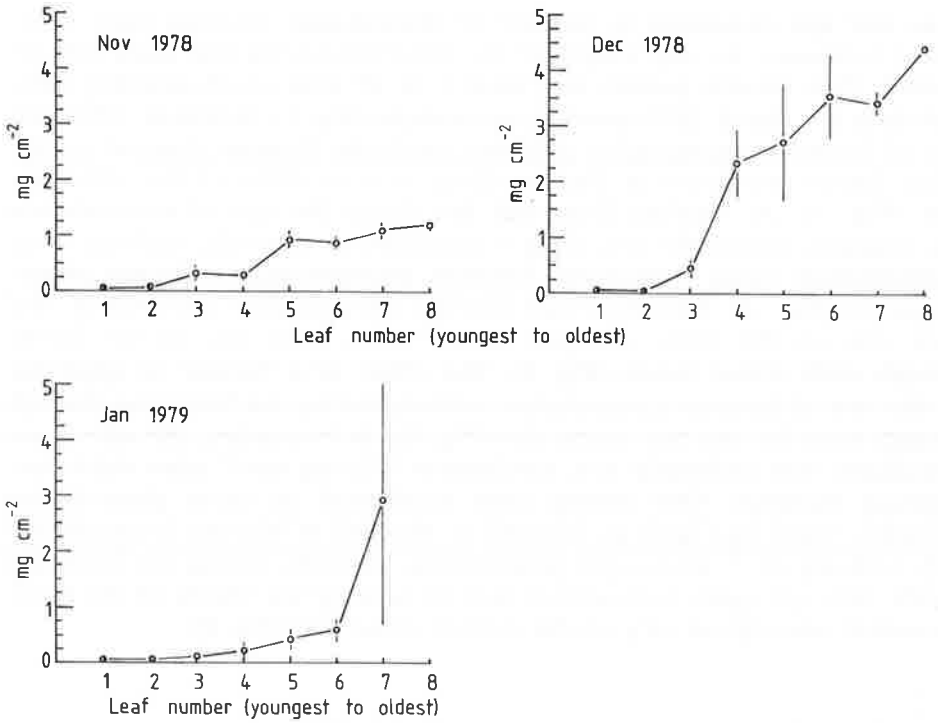

Fig. 2. Dry weight of epiphytes on successively older leaves of *Heterozostera tasmanica* at San Remo, Western Port before, during and after an epiphyte 'bloom' in December 1978. Mean ± 1 s.e., n = 3—6 leaves.

Ash-free dry weight of the epiphytes as a percentage of the dry weight did not change significantly ($P > 0.05$) at Charing Cross as leaf age increased (Table II). At San Remo, however, the percentage of ash-free dry weight decreased on older leaves. At San Remo, a greater abundance of encrusting coralline red algae was noted on older leaves, and these may have contributed to the increased ash content.

TABLE II

Organic weight (as a percentage of dry weight) of epiphytes on successively older leaves of *Heterozostera tasmanica* at an inter-tidal (Charing Cross) and subtidal (San Remo) site in Western Port. Mean + s.e., n = 10 sample dates with 2—6 leaves per sample date

Site	Leaf number (youngest to oldest)						
	2	3	4	5	6	7	8
Charing Cross	75.7	76.6	74.6	71.5	72.9	66.2	71.1
	±2.0	±2.1	±2.7	±3.3	±2.3	±4.2	±3.1
San Remo	79.5	78.7	71.9	68.2	64.6	63.2	58.5
	±2.5	±1.7	±2.3	±2.7	±3.8	±2.5	±3.6

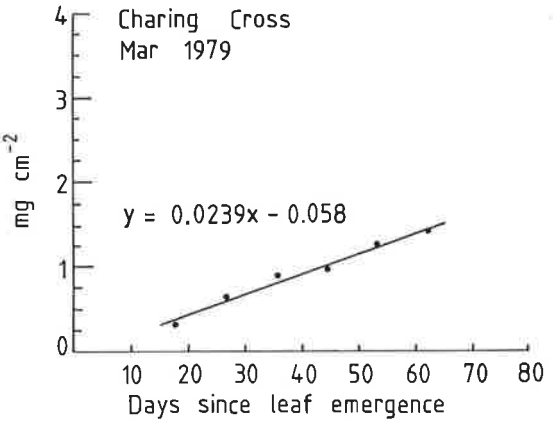

Fig. 3. Rate of epiphyte biomass accumulation on leaves of *Heterozostera tasmanica* at Charing Cross, Western Port, in March 1979. The line and equation are the least squares linear regression of the points shown (r^2 = 0.978). The slope (0.0239) is in mg cm^{-2} day^{-1}. The slope was calculated for each sampling date and used as the best estimate of epiphyte biomass accumulation rate for that date.

TABLE III

Rates of biomass accumulation of epiphytes on leaf blades of *Heterozostera tasmanica* at three sites in Western Port and Port Phillip Bay in μg cm^{-2} day^{-1}. Rates were determined by linear regression as illustrated in Fig. 3. r^2 for the linear regressions are given in parentheses

Month	Charing Cross	San Remo	Edwards Point
Aug. '78	5.7 (0.80)	44.6 (0.92)	31.3 (0.86)
Oct. '78	9.7 (0.93)	15.7 (0.95)	36.8 (0.99)
Nov. '78	9.8 (0.91)	19.5 (0.90)	*
Dec. '78	24.4 (0.95)	58.4 (0.92)	35.8 (0.80)
Jan. '79	8.8 (0.72)	14.9 (0.99)	46.4 (0.95)
Feb. '79	12.9 (0.82)	48.3 (0.99)	104 (0.92)
Mar. '79	23.9 (0.98)	50.1 (0.99)	91.8 (0.95)
May '79	27.4 (0.97)	15.7 (0.98)	21.8 (0.99)

*No data available.

When the leaf number is replaced by the length (in days) of the plastochrone interval, the rate of biomass accumulation can be expressed in μg cm^{-2} day^{-1} (Fig. 3). Least squares linear regression of these points from Charing Cross, March 1979, had an r^2 of 0.978 and a slope of 0.0239. That is, biomass of epiphytes accumulated on the leaf blades of *H. tasmanica* at a rate of 0.0239 mg cm^{-2} day^{-1} (or 23.9 μg cm^{-2} day^{-1}). Similarly, least squares linear regression for the straight line portion (e.g., leaves 2—6 for San Remo, January 1979, Fig. 2) on each sampling date was used to estimate the rates of epiphyte biomass accumulation (Table III). Rates at San Remo

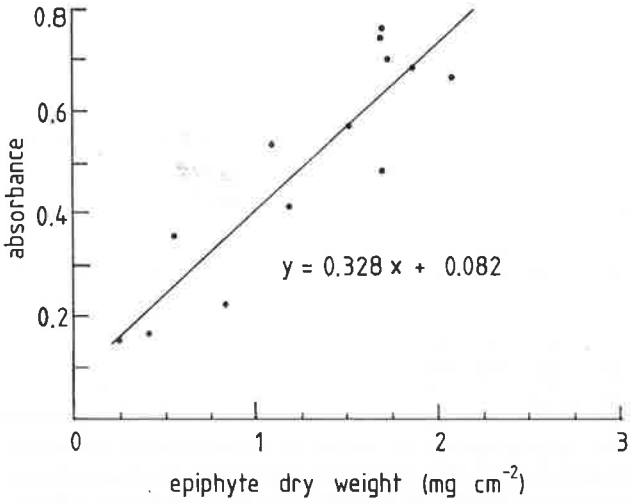

Fig. 4. Dry weight vs. absorbance of epiphytes on leaves of *Heterozostera tasmanica* at Charing Cross, Western Port, August 1979. The line and equation are the least squares linear regression of the plotted points (r = 0.878).

for November, December and January indicate the sharp increase in December at the time of a 'bloom' of epiphytes (Table III, Fig. 2). The rates of accumulation of epiphytes at Charing Cross, San Remo and Edwards Point varied from 8.8 to 104 μg dry weight cm^{-2} leaf surface day^{-1} during the spring and summer months of October to March. Rates above 40 μg cm^{-2} day^{-1} were recorded during December, February and March at San Remo and during January to March at Edwards Point. The highest rate of epiphyte biomass accumulation recorded in the present study was 104 μg cm^{-2} day^{-1} at Edwards Point during February 1979. Biomass accumulation rates during spring and summer were generally highest at Edwards Point and lowest at Charing Cross (Table III). Rates during May and August (autumn and winter) were usually lower than during summer (December to March).

The accumulated biomass of epiphytes on the leaf blades of *H. tasmanica* reduced light penetration to the leaf surface (Fig. 4). There was a direct relationship between dry weight of epiphytes and light absorbance over the range of 0.35—2.05 mg epiphytes cm^{-2} leaf surface. At an epiphyte dry weight of 2 mg cm^{-2} and, thus, an absorbance of 0.7 (Fig. 4), only 20% of the irradiance reaching the upper surface of the epiphytes would be transmitted to the upper surface of the leaf blade.

DISCUSSION

The present study has demonstrated a method for quantifying the rate of biomass accumulation of epiphytes on leaf blades of *H. tasmanica*. With minor modifications in measuring the plastochrone interval, the same meth-

od is applicable to most other seagrasses. Because seagrasses continually produce new substrate for epiphyte colonisation, a set of samples from a single date (plus an estimate of the plastochrone interval) can be used to estimate a rate.

The method also was attempted in an area of high silt accumulation where fine silt becomes enmeshed in the epiphyte community and may account for more than 50% of the total dry weight. This fine silt, however, was very easily disturbed and the physical handling involved in removing leaf blades from the field to the laboratory jarred various amounts of silt off the leaf. The method is not applicable at such sites.

The increase in epiphyte dry weight with leaf age found in the present study is consistent with the qualitative description of epiphyte colonisation on the seagrass *Z. marina* by Sieburth and Thomas (1973) and the higher epiphyte biomass reported on older than on younger leaves for various seagrasses (van den Ende and Haage, 1963; van der Ben, 1969; Johnstone, 1979; Borum and Wium-Andersen, 1980; Harlin, 1980).

The accumulated dry weight of epiphytes in the present study includes both living and dead plant and animal epiphytes and any debris which may have become enmeshed in the community. The rates measured in the present study are a measure of changes in the total epiphyte biomass over time and indicate the magnitude of the effect that epiphytes may have on seagrasses (for example, in reducing light intensity at the leaf surface, Fig. 4). The rate of biomass accumulation is not an estimate of net primary production because no attempt has been made to measure dissolved organic carbon losses, physical sloughing of epiphytes off the leaves, senescence of epiphytes or grazing. Grazing, particularly, may significantly reduce epiphyte biomass on seagrass leaves (Mook, 1977; Howard, 1982; Robertson and Mann, 1982; Van Montfrans et al., 1982).

The conditions for epiphyte growth and accumulation of biomass were more favourable at Edwards Point than at either San Remo or Charing Cross (Table III). At Edwards Point, ammonium concentration of the water was slightly higher and phosphate concentration was eight times higher than at the other two sites (Bulthuis and Woelkerling, 1983). These higher nutrient levels in the water may account for the higher rates of biomass accumulation of epiphytes observed at Edwards Point. Rates of epiphyte biomass accumulation also were higher at San Remo than at Charing Cross (Table III). Nutrient levels in the water were similar at these two sites (Bulthuis and Woelkerling, 1983), but snail populations were conspicuously abundant at Charing Cross and may account for the lower epiphyte biomass observed at this site (cf. Mook, 1977; Robertson and Mann, 1982; Van Montfrans et al., 1982). Rates of biomass accumulation of epiphytes at all sites were generally higher during December through March than during the other months that were measured (Table III). These may indicate seasonal differences in the rate of biomass accumulation of epiphytes and further study of seasonal trends is warranted. Increases in the rate of biomass accumulation

during summer may be particularly deleterious to *H. tasmanica* because field (Bulthuis, 1983b) and laboratory (Bulthuis, 1983a) studies indicate that *H. tasmanica* is most sensitive to light reduction during the warmer months.

Epiphytes occur ubiquitously on seagrasses and the effect on the seagrass may be deleterious because of shading, lowering of the bicarbonate concentration at the leaf surface (Sand-Jensen, 1977; Borum and Wium-Andersen, 1980) or competition for water-borne nutrients. In freshwater, Phillips et al. (1978) suggested that under conditions conducive to rapid growth of epiphytes, submerged angiosperms may die and be excluded from certain lakes. Similarly, the disappearance of the seagrass, *Posidonia australis*, from much of Cockburn Sound, Western Australia, has been attributed to growth and development of epiphytes (Cambridge, 1979). Sand-Jensen (1977) and Johnstone (1979) have suggested that seagrasses generally have high leaf growth rates and thus produce new photosynthetic tissue faster than epiphytes can shade, nutrient-filter, or damage the leaf tissue. Data from the present study provide evidence that epiphyte biomass accumulates during a 'bloom' at a rate fast enough to lower leaf photosynthesis significantly. For example, during December 1978, epiphyte biomass accumulation at San Remo was 0.0584 mg cm^{-2} day^{-1} (Table III), irradiance at the water surface at noon on a cloudless December (summer) day is about 1500 μmol m^{-2} s^{-1}, irradiance at the top of the seagrass canopy at San Remo was 12% of surface irradiance (Bulthuis and Woelkerling, 1983), the instantaneous light compensation level for a leaf blade of *Heterozostera tasmanica* at 20° C is about 30 μmol m^{-2} s^{-1} (Bulthuis, 1983a) and epiphyte dry weight vs. light absorption is characterised by absorbance = 0.328 dry weight + 0.0819 (Fig. 4). Under these conditions, 36 days after leaf emergence the epiphytes reduced light intensity below the light compensation point; and at noon on cloudy December days, this point was reached for leaves 11 days after emergence. Mean leaf life span at San Remo in December was 64 days from emergence to abscission (Bulthuis and Woelkerling, 1983). Thus, leaf blades at San Remo in December 1978 were so quickly shaded by epiphytes that they did not have a positive net photosynthesis, even at noon, for more than half of their life span. Similar conclusions were indicated for the 'bloom' at Edwards Point in February 1979. Therefore, high rates of biomass accumulation of epiphytes on *H. tasmanica* leaves may significantly lower photosynthesis of the seagrass by shading and deleteriously alter the chances of survival. On the other hand, at Charing Cross, where rates of epiphyte biomass accumulation were lower and light at the top of the seagrass canopy higher, on clear December days at noon, even the oldest and most heavily encrusted leaves received more than the light saturation level of irradiance. Shading by epiphytes, thus, would not be expected to be a major factor for *H. tasmanica* at Charing Cross, Western Port.

The present study has shown that rates of biomass accumulation of epiphytes on *H. tasmanica* leaves varied from 5.7 to 104 μg cm^{-2} day^{-1} at

three sites in Western Port and Port Phillip Bay. Rates were highest at Edwards Point where nutrient concentration of the water was highest, lowest at Charing Cross where the snail population was the densest and generally higher during December through March (summer) than during May (autumn), August (winter) or October (spring). At the rates measured in the present study, epiphyte biomass can accumulate fast enough to shade *H. tasmanica* leaf blades and significantly reduce the time span in which positive net photosynthesis of the leaf blade is possible.

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Some effects of light and temperature on growth and conceptacle production in *Fosliella cruciata* Bressan (Corallinaceae, Rhodophyta)

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Although taxa of the *Pneophyllum* (syn. *Heteroderma*; see Chamberlain, 1983)–*Fosliella* complex (Corallinaceae, Rhodophyta) are among the most common and prolific marine epiphytes in many parts of the world (e.g. Chamberlain, 1977a; Ducker *et al.*, 1977; Harlin, 1980; Humm, 1974), data on their growth rates and conceptacle production are almost entirely lacking. However, during the course of experimental studies on morphological and anatomical variability in southern Australian representatives of this complex, some data were obtained on the effects of differing photon flux densities and temperatures on growth rates and conceptacle production in plants of *Fosliella cruciata* Bressan (in Bressan *et al.*, 1977). These data are considered here in relation to results published by Bressan *et al.* (1979), Bressan & Tomini (1980, 1982), and Chamberlain (1977b) for species of *Fosliella* and in relation to available growth data for other taxa of non-geniculate Corallinaceae.

Populations of *Fosliella cruciata* (Fig. 1) growing on leaves of the seagrass *Amphibolis antarctica* (Labillardiere) Sonder & Ascherson ex Ascherson were collected periodically during April–June (autumn) from tidepools on the reef at the Sorrento back beach, Victoria, Australia and returned to the laboratory for subseqent spore inoculation within 24–48 h. At this locality, tetrasporangial plants of *Fosliella cruciata* are present throughout the year, but the tetraspores appear to be viable only at certain seasons; virtually all tetraspores isolated from plants collected at times other than April–June failed to germinate.

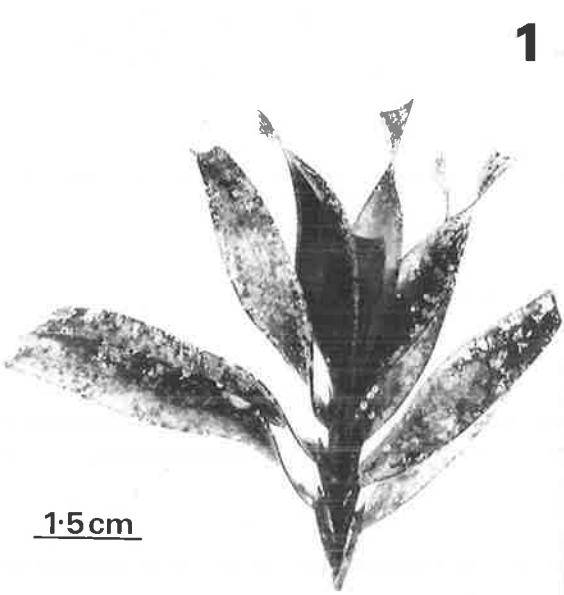
Experiments were conducted on a cross-gradient growth table (Yarish *et al.*, 1979) using all combinations of two light and three temperature regimes. The two light regimes, supplied by cool white fluorescent tubes, provided a photon flux density of 3–6 μmol m^{-2} s^{-1} or 12–25 μmol m^{-2} s^{-1} on an 18 h light : 6 h dark photoperiod. These are referred to as the low and high light regimes, respectively. The temperatures used for both light regimes were 9.5°C ± 1.5°C, 15°C ± 1°C and 21.5°C ± 1.5°C and are referred to as the 10°C, 15°C and 22°C temperature regimes, respectively. These temperatures and light regimes fall within the range of conditions found in the tidepool from which the plants were obtained.

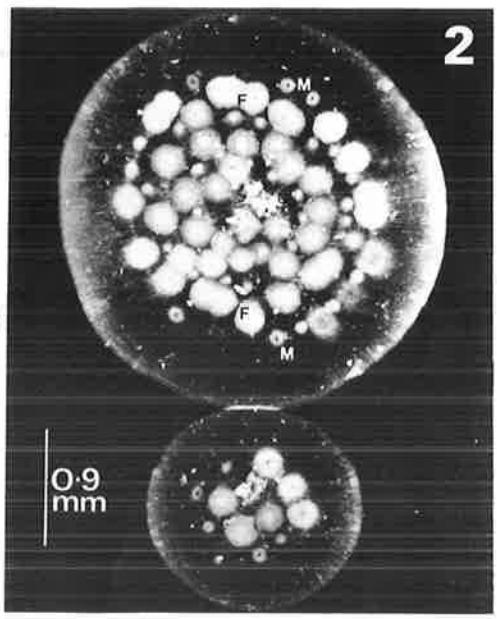
For spore isolation, field collected plants were placed in 90 mm diameter petri dishes containing 15–20 ml seawater, and conceptacles were broken open with small forceps to expose tetrasporangia. Within 2 min, mature tetrasporangia swelled up and burst, releasing the spores. Using micropipettes, relased spores were transferred onto 22 × 22 mm coverslips which had been placed in 35 mm diameter plastic petri dishes, each containing 5 ml of PES culture medium (McLachlan, 1973) modified by using orthophosphate instead of glycerophosphate, by adding 0.5 mg/l GeO_2 to prevent diatom growth, and by omitting Tris. For each treatment, 10–25 replicate 35 mm diameter petri dishes, each containing approximately 20 spores, were employed.

The inoculated petri dishes were placed on the cross-gradient growth table at loci representing the various light–temperature regimes. During preliminary experiments, a high percentage of germination resulted at 15°C and 22°C, but no spores germinated at 10°C. Subsequently, all spores were germinated at 15–22°C in the high light regime and then some were transferred to 10°C after 5 days. Once germinated (i.e. 5 days after inoculation), all plants from each petri dish were placed in one of a series of 120 ml glass culture dishes containing 80 ml of modified PES. Media were changed weekly and where necessary, 50 mg/l benzylpenicillin was used to destroy blue-green algae and bacteria.

After 26–33 days and/or after 65–72 days, all plants were photographed, surface areas of individual plants were determined from the photographs, and growth rates (increase in surface area per day) of individual plants were calculated. In addition, the percentage of plants producing conceptacles for each regime was determined and the density of conceptacles per mm^2 of thallus surface was calculated for reproductively mature individuals.

The growth and development of *Fosliella cruciata* plants from spores is affected both by temperature and photon flux density (Table 1). Based on results of Mann–Whitney tests, thallus growth after 26–33 days in culture is significantly greater ($P < 0.001$) at 15°C and at 22°C than at 10°C within both the low and high light regimes. With-





Figs 1, 2.
Fig. 1. Population of *Fosliella cruciata* plants on leaves of *Amphibolis antarctica* from Sorrento, Victoria, Australia. LTB 12528.
Fig. 2. Sixty-five day old conceptacle bearing plants of *Fosliella cruciata* cultured at 22°C and a photon flux density of 12–25 μmol m^{-2} s^{-1}. Note male (M) and female (F) conceptacles.

in a given light regime, however, significant differences ($P < 0.05$) did not occur between plants grown at 15°C and 22°C.

It appears that 10°C is not conducive to spore germination or thallus development. Spores could not be germinated at 10°C, and 75–80% of the sporelings transferred to 10°C after germination at higher temperatures died within 14 days. After 26–33 days, the growth rate of surviving plants cultured at 10°C in the low light regime was not significantly different ($P < 0.05$) from those cultured at 10°C in the high light regime, and based on differences in mean growth rates (Table 1), thallus growth at 10°C was only 0.04–0.15 times that of plants grown at 15°C. Moreover, with a single exception, all plants grown at 10°C remained sterile. Thus at 10°C, the adverse effects of low temperature appear to override any influence of differences in photon flux density in these experiments.

For plants cultured at 15°C and 22°C (Fig. 2), photon flux density differences influenced thallus growth more than temperature differences. At both temperatures, growth rates of plants cultured in the high light regime were significantly greater ($P < 0.001$) than those grown in the low light regime. Mean growth rates after 26–33 days were 3.2–5.4 times greater for plants grown in the high light regime than for plants grown in the low light regime (Table 1), and while 68–72% of the high light regime plants had produced conceptacles after 26–33 days, all plants grown in the low light regime remained sterile.

To determine whether time in culture could affect growth and conceptacle production, the plants cultured at 15°C and 22°C in the low light regime were allowed to develop further and examined again after 65–72 days (Table 1). After 65–72 days, 56–63% of the plants had produced conceptacles whereas none had produced conceptacles after 26–33 days. Moreover, the growth rates of the 65–72 day plants cultured at 15°C were significantly higher ($P < 0.001$) than those maintained at 22°C. No such differences occurred between the two groups of plants after 26–33 days, however, and this implies that at photon flux densities of 3.0–6.0 μmol m^{-2} s^{-1}, *sustained* growth is better at 15°C than at 22°C.

Plants maintained in low light at 15°C or 22°C for 65–72 days grew significantly more slowly ($P < 0.001$) than plants cultured in high light at 15°C or 22°C for 26–33 days, and fewer

Table 1. Growth rates and conceptacle production for *Fosliella cruciata* plants cultured on an 18 h light : 6 hr dark photoperiod under various experimental conditions

Temp. (°C)	Photon flux density (μmol m^{-2} s^{-1})	No. of plants examined	26–33 days in culture: Growth rate (μm^2/day) Mean	26–33 days in culture: Growth rate (μm^2/day) Range	Plants with conceptacles (%)	65–72 days in culture: Growth rate (μm^2/day) Mean	65–72 days in culture: Growth rate (μm^2/day) Range	Plants with conceptacles (%)
10	3.0–6.5	23	14	7–30 (45)	0			
15	3.0–6.5	120	93	(25) 50–150 (200)	0	342	(50) 120–550 (850)	63
22	3.0–6.5	100	94	(20) 40–140 (260)	0	156	(50) 75–350 (710)	56
10	12–25	20	20	10–40 (70)	5			
15	12–25	116	494	(150) 200–850 (1000)	72			
22	12–25	86	510	(140) 250–800 (1200)	68			

low light plants had produced conceptacles (Table 1). While growth occurred most rapidly at 22°C in high light over a period of 26–33 days, the 65–72 day experiments provide an indication that 15°C may be a more favourable temperature for long term growth. Plants grown under all four sets of conditions, however, had reached reproductive maturity, and this implies that under field conditions, reproduction will occur over a range of photon flux densities provided water temperatures of 15°C–22°C occur for periods of up to 72 days.

Among reproductively mature individuals, conceptacle density was not affected significantly by photon flux density or temperature (15°C *vs* 22°C). In all regimes tested, conceptacle densities of (1–)3–7(–11) conceptacles per 10 mm^2 thallus surface were found (Fig. 2), with mean densities ($n = 30$) of 4.0–6.0 conceptacles per 10 mm^2 (S.D. 2.0–2.7), depending on the treatment.

The only other published data on growth rates in the *Pneophyllum–Fosliella* complex are provided by Bressan *et al.* (1979) and Bressan & Tomini (1980, 1982). Based on 27 day experiments, Bressan *et al.* (1979) concluded that light is one of the primary factors affecting growth, that growth of some species was greater under 'high light intensities', and that *F. cruciata* grew more rapidly under 'diffuse lighting conditions' than under 'artificial incident light'. Unfortunately *Bressan et al.* (1979) did not empirically define the light regimes used or record the growth rates in terms of increase in thallus surface area, thus precluding meaningful comparisons with results from the present study. Subsequently, Bressan & Tomini (1982) concluded from similar experiments that temperature had the greatest effect on the growth of *Pneophyllum–Fosliella* crusts and that growth was fastest under summer conditions and slowest in winter and spring. The identical data also appeared in a second version (Bressan & Tomini, 1980), and in both instances it is not clear exactly what levels of illuminance were employed during the temperature experiments or whether the photoregime was varied or kept constant. Moreover, the graphic data of Bressan & Tomini (1980, 1982) do not allow for meaningful comparisons with data obtained during the present study. Data on conceptacle production were not provided in any of the above papers.

Chamberlain (1977b), working with plants of *Fosliella farinosa* (Lamouroux) Howe, found that the first signs of conceptacle production appeared 22.5 wk after inoculation of bispores and that mature bisporangia were produced after an additional 4 wk. In southern Australian plants of *F. cruciata,* in contrast, gametic conceptacles were produced within 4–4.5 wk of inoculation of tetraspores. The comparatively slower development reported by Chamberlain (1977b) may be due to differences in the species examined, differences in the spore types used, or differences in the temperatures (Chamberlain used 10°C) or photoperiods (Chamberlain used a 8 h light : 16 h dark photoregime) employed in the two studies.

The rates of growth and of conceptacle production in *Fosliella cruciata* reported here may be much higher than in plants of more massive epilithic taxa of nongeniculate Corallinaceae (see Johansen 1981, p. 149 for a summary of avail-

able data), and this may help explain why taxa of the *Pneophyllum–Fosliella* complex are capable of surviving and developing so prolifically as epiphytes on hosts whose leaves (seagrasses) or thalli (algae) normally live for less than 12 months. The short life spans of epiphytic taxa of the *Pneophyllum–Fosliella* complex contrast markedly with those of certain deep water rhodolites (coralline algal nodules). Bosellini & Ginsburg (1971) estimated that 3 cm diameter rhodolites growing off Bermuda were 75 yr old while Adey & MacIntyre (1973, p. 887) suggested that 20–30 cm diameter rhodolites from deep water could have core ages of at least 500–800 yr. However, in common with data provided by Adey (1970) for six epilithic species, it appears that temperature and light are major factors affecting the growth rates of both thin crusted epiphytic taxa and the thick crusted epilithic taxa of Corallinaceae. It also appears that different species may have different light and temperature optima, and further studies of other taxa are now required to elucidate more fully the effect of these parameters on the growth and reproduction of nongeniculate Corallinaceae.

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PHYCOLOGICAL REVIEWS 8

The *Audouinella* (*Acrochaetium–Rhodochorton*) complex (Rhodophyta): present perspectives

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CONTENTS

I. INTRODUCTION

The *Audouinella* (*Acrochaetium-Rhodochorton*) complex contains a diverse but distinctive assemblage of marine and freshwater red algae (*Rhodophyta*). Marine forms occur in all seas, and although dense populations sometimes develop, plants of most species generally constitute an inconspicuous but often regular component of many littoral and sublittoral communities. Freshwater forms, which account for less than 10% of the described species, most commonly grow in streams where, occasionally, they can become a dominant organism within localized areas. Individual plants may be epiphytic, endophytic, epizoic, endozoic, or epilithic. Some species occur regularly on rock but most usually grow on/in a biotic substrate. Collectively, members of this complex often are referred to as acrochaetioid or audouinelloid algae, both terms being derived from generic names.

Compared to most other Rhodophyta, acrochaetioid algae have a simple morphology, but their taxonomy is rather more complex. During the period 1971–1980, numerous floristic, monographic, morphological, ecological and other accounts containing data on these algae have been published, and although our understanding of certain aspects of their biology has improved measurably, acrochaetioid taxonomy appears to have become more confused and bewildering than ever (e.g. see comments by Abbott & Hollenberg, 1976, p. 308; Dixon & Irvine, 1977, p. 57; Garbary, 1979d, p. 477; Kornmann & Sahling, 1977, p. 174; Stegenga, 1979, p. 6). Since 1970, at least fourteen different classification systems have been used for these algae. Moreover, species concepts and delineations generally continue to be vague and changeable; generic concepts remain unresolved; and higher level taxonomic concepts have become the subject of inconclusive debate. This problematical situation has deep historical roots, and a widespread consensus on acrochaetioid taxonomy still appears to be rather elusive since much remains to be learned about the life histories (i.e. both sexual cycles and apomictic cycles) of these organisms and about the extent of variability which can occur in attributes considered to be of taxonomic importance.

Following a brief background summary of the basic morphological features of acrochaetioids, the current taxonomic problems associated with this group of algae will be examined. Specific topics to be considered include an analysis of the relevant taxonomic literature, recent nomenclatural developments, current generic concepts and classification schemes, assessments of generic attributes, species level taxonomy, family and ordinal classification schemes, and other studies of potential taxonomic interest. With two exceptions, this account does not include papers published after 1981.

Because so many classification schemes are currently used, the concepts associated with many of the generic names differ from paper to paper. Throughout this review, the generic epithets used in conjunction with particular species are those employed in the paper cited. No single classification scheme is adopted here since this would necessitate making new nomenclatural combinations and could also potentially bias an assessment of the present state of affairs. Unless otherwise indicated, all the binomials used in conjunction with a particular specific epithet refer to the same biological species, and nomenclature (author citations) follows that used in the papers cited.

II. BASIC MORPHOLOGY

Thalli of acrochaetioid algae are heterotrichous and composed of simple or branched monosiphonous filaments (Figs 1–18). Anchorage to the substrate is effected by a single cell (Figs 1–4, 7–9) or by a multicellular prostrate system (Figs 5, 10). The latter type of prostrate system may be filamentous or pseudoparenchymatous, and sometimes forms the bulk of the thallus. Erect filaments never become pseudoparenchymatous, may be rare or abundant, and vary in extent from one to two celled unbranched structures to sparsely or highly branched structures up to 5 mm (rarely to 50 mm) long (Figs 1–5, 7–11, 13–18). Cells of erect filaments vary in shape from moniliform to cylindrical (Figs 1–5, 7–10) and depending upon the species, cells each contain one or more chromoplasts of various shapes (Figs 4, 6, 12). Chromoplasts of many species also may contain one or several pyrenoids (Figs 6, 12).

In most species, apomictic (asexual) reproduction occurs by means of monospores; these are produced in monosporangia borne in various arrangements on the erect or in some species

also on the prostrate filaments (Figs 5, 7–10). Monospores appear to be the most common and/or the only known mode of reproduction in the majority of acrochaetioid algae, although in a few species monospores have never been recorded. In some taxa, apomictic reproduction may also occur by means of bispores, apomeiotic tetraspores and/or multipartite spores, all of which are also produced in sporangia. Under culture conditions, new plants can also be grown from vegetative fragments of older plants (e.g. see Pearlmutter & Vadas, 1978).

Sexual reproduction has been documented only for a small minority of species and the complete sexual cycle is known for fewer species still. Gametangial plants may be monoecious or dioecious. Male gametes are produced within spermatangia (Figs 1, 2, 13, 14), which may look like miniature monosporangia and are borne singly or in clusters on erect or in some cases also on prostrate filaments. Female gametangia or carpogonia (Figs 3, 15) may be sessile on cells of vegetative filaments, intercalary in vegetative filaments, or terminal on 1–2 celled stalks. Postfertilization development can follow one of several distinct patterns; these are considered in greater detail in Section VI below.

The complete sexual cycle may involve two or three distinct morphological phases (see Figs 19–22 in Section VI). In species with three distinct phases, two may be concordant morphologically or all three may differ in appearance from one another. With several known exceptions, postfertilization development involves the production of a carposporophyte (Figs 4, 16–18), a small spore-producing phase which remains permanently attached to the old parent progenitor plant. With a single known exception, the spores are borne singly (undivided) within sporangia, are presumably diploid and upon germination give rise to a third distinct, free-living tetrasporangial phase (or tetrasporophyte) which may or may not have a morphology similar to the gametangial phase. So far as is known, meiosis in this sequence ultimately occurs within sporangia formed on filaments of the final morphological phase and results in the production of four spores. Such spores are termed tetraspores and are said to develop within tetrasporangia (Fig. 11). In the absence of cytological data or culture-based evidence, it apparently is not possible at present to distinguish morphologically between tetrasporangia in which the spores are produced meiotically and tetrasporangia in which the spores are produced mitotically.

Further data on the basic morphology of acrochaetioid algae can be found in the papers of Stegenga, West, and Woelkerling listed in the references (Section XI).

III. THE TAXONOMIC LITERATURE

The taxonomic literature on acrochaetioid algae can be categorized into four groups: monographic accounts (Table 1), containing data generated from the direct, comparative examination of plant material; taxonomic reviews and proposals (Table 2), containing ideas generated mostly from analyses of pre-existing literature; regional floristic accounts (Table 3), commonly summarizing and consolidating previously published descriptive data; and checklists and catalogues (Table 4), primarily containing records of species occurrence. In addition, censuses of described taxa have been published by De Toni (1897 *et seq.*), Hamel (1927, 1928b), Papenfuss (1945, 1947) and Dawson (1962). A further unpublished census has been prepared by Aziz (1965) and extensive data are contained in the *Index Nominum Algarum* (Silva, 1977).

A number of important points emerge from analyses of the above tables and of the census data. Firstly, a world monograph of the group never has been published. Since 1950, only six regional monographic accounts have appeared (Table 1) of which only one (Woelkerling, 1971) is southern hemisphere based. No critical monographic studies of freshwater representatives have appeared since Israelson (1942). Secondly, virtually all of the floristic accounts (Table 3) and a vast majority of recent checklists (Table 4) involve regions in the northern hemisphere; comparatively few data are available for the southern hemisphere. Moreover, many of these publications list few species, suggesting that other inconspicuous taxa may have been overlooked. Thus while acrochaetioid algae are recorded from many regions, it has not been possible to produce any reliable biogeographic analysis of the group because data are still too scant. Thirdly, with the exceptions of Dixon & Irvine (1976) and Garbary (1979d), all classification proposals emanating from review type papers (Table 2) have involved recognition of two or more genera,


1
2
3
4
5
6
10 μm 1-4
60 μm 5
20 μm 6

whereas most classification proposals emanating from monographic accounts (Table 1) involve recognition of a single genus or of one 'natural' genus and one form-genus. The only taxonomic proposals based primarily on experimental data obtained from laboratory cultures are those of Stegenga (1979, see also Stegenga & Vroman, 1977) who recognized 5(–7) genera.

An analysis of data obtained from the *Index Nominum Algarum* in April 1980 together with additional non-overlapping data from other sources shows that at least 390 species and infraspecific taxa have been described, that at least 24 generic names have been employed, and that at least 1007 nomenclatural combinations have been made for acrochaetioid algae (Table 5). Over half of the species were described during the period 1900–1949 with declining numbers since (Table 6), but the nomenclatural shuffling has continued unabated (e.g. Dixon & Irvine, 1976; Garbary, 1979d; Woelkerling, 1971).

IV. RECENT NOMENCLATURAL DEVELOPMENTS

Historical accounts of generic and familial nomenclature have been provided by Drew (1928) and Woelkerling (1971). Since 1971, additional data have appeared for four generic names and one family name. According to Silva (in Farr *et al.*, 1979), the name *Acrochaetium* was first published by Naegeli in 1858 (in Naegeli & Cramer) and not in 1862 as is usually quoted. Moreover, the generally cited lectotype species, *A. daviesii* (see Drew, 1928, p. 147; Papenfuss, 1945, p. 302), is not tenable because it was not mentioned in the initial presentation of the genus. Naegeli (1858, p. 532) originally included four species: *A. secundatum* (Lyngbye) Naegeli, *A. lanuginosum* (Dillwyn) Naegeli, *A. griffithsianum* Naegeli, and *A. microscopicum* (Naegeli in Kuetzing) Naegeli. Of these, the present author has examined the type collections of *A. secundatum* and *A. microscopicum* and on this basis, *A. secundatum* (Lyngbye) Naegeli, 1858, p. 532 (basionym: *Callithamnium daviesii* var *secundatum* Lyngbye, 1819, p. 129, pl. 41, Figs B4–6) is chosen here to serve as lectotype species of *Acrochaetium*. The species has been studied recently by Garbary (1979a, 1979c, as *Audouinella*), by Stegenga & Mol (1980, as *Chromastrum*) and by Woelkerling (1973b, as *Colaconema*).

Silva (1980a) has proposed official conservation of the widely used orthographic variant *Audouinella* Bonnemaison (1828, p. 146) against the original spelling *Auduinella* Bory (1823, p. 340). Silva (1980a; also Silva in Farr *et al.*, 1979) also has noted that *A. miniata* Bory is the correct lectotype species but that *A. miniata* is a taxonomic synonym of *A. hermanii* (Roth) Duby, which is usually listed as lectotype species.

Garbary (1980) concluded that *Liagorophila* Yamada was congeneric with *Audouinella* and he transferred the type species of *Liagorophila, L. endophytica* Yamada, into *Audouinella* using the name *A. yamadae* Garbary because the specific epithet 'endophytica' has been used previously in *Audouinella*.

Rhodothamniella, first introduced as a nomen nudum by Feldmann (1954, introduction and p. 68), has been published validly by Christensen (1978, see also Feldmann, 1981). Both authors list *R. floridula* (Dillwyn) J. Feldmann as type species. Garbary (1979d, p. 488) rejected *Rhodothamniella* '. . . as a distinct genus even pending valid publication'.

The family name Acrochaetiaceae was first published validly by Taylor (1957) rather than Fritsch (1944) and has been proposed for conservation against Rhodochortonaceae Nasr (1947) by Silva (1980b).

With the realization that different phases in the sexual cycle of some species had been described originally as distinct taxa (see Section VI and Table 8), several opinions have arisen with respect to which of the available names is

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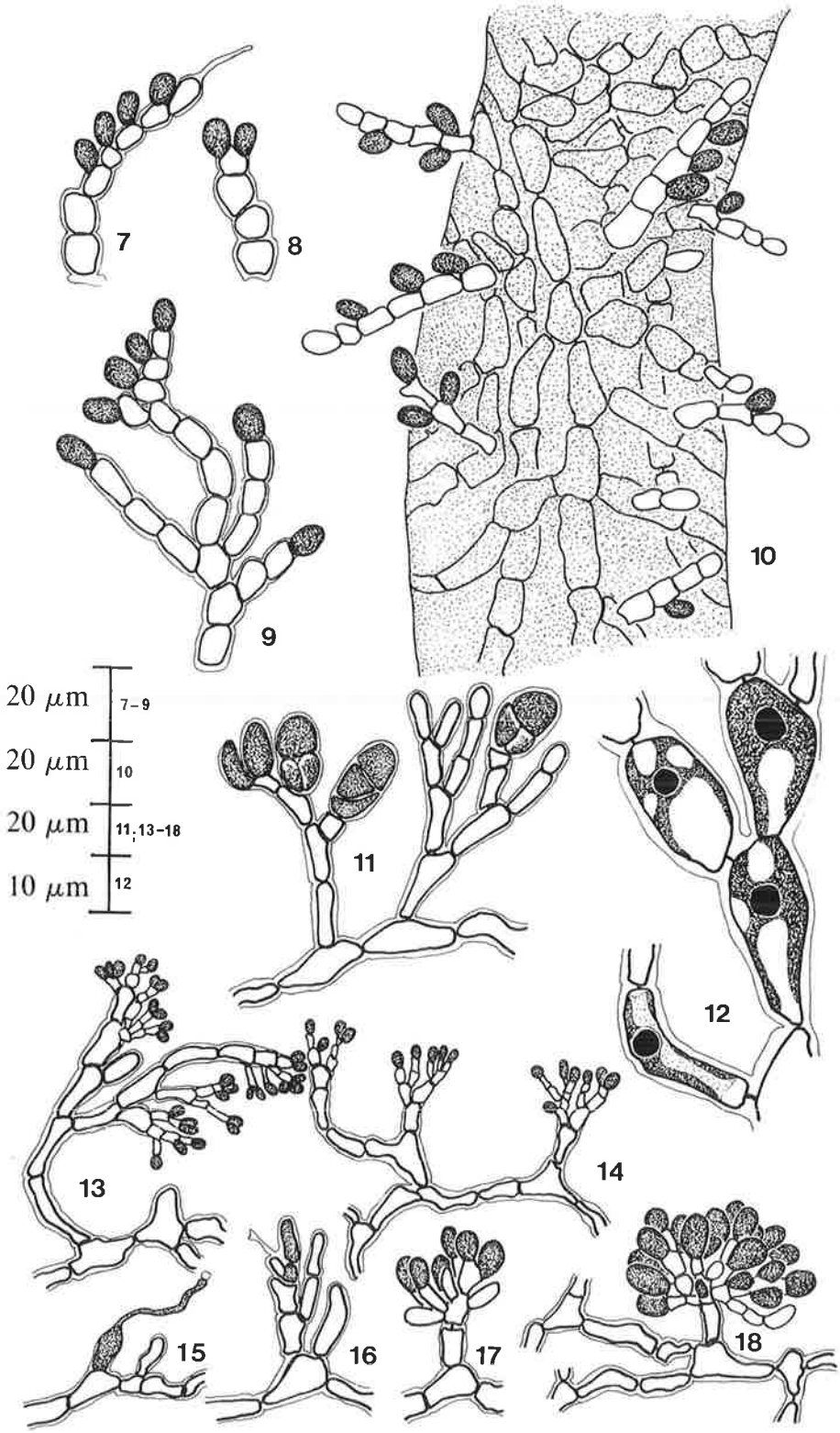
Figs 1–6. Representative acrochaetioid algae. Figs 1–4 adapted from Woelkerling, 1971; Figs 5–6 adapted from Woelkerling, 1973b.

Figs 1, 2. Male plants of *Audouinella unifila* (Jao) Woelkerling with spermatangia.

Figs 3, 4. Female plants of *A. unifila* bearing carpogonia (Fig. 3) and a carposporophyte (Fig. 4). Note chromoplasts.

Fig. 5. Monosporangial plant of *A. secundata* (Lyngbye) Dixon.

Fig. 6. Chromoplasts in cells of *A. secundata*. Note pyrenoids.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correct in such cases. In this paper, the oldest available legitimate specific epithet will be used for all phases in the sexual cycle; this conforms to Article 11.3 of the International Code of Botanical Nomenclature. This approach contrasts with the suggestion of Garbary (1979d, p. 481–2) that nomenclatural priority be given to the tetrasporangial generation rather than the gamete bearing generation. It also contrasts with the practice of using different binomials for the various phases (e.g. see Stegenga & Van Wissen, 1979).

V. GENERIC CONCEPTS AND CLASSIFICATION SCHEMES

The generic classification of acrochaetioid algae has been attended by several rather different taxonomic philosophies in recent years. Dixon & Irvine (1976, p. 537; 1977, p. 75) have concluded that the described species '. . . form an interrelated reticulum and there appears to be no logical basis for the delineation of genera', a view shared by Garbary (1979d). Similarly, Russell (1978, p. 350) draws an analogy between the Acrochaetiaceae and Ectocarpaceae (Phaeophyta) where he indicates that '. . . we have been overliberal in the establishment of genera'. These views contrast with those of Stegenga (1979, p. 22, 23) who defines a genus as a cluster of related species, indicates that these clusters need not be determined solely by the existence of obvious discontinuities and concludes '. . . that division into a number of different genera would be rather convenient in a group as large as the Acrochaetiaceae'. Other authors (e.g. Bold & Wynne, 1978, p. 481, Kornmann & Sahling, 1977, p. 174) also maintain multigeneric systems noting various reservations.

At least twenty-four different classification schemes involving taxa of generic and higher rank have been proposed for acrochaetioid algae since 1900 and at least fourteen of these have been employed in papers published since 1970 (see Tables 1–4). In these post-1970 schemes, twelve different generic names have been involved and the concepts attached to most of these names have varied widely.

Three of the post-1970 schemes do not involve use of any attributes related to sexual reproduction. Two single genus schemes (one based on *Rhodochorton* sensu Drew, 1928 and one based on *Audouinella* sensu Dixon & Irvine, 1976) have been employed; *Audouinella* has nomenclatural priority as a name (Woelkerling, 1971). A four genus scheme based on chromoplast shape/position has been used rather extensively since introduced by Papenfuss (1945, 1947).

Five other classification schemes utilized since 1970 involve, at least in part, attributes associated with sexual reproduction. Woelkerling (1971) referred all taxa known to reproduce sexually to *Audouinella* (the status of *Kylinia* and of *Liagorophila* were considered doubtful) and all other taxa to the form-genus *Colaconema*. Humm (1979) has used spermatangial arrangement to delineate two genera (*Acrochaetium, Kylinia*) while Abbott & Hollenberg (1976) have employed spermatangial arrangement and chromoplast morphology to distinguish three genera (*Acrochaetium, Kylinia, Rhodochorton*). Stegenga & Vroman (1977; see also Stegenga, 1979) have delineated 5(–7) genera based on sexual cycle 'isomorphy' or 'heteromorphy', chromoplast morphology, pyrenoid occurrence, and mode of spore germination. Some authors have employed the older scheme of Feldmann (1962) in which eight genera are recognized based on sexual cycle 'haplobionty' or 'diplobionty', chromoplast morphology, spermatangial ar-

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Figs 7–18. Representative acrochaetioid algae. Figs 7–9 adapted from Woelkerling, 1972; Fig. 10 adapted from Woelkerling, 1973a; Figs 11–18 adapted from Woelkerling, 1971.

Figs 7–9. Monosporangial plants of *Audouinella microscopica* (Naegeli ex Kuetzing) Woelkerling.

Fig. 10. Monosporangial plant of *A. infestans* (Howe & Hoyt) Dixon endozoic in a hydroid.

Fig. 11. Portion of a tetrasporangial plant of *A. liagorae* (Boergesen) Woelkerling.

Fig. 12. Chromoplasts in cells of *A. liagorae*. Note pyrenoids.

Figs 13, 14. Portions of male plants of *A. liagorae* bearing spermatangia.

Figs 15–18. Portions of female plants of *A. liagorae*. Note carpogonia just prior to (Fig. 15) and shortly after (Fig. 16) karyogamy, and two subsequent stages in carposporophyte development (Figs 17–18).

Table 1. Important monographic accounts of acrochaetioid algae.

Author and date	Geographic region	No. species	No. genera	Comments
Abbott, 1962	Tropical Pacific and Bermuda	15	1	Marine taxa associated with *Liagora* (Rhodophyta)
Boergesen, 1915	Virgin Islands	22	1	Marine
Brand, 1897	Germany	7	1	Freshwater
Collins, 1906	North America	12	1+1*	Marine
Drew, 1928	Pacific Coast of North America	34	1	Marine
Hamel, 1925	France	7	3	Freshwater
Hamel, 1927 (1928a)	France	28	2	Marine
Israelson, 1942	Sweden	5	2	Freshwater
Jao, 1936	U.S.A. (Massachusetts)	11	2	Marine
Jao, 1941	China	6	1	Freshwater
Kylin, 1944	Sweden (W. coast)	26	5	Marine
Lee & Lee, 1974	Korea	9	1	Marine
Nakamura, 1941, 1944	Japan	20	1	Marine
Rosenvinge, 1909, 1923, 1935	Denmark	28	1**	Marine
Stegenga & Mol, 1980	Netherlands	12	3	Marine
Woelkerling, 1971	Southern Australia	26	1+1*	Marine
Woelkerling, 1973a	Western Sargasso Sea	6	1+1*	Marine
Woelkerling, 1973b	Northeastern U.S.A.	11	1+1*	Marine

* One true genus and one form genus. ** Based on statements in 1935.

rangement, and immediate postfertilization events.

There is no consensus as to which, if any, of the above schemes should be employed for acrochaetioid algae. In spite of whatever theoretical and phylogenetic merits underlie the Humm, Abbott & Hollenberg, Stegenga & Vroman, and Feldmann schemes, they have serious pragmatic shortcomings because data on sexual stages are lacking totally for over 80% of the described species (Stegenga, 1979; Woelkerling, 1971), thus making reliable generic placement difficult, presumptive or impossible. The Woelkerling (1971) scheme will allow for generic placement of all taxa but has been criticized as being unnatural (Garbary, 1979d), as causing an unnecessary proliferation of nomenclatural synonymy (Garbary, 1979d; Pedersen, 1976), and as '. . . carrying things too far' (Kumano, 1978). The three schemes which do not depend on sexual reproduction attributes also readily accommodate all taxa and thus potentially have considerable merit on utilitarian grounds. As noted below, however, these schemes have been criticized as well.

The remaining post-1970 classification schemes (Cordero, 1977; Guiry, 1978a; Kornmann &

Table 2. Important taxonomic proposals on and reviews of acrochaetioid algae.

Author and date	No. species listed		No. genera recognized	Comments
	Freshwater	Marine		
Agardh, 1892		4	2	Generic concepts and names
Batters, 1902		24	3	Generic names
Bornet, 1904		26	1+1*	Generic and specific concepts
Brand, 1910	8		2	Generic concepts
Dixon & Irvine, 1976		33	1	Generic concepts
Feldmann, 1962			8	Generic and family concepts
Garbary, 1979d	1	111	1	Generic concepts
Hamel, 1927 (1928b)		117	2	Generic concepts
Kylin, 1956			7	Generic concepts
Papenfuss, 1945, 1947	10	211	4	Generic concepts
Stegenga, 1979			5 (–7)	Generic concepts
Stegenga & Vroman, 1977			5 (–7)	Generic concepts

* One true genus and one form genus.

Table 3. Selected floristic accounts and descriptive studies published since 1900 which contain information on acrochaetioid algae. Species are marine unless otherwise indicated.

Author and date	Geographic region	No. species	Classification system used
Abbott & Hollenberg, 1976	U.S.A. (California)	18	Abbott & Hollenberg, 1976
Ardré, 1970	Portugal	13	Feldmann, 1962
Baardseth, 1941	Tristan du Cunha	8	Hamel, 1927 (?)
Boergesen, 1902	Faeroes	16	uncertain
Boergesen, 1927	Canary Is.	10	Boergesen, 1915
Boergesen, 1937	South India	7	Boergesen, 1915
Boergesen, 1942, 1952	Mauritius	6	Boergesen, 1915
Chapman, 1969	New Zealand	16	Papenfuss, 1945, 1947
Collins & Hervey, 1917	Bermuda	11	uncertain
Dawes, 1974	U.S.A. (Florida west coast)	5	Papenfuss, 1945, 1947
Dawson, 1953	Mexico (Pacific coast)	22	Papenfuss, 1947
Dawson *et al.*, 1964	Peru	6	uncertain
Dixon & Irvine, 1977	British Isles	33	Dixon & Irvine, 1976
Edwards, 1970	U.S.A. (Texas)	5	uncertain
Feldmann, 1939	France (Albères)	13	Hamel, 1927
Humm, 1979	U.S.A. (Virginia)	9	Aziz, 1965
Jaasund, 1965	Northern Norway	16	Feldmann, 1962 (?)
Jaasund, 1976	Tanzania	2	Woelkerling, 1971 (?)
Joly, 1965	Brazil (Sao Paulo)	6	Kylin, 1956
Jonsson, 1901	Iceland	3	uncertain
Kapraun, 1980	U.S.A. (N. Carolina)	6	Woelkerling, 1971
Kornmann & Sahling, 1977	Germany (Helgoland)	6	uncertain; possibly Papenfuss, 1947
Levring, 1937	Norway (west coast)	25	Levring, 1937
Levring, 1941	Juan Fernandez	6	Levring, 1937
Lund, 1959	Greenland (east coast)	6	uncertain
Nagai, 1941	Kurile Is.	2	Drew, 1928
Noda & Konno, 1981	Mid-Japan Sea	14	Papenfuss, 1947
Pankow, 1971	Baltic Sea	17	Papenfuss, 1947
Pascher & Schiller, 1925	Germany, Austria and Switzerland	4	Rosenvinge, 1909
Pedersen, 1976	Greenland (southern)	6	Papenfuss, 1945
Perestenko, 1980	Zaliv Petra Velikogo	5	uncertain
Pham-Hoang Ho, 1969	South Viet Nam	14	uncertain
Rueness, 1977	Norway	24	Papenfuss, 1947
Starmach, 1977	Poland	5 freshwater	uncertain
		8 marine	Papenfuss, 1947
Taylor, 1945	Pacific Ocean (eastern)	2	uncertain
Taylor, 1960	Tropical and subtropical Western Atlantic	38	Papenfuss, 1947
Weber van Bosse, 1921	Idonesia and adjacent regions	9	Weber van Bosse, 1921
Zinova, 1955	U.S.S.R. (Northern seas)	5	Papenfuss, 1947
Zinova, 1967	U.S.S.R. (Southern seas)	14	Papenfuss, 1947

Sahling, 1977; Kuhnemann, 1972; Levring, 1974; Starmach, 1977) provide no clear information on generic delineation and thus merit little consideration. Several, however, contain novel proposals, among which are the placement of *Rhodochorton* in the Bangiophyceae (Cordero, 1977, p. 20, 21) and the inclusion of *Nemalion* in the Acrochaetiaceae (Kuhnemann, 1972).

This plethora of classification schemes reflects not only how a number of different generalizations can emerge from a limited data bank but also how these generalizations are dependent both on which taxa have been examined and on the relative taxonomic importance various authors attach to different attributes. It also indicates that many uncertainties exist over the taxonomic reliability of the attributes used to delineate genera. As an end result, acrochaetioid classification at the generic level often is regarded as difficult or confusing (e.g. Abbott & Hollenberg, 1976; West, 1978). The single published attempt (Garbary, 1979d) to assess generic cir-

Table 4. Selected checklists and catalogues published during the period 1950–1980 which contain information on acrochaetioid algae.

Author and date	Geographic region	No. species	Classification system used
Adams, 1972	New Zealand (Wellington)	6	Woelkerling, 1971
Adams *et al.*, 1974	New Zealand (Stewart Is.)	8	uncertain
Basson, 1979	Saudia Arabia (Arabian Gulf)	3	uncertain
Boudouresque & Perret, 1977	Corsica	7	Feldmann, 1962
Caram & Jonsson, 1972	Iceland	10	uncertain
Christensen & Thomsen, 1974	Denmark	30	Papenfuss, 1945
Cordero, 1977	Philippines	9	Cordero, 1977
Dawson, 1954	Viet Nam (Nha Trang)	5	Papenfuss, 1947
Dawson, 1957	Eniwetok	4	uncertain
Dawson, 1961	Pacific Ocean (eastern)	49	Papenfuss, 1947
Feldmann, 1954	France (Roscoff)	26	Feldmann, 1954
(Additions: Magne 1978b)	France (Roscoff)	4	Feldmann, 1962
Funk, 1955	Gulf of Naples	11	uncertain
Giaccone, 1969	Italy	10	uncertain, possibly Hamel, 1927
Giaccone *et al.*, 1972	Sicily (Straits)	6	Feldmann, 1962
Guiry, 1978a	Ireland	19	Guiry, 1978
Hawkes *et al.*, 1978	N. British Columbia	7	Abbott & Hollenberg, 1976
Jorde, 1966	Norway (Bergen area)	14	Papenfuss, 1947
Kang, 1966	Korea	5	uncertain
Klavestad, 1978	Norway (Oslo Fjord)	12	Papenfuss, 1947
Kuhnemann, 1972	Argentina	9	Kuhnemann, 1972
I.K. Lee & Kim, 1977	Korea (Kwang Yan Bay)	4	Drew, 1928
R.K.S. Lee, 1980	Canada (Arctic)	6	Woelkerling, 1971
Levring, 1960	Chile	7	Hamel, 1927
Levring, 1974	Madeira	10	Levring, 1974
Lindstrom, 1977	U.S.A. (Alaska)	5	Abbott & Hollenberg, 1976
Munda, 1978	Iceland (Dyrafjordur)	7	Abbott & Hollenberg, 1976
Munda, 1980	Iceland (Borgarfjordur)	5	Dixon & Irvine, 1976
Nizamuddin *et al.*, 1979	Libya	2	uncertain
Noda, 1974	Japan (Sado Is.)	10	uncertain
Papenfuss, 1964	Antarctic and Subantarctic	7	Papenfuss, 1947
Papenfuss, 1968	Red Sea	4	Papenfuss, 1945
Pujals, 1963, 1977	Argentina	8	Papenfuss, 1947
Scagel, 1957	Canada (Br. Columbia) U.S.A. (N. Washington)	15	Papenfuss, 1947
Schneider *et al.*, 1979	U.S.A. (Connecticut)	3	Dixon & Irvine, 1976
Searles & Schneider, 1978	U.S.A. (N. Carolina)	12	Woelkerling, 1971 Papenfuss, 1947
Silva, 1979	U.S.A. (San Francisco Bay)	8	probably Abbott & Hollenberg, 1976
South, 1976a	Newfoundland, Labrador, St Pierre, Miquelon	9	Woelkerling, 1971
South, 1976b	Canada (East Coast)	14	Woelkerling, 1971
South & Adams, 1976	New Zealand (Kaikoura)	5	Woelkerling, 1971
South & Hooper, 1980	Newfoundland	8	Dixon & Irvine, 1976
Tsuda and Wray, 1977	Micronesia	4	uncertain
Velasquez *et al.*, 1975	Philippines	9	uncertain
Womersley & Bailey, 1970	Br. Solomon Is.	3	uncertain

cumscription with numerical taxonomic techniques unfortunately appears to be of limited value because all of the data were derived from second or third hand sources rather than from original observations, because the characters examined did not include ones related to the *types* of sexual cycles present because the character expressions were divided in an arbitrary manner which in many cases has little practical biological meaning (especially those relating to cell and spore size classes) and because no apparent discrimination was made in the data matrix between 'absent' and 'unknown' (the descriptions used for many taxa do not contain data for all

Table 5. Historical summary of generic names and numbers of basionyms and specific and subspecific taxa associated with acrochaetioid algae.

Generic name	No. of[1] basionyms	No. of specific and subspecific names	Generic name	No. of basionyms	No. of specific and subspecific names
Acrochaetium	153	287	*Erythrocladia*	1	1
Audouinella	11	141	*Grania*	—	1
Balbiana	1	2	*Kylinia*	4	54
Byssus	1	1	*Liagorophila*	1	1
Callithamnion	29	32	*Microthamnium*	1	1
Ceramium	—	1	*Pseudacrochaetium*	2	1
Chantransia	113	246	*Pseudochantransia*	2	9
Chantransiella	1	1	*Rhodochorton*	49	116
Chromastrum	—	65	*Rhodochortonopsis*	1	1
Cladophora	1	1	*Rhodothamniella*	—	4
Colaconema	9	25	*Thamnidium*	3	8
Conferva	7	7	*Trentepohlia*	—	1

[1] Excludes those names rejected on nomenclatural grounds for which new names have been established. Totals: basionyms, 390; names, 1007.

the characters and although these data are totally unknown they were scored as absent).

Against this background, data on the various generic attributes now can be considered.

VI. GENERIC ATTRIBUTES

Chromoplasts and pyrenoids

Chromoplast attributes have been employed more extensively than any other vegetative characteristics in delineating genera, and recently Magne (1978a, p. 153) has emphasized the variety of plastid construction present in acrochaetioid algae. Papenfuss (1945, p. 300) noted that cells of particular taxa may contain a few to many small discoid plastids, one parietal or laminate plastid, one or more spiral plastids, or one or more stellate plastids. Unfortunately, some subsequent authors (e.g. Dawson, 1953; Humm, 1979; Lee & Lee, 1974; Noda & Konno, 1981) adopted the term parietal rather than laminate, thus confusing plastid position (parietal) with plastid shape (laminate).

Moreover, chromoplast shape and number have not been used in a consistent manner for generic delineation. Thus, for example, *Rhodochorton* has been characterized as having cells which contain a few to many discoid plastids (Feldmann, 1962; Papenfuss, 1945; West, 1979) or as having cells which contain one or several parietal plastids (Stegenga, 1979). Abbott & Hollenberg (1976) characterized *Rhodochorton* both as having one to several plastids (p. 308) and as having a few to many small discoid plastids (p. 321). *Chromastrum* sensu Papenfuss (1945; see also Pedersen, 1976) includes taxa with one or more stellate plastids while *Chromastrum* sensu Stegenga (1979) is restricted to taxa with a single stellate plastid. Abbott & Hollenberg (1976) merge taxa with single stellate and single laminate plastids into one genus (*Acrochaetium*) while Feldmann (1981) places taxa with more than one parietal lobate-stellate plastid per cell into *Rhodothamniella*. The type species, *Rhodothamniella floridula* (Dillwyn) J. Feldmann also has been referred to *Chromastrum* (Papenfuss, 1945), to *Kylinia* (Papenfuss, 1947) and to *Rhodochorton* (Stegenga, 1979) partly on the basis of plastid structure.

Table 6. Numbers of new acrochaetioid taxa described during specified time periods. Cumulative total of taxa given in parentheses.

Time period (y)	No. of new taxa	Time period (y)	No. of new taxa
1777–1799	2 (–)	1890–1899	21 (110)
1800–1809	6 (8)	1900–1909	57 (167)
1810–1819	1 (9)	1910–1919	36 (203)
1820–1829	2 (11)	1920–1929	49 (252)
1830–1839	5 (16)	1930–1939	39 (291)
1840–1849	28 (44)	1940–1949	38 (329)
1850–1859	8 (52)	1950–1959	26 (355)
1860–1869	11 (63)	1960–1969	22 (377)
1870–1879	19 (82)	1970–1979	12 (389)
1880–1889	7 (89)	1980–	1 (390)

Although chromoplast shape appears to be more or less constant in some species, considerable variation occurs in other species. Woelkerling (1971, p. 14) summarizes much of the earlier literature, and variation within single plants has been reported since in field populations by a number of authors (e.g. Abbott & Hollenberg, 1976, p. 310, 317, 321; Boney, 1972a, p. 177; Dixon & Irvine, 1977, p. 99, 103, 114; Feldmann, 1981; Rueness, 1977, p. 34). West (1970a, p. 180) has noted that in cultures, plastid appearance can vary with cell age, and when plants are fixed in alcohol or formalin, plastids may lose their identity (West, *op. cit.*). In *Acrochaetium pectinatum*, West (1968, p. 97) found that in cultures, plastid shape could be affected by day length.

Stegenga (1979, p. 10) reported that chromoplast shape may differ in endophytic and erect filaments of a plant (see also Woelkerling, 1971, p. 14) as well as in separate parts of the erect system, but nevertheless Stegenga (*op. cit.*) concluded that chromoplast shape '. . . is a very reliable character if young cells, say those in 2nd to 6th position below the apical cell of the erect filaments, are considered'. Stegenga (1979, p. 17) also has advocated using plastid structure to assign to genera all species for which sexual cycle data are lacking (including endophytes which do not produce erect filaments). In view of the available evidence, however, such assignments could not be made confidently, especially for endophytic taxa. Woelkerling (1971, p. 67) moreover has shown that in field populations plastid shape can vary even in the first six cells of a filament and Boney (1972a, p. 177, Fig. 6) has noted similar variability in erect filaments of a predominantly endophytic species. Illustrations provided by Stegenga & Borsje (1977, p. 458, Fig. 5g, h) also show parietal lobate to stellate plastids in the second to sixth cells of a single erect filament; Stegenga & Borsje (1977, p. 461) describe all these plastids as stellate. Similar variation also has been found in plants of *Rhodochorton floridulum* (Stegenga, 1978, p. 285, Fig. 20). Finally, as noted by Stegenga & van Wissen (1979, p. 111), exact chromoplast structure is difficult to determine in taxa with small cells.

Some authors have used pyrenoid occurrence in conjunction with chromoplast attributes to help delineate genera. *Audouinella* sensu Stegenga (1979, p. 14) has been restricted to taxa in which cells possess one to several parietal plastids of irregular or spiral shape without pyrenoids. *Rhodochorton* sensu Abbott & Hollenberg (1976; see also Papenfuss, 1945; West, 1979, p. 114) has been delimited by the occurrence in each cell of a few to many discoid plastids without pyrenoids while Bold & Wynne (1978, p. 483) state that *Rhodochorton* has cells which contain several small discoid plastids with several pyrenoids. *Rhodothamniella* sensu Feldmann (1981; see also Christensen, 1978) has been characterized as having cells with three to twelve parietal lobate to stellate plastids each with a single pyrenoid.

Stegenga & Van Erp (1979, p. 446), however have concluded that: 'At present we have no insight into the importance of presence or absence of pyrenoids in determining systematic relationships . . .'. Woelkerling (1971, p. 15) concluded from field studies that the number of pyrenoids per plastid (zero, one, two or more) appeared to be a stable character and organized species into three groups on that basis (see also Woelkerling, 1973b) but Stegenga & Borsje (1977, p. 461) and Stegenga & Vroman (1976, p. 260, 274) have found subsequently that plastids in some taxa may have one or two pyrenoids and that high light intensity seemed to promote production of more than one pyrenoid per plastid. In addition, Garbary & Rueness (1980, p. 20) suggested that in *Audouinella tetraspora* some stages in the life history may have pyrenoids while others do not. Abbott & Hollenberg (1976, pp. 310, 313, 319, 321) moreover, described one species as having one or two pyrenoids present per plastid and indicated that pyrenoids may be present or absent in plastids of three other species. Thus it would appear that pyrenoid occurrence and numbers may have relatively limited value as taxonomic characters, and the same appears to be true of chromoplast attributes, at least at the generic level. In some cases, however, pyrenoid and chromoplast characters may be useful in keys to help separate taxa in which particular character states are known to be constant.

Spore germination and persistence

Spores of acrochaetioid algae may be septate (i.e. divide into two or more cells prior to producing filaments) or aseptate (i.e. give rise to filaments directly, and spores may be persistent (i.e. the spore remains readily recognizable in mature plants) or non-persistent (i.e. the spore soon loses its identity). Based on field and literature studies, Woelkerling (1971, p. 12) con-

cluded that these characters were too variable for purposes of taxon delineation.

Subsequently, however, these attributes have been used to help delineate several genera. Stegenga & Mulder (1979, p. 301, 305) limited *Chromastrum* to species in which the tetrasporophytes developed from septate spores; of the sixty species included in the genus (*op. cit.*, p. 305), thirty-five were placed generically *primarily* on the presence of septate spores. Stegenga (1979, p. 19) also limited *Kylinia* to taxa in which the tetrasporophyte developed from spores which germinated in a unipolar manner (one filament per spore).

Evidence obtained from culture studies appears to indicate clearly that spore germination and persistence attributes are of little taxonomic importance. Stegenga & Mulder (1979, p. 297, Figs 31–36) found that within a single sexual cycle of *Chromastrum collopodum*, spore germination may or may not be septate. West (1970a, p. 180, Fig. 13; 1979, p. 112) found both septate and non-septate spore germination patterns in *Rhodochorton concrescens* and *R. membranaceum*, and Stegenga & Vroman (1976, p. 260, Figs 1, 3) found the same situation in *Acrochaetium densum*. Stegenga & Van Erp (1979, p. 437) reported that in *Acrochaetium nemalionis*, haploid monospores showed bipolar germination while diploid monospores and carpospores showed unipolar germination. In *Rhodochorton purpureum*, tetraspores germinate either in a bipolar or unipolar fashion (Ohta & Kurogi, 1979; Stegenga, 1978; West, 1969). White & Boney (1969, p. 269) recorded the same patterns for monospores of *Acrochaetium endophyticum* Batters (non *Liagorophila endophytica* Yamada) and *A. infestans* as did West (1972a, p. 379) for *A. proskaueri*. Moreover Stegenga & Borsje (1976) found that spores persisted in haploid plants of *Acrochaetium dasyae* but not in diploid plants; West (1968) noted that spores may or may not persist in *Acrochaetium pectinatum*; and White & Boney (1971, p. 872) reported both persistent and nonpersistent spores in cultures of *A. asparagopsis*. These data do not support use of spore germination and persistence characters for use in generic delineation.

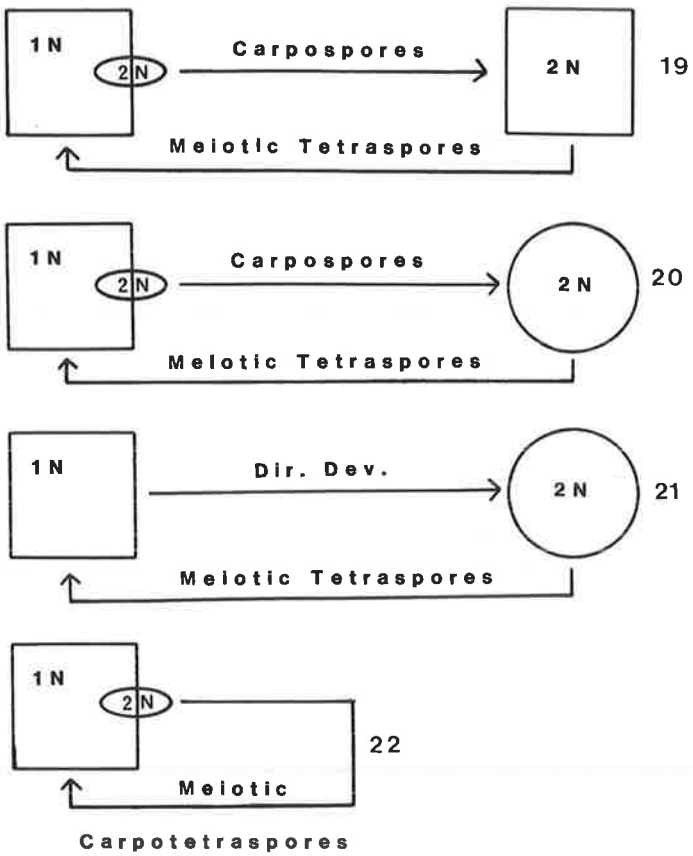
Spermatangial arrangement

In most species where they are known, spermatangia occur terminally or laterally in groups on small stalk cells or on a branched stalk system (Woelkerling, 1971, p. 18). In several species, however, spermatangia may occur on more elongate hyaline cells which have been termed androphores. Rosenvinge (1909, p. 141) established the genus *Kylinia* for taxa which possessed 'androphores' and this concept has been maintained in the classification schemes of Abbott & Hollenberg (1976) and of Humm (1979). In the Feldmann (1962) scheme, both *Kylinia* and *Balbiania* were characterized by the presence of androphores.

Papenfuss (1945, p. 304) regarded the presence of androphores as insignificant generically, and a similar conclusion was reached by Woelkerling (1971). Based on field and culture studies of *K. rosulata*, the type species of *Kylinia*, Stegenga & van Wissen (1979, p. 112) concluded that 'the recognition of androphores. . . is probably a matter of taste'. Moreover, their illustrations (*op. cit.*, p. 105, Figs 38–40, 45–47) show spermatangia both on elongate cells and on more ordinary stalk cells. Stegenga (1979, p. 19) does not consider 'androphores' to be of taxonomic significance. Thus, continued recognition of a genus for 'androphore' bearing taxa does not appear to be supported by the available evidence.

Postfertilization development

The fertilized carpogonium may divide either transversely or longitudinally or give rise directly to diploid filaments. Feldmann (1962) delineated the genera *Acrochaetium, Balbiania, Kylinia, Liagorophila* primarily on differences in immediate postfertilization development. Woelkerling (1970, 1971), however, found that fertilized carpogonia in *Audouinella botryocarpa* and *A. dictyotae* may or may not divide prior to filament production and noted that studies of other species should be undertaken. Stegenga & Borsje (1977, p. 458) also reported both divided and undivided fertilized carpogonia in cultures of *Acrochaetium hallandicum*. More recently, Stegenga (1979, p. 22) reaffirmed the need for more studies and advised caution in the use of such characters. In addition, Garbary (1980) did not consider that a longitudinal division of the fertilized carpogonium was worthy of generic recognition for *Liagorophila*, but apparently he examined no material of the relevant taxon. Further critical studies of field populations and cultured plants are needed before the generic significance of this character can be evaluated more fully.



Figs 19–22. Diagrams of sexual cycles known to occur in acrochaetioid algae. Ellipses represent carposporophyte (Figs 19–20) or carpotetrasporophyte (Fig. 22) stages. Dir. Dev. = direct development.
Fig. 19. Triphasic, dimorphic cycle.
Fig. 20. Triphasic, trimorphic cycle.
Fig. 21. Diphasic, dimorphic cycle—no carposporophyte stage.
Fig. 22. Diphasic dimorphic cycle—carpotetrasporophyte stage present.

Stegenga (1979, see also Stegenga & Van Erp, 1979) delineated the genera *Acrochaetium* and *Chromastrum* in part on apparent differences in carposporophyte size. Species of *Acrochaetium* are said to have well developed carposporophytes while those of *Chromastrum* are said to be relatively small. These authors did not quantify the meanings of 'well developed' and 'relatively small', however, and it is difficult to determine the reliability of such characters in the absence of more precise and extensive data.

Sexual cycles: morphology

Differences in sexual cycles have been employed to help delineate genera (Stegenga, 1979; Stegenga & Vroman, 1977) and to delineate families and genera (Feldmann, 1962). Since 1968, culture studies have led to the realization that a number of distinct types of sexual cycles occur among acrochaetioid algae, and a consideration of these is a necessary prelude to discussing the taxonomic matters which have emerged.

Although some form of reproduction is recorded for nearly all of the 390 described species, sexual stages have been found in only about sixty acrochaetioid taxa and the complete sexual cycle has been worked out for only sixteen species in culture and an additional seven species from field collected populations. At least four distinctive sexual cycles involving gametangial phases of acrochaetioid morphology are now known.

Ten species (Table 7) have been shown to possess a triphasic, dimorphic sexual cycle in which

Table 7. Taxa with triphasic dimorphic sexual cycles. F = field based data; C = culture based data.

Specific epithet	Reference(s) and generic name used	Comments
botryocarpa	Woelkerling, 1970 (as *Acrochaetium*) Woelkerling, 1971 (as *Audouinella*)	F
dasyae	Stegenga & Borsje, 1976 (as *Acrochaetium*)	C
daviesii	Woelkerling, 1971, 1973b (as *Audouinella*)	F
efflorescens	Kylin, 1906; Rosenvinge, 1909 (both as *Chantransia*)	F
investiens	Swale & Belcher, 1963 (as *Rhodochorton*)	F, C
liagorae	Woelkerling, 1971 (as *Audouinella*)	F; see also Aziz, 1966
nemalionis	Stegenga & Van Erp, 1979 (as *Acrochaetium*)	C
saviana	Woelkerling, 1973b (as *Audouinella*)	F; see also Woelkerling, 1971 (*A. thuretii*)
subtilissimum	Abdel-Rahman, 1980	C
violaceum	Drew, 1935 (as *Rhodochorton*)	F; = *Audouinella hermanni*; see Israelson, 1942

free living, more or less isomorphic gametangial and tetrasporangial phases (both producing multicellular prostrate systems) occur along with a carposporophyte phase which develops on and remains attached to the gametangial plant but is distinctly different morphologically (Fig. 19). Gametangial plants are presumably haploid while carposporangial and tetrasporangial stages are presumably diploid. Confirmatory chromosome data are lacking, although karyogamy has been documented in one species (Woelkerling, 1970). In four species (Table 7), this type of sexual cycle has been demonstrated in culture; in the other six species the sexual cycle has been elucidated from field data. Among species in this latter group is *Audouinella miniata* (*A. hermanii* (Roth) Duby) Bory, the type species of *Audouinella,* whose sexual cycle was determined by Drew (1935, as *Rhodochorton violaceum*; for nomenclatural details see Israelson, 1942; Papenfuss, 1945; and Silva, 1980a).

Triphasic, trimorphic sexual cycles have been found in nine species studied in culture (Table 8). The free-living gametangial phase differs morphologically from the free-living tetrasporangial phase primarily in possessing a unicel-

Table 8. Taxa with triphasic trimorphic sexual cycles. All data based on culture studies. S = sexual generation; T = tetrasporophyte generation.

Specific epithet	Reference(s) and generic names used	Comments
collopodum	Stegenga & Mulder, 1979 (as *Chromastrum*)	
densum	Stegenga & Vroman, 1976 (as *Acrochaetium*)	S = *Chromastrum catenulatum*; see Stegenga & Mulder, 1979
hallandicum	Stegenga & Borsje, 1977 (as *Acrochaetium*)	T = *A. polyblastum*
moniliforme	Stegenga & Mulder, 1979 (as *Chromastrum*)	T = *C. humile*
pectinatum	West, 1968 (as *Acrochaetium*)	
reductum	Stegenga & van Wissen, 1979 (as *Chromastrum*)	S = *A. kylinioides*
rosulata	Stegenga & van Wissen, 1979 (as *Kylinia*) Boillot & Magne, 1973 (as *Kylinia*)	T = *Acrochaetium strictum* T = *A. pectinatum*
unifilum	Abdel-Rahman, 1981 (as *Acrochaetium*)	
virgatulum	Borsje, 1973 (as *Acrochaetium*) Stegenga & Mulder, 1979 (as *Chromastrum*) Stegenga & Mol, 1980 (as a synonym of *C. secundatum*)	S = *C. rhipidandrum*

Table 9. Taxa with diphasic dimorphic sexual cycles. F = field based data; C = culture based data; CT = carpotetrasporophyte present.

Specific epithet	Reference(s) and generic names used	Comments
floridulum	Stegenga, 1978, Stegenga & Mol, 1980 (as *Rhodochorton*)	C
purpureum	West, 1969 (as *Rhodochorton*)	C
	Stegenga, 1978 (as *Rhodochorton*)	C
	Ohta & Kurogi, 1979 (as *Rhodochorton*)	C
subimmersum	Lee & Kurogi, 1978 (as *Rhodochorton*)	F, CT; see Stegenga, 1979, p. 20.

lular rather than a multicellular prostrate system, and the carposporangial phase, which develops on and remains attached to the gametangial plant, differs morphologically from both (Fig. 20). Stegenga and coworkers (see Table 8 for references) have indicated that in most cases the gametangial and tetrasporangial phases originally were described as distinct species. Among species in this group are *Chromastrum virgatulum*, the type species of *Chromastrum* and *Kylinia rosulata*, the type species of *Kylinia*.

Abdel-Rahman & Magne (1981) have reported a different type of triphasic, trimorphic sexual cycle in *Acrochaetium asparagopsis* (Chemin) Papenfuss, which is known only as an endophyte under field conditions. In culture, both the gametangial and the tetrasporangial phases produce multicellular prostrate systems. The erect system of tetrasporangial plants develops to a much greater extent than does the erect system of gametangial plants. Tetrasporangial plants have not been identified from field material to date, however.

Diphasic, dimorphic sexual cycles are known for three species (Table 9) and each shows some distinctive characteristics. In *Rhodochorton purpureum* (the type species of *Rhodochorton*) culture studies (West, 1969, 1970b, 1972b; Stegenga, 1978; Ohta & Kurogi, 1979) have shown that comparatively small (<1 mm tall) haploid gametangial plants alternate with much larger (up to 25 mm tall) diploid tetrasporangial plants and that a distinct *spore bearing* carposporangial phase does not develop (Fig. 21). After karyogamy, the fertilized carpogonium elongates and divides transversely. The upper cell develops into a more or less clavate gonimoblast filament usually one to four cells long, and the erect system of the tetrasporangial plant develops directly from the terminal gonimoblast cell. The lower cell may form additional gonimoblasts and always produces rhizoidal filaments which eventually anchor the tetrasporangial plant to the substrate after the old female plant dies. Thus no carpospores are produced, and the tetrasporangial plant develops directly into an independent free-living organism after an early period of attachment to the progenitor haploid female plant. Similar sexual cycles occur in the Palmariales (see West & Hommersand, 1981). Dixon & Irvine (1977, p. 109), Magne (1970) and Stegenga (1978, p. 288), refer to the gonimoblast stage as a carposporophyte but West (1969) and West & Hommersand (1981, p. 148) state that a carposporophyte stage is absent. Because carpospores never develop, it seems best not to employ the term carposporophyte. Moreover the 'gonimoblasts' represent only an ephemeral, juvenile stage of development and thus may not even warrant recognition as a distinct structure.

Stegenga (1978) found in culture that *Rhodochorton floridulum* (the type species of *Rhodothamniella*) had a similar sexual cycle, except that 'gonimoblasts' did not occur. Instead, the erect filaments and a rhizoid develop directly from the distal cell of the fertilized, divided carpogonium. The single rhizoid branches, anchors the plant to the substrate and gives rise to other erect axes. The tetrasporangial plant soon becomes independent of the progenitor gametangial plant.

Lee & Kurogi (1978) concluded that a diphasic, dimorphic sexual cycle occurs in *Rhodochorton subimmersum* from studies of field collected material. In this taxon, however, a free-living tetrasporangial plant apparently does not occur and the haploid gametangial phase is dominant in terms of size (Fig. 22). After karyogamy, a small group of 2 or 3 celled gonimoblast filaments develop and these eventually produce ter-

Table 10. Taxa known to produce gametes but not tetrasporangia. List includes only taxa for which data were not recorded by Papenfuss (1945, 1947). M = male; F = female; C = carposporophyte.

Specific epithet	Selected reference(s) and generic name used	Known reproduction	Comments
barbadense	Woelkerling, 1971 (as *Audouinella*)	M, F, C	
battersianum	Hamel, 1927 (as *Acrochaetium*) Dixon & Irvine, 1977, (as *Audouinella*)	M, F, C M, F, C	
blumii	Woelkerling, 1971 (as *Audouinella*)	F, C	
bornetii	Papenfuss, 1945 (as *Acrochaetium*) Dixon & Irvine, 1977 (as *Audouinella corymbifera*)	M, F, C, M, F, C	
boweri	Hamel, 1925 (as *Audouinella*)	M, F, C	Freshwater
callithamnioides	Nakamura, 1944 (as *Rhodochorton*)	M	
dictyotae	Woelkerling, 1971 (as *Audouinella*)	M, F, C	
dotyi	Abbott, 1962 (as *Acrochaetium*)	M, F	
endophytica	Abbott, 1966 (as *Liagorophila*)	M, F, C	
imitator	Abbott, 1962 (as *Acrochaetium*)	M, F	
kurogii	Lee & Lindstrom, 1979 (as *Audouinella*)	M, F, C	
laxum	Abbott, 1962 (as *Acrochaetium*)	M, F, C	
magnificum	Lee & Lee, 1974 (as *Rhodochorton*)	M, F, C	
microscopica	Woelkerling, 1972 (as *Audouinella*) Abbott & Hollenberg, 1976 (as *Acrochaetium*)	M, F, C M, F	Schiffner 1931 records tetraspores, but see Dixon & Irvine 1977
papenfussii	Abbott, 1962 (as *Acrochaetium*)	M, F, C	
parvula	Dixon & Irvine, 1977 (as *Audouinella*)	M, F	
punctatum	Dawson, 1953 (as *Acrochaetium*)	M	
repens	Woelkerling, 1971 (as *Audouinella*)	M, F, C	
rhipidandrum	Hamel, 1927 (as *Acrochaetium*)	M, F, C	See also Stegenga & Mulder, 1979
rongelapense	Abbott, 1962 (as *Acrochaetium*)	M, F, C	
trichogloeae	Abbott, 1962 (as *Acrochaetium*)	M, F, C	

minal sporangia, each containing four spores. Thus it appears that this species possesses a carpotetrasporophyte and carpotetraspores similar to those found in some taxa of Helminthocladiaceae (for references see Lee & Kurogi, 1978; West & Hommersand, 1981). Presumably these spores give rise to new haploid gametangial plants. If confirmed by culture studies, the sexual cycle of *R. subimmersum* would be the first demonstrated occurrence of haplobionty in the sense of Feldmann (1962; see also Bold & Wynne, 1978, p. 587 and Dixon, 1973, p. 184 *et seq.*).

In addition to the twenty-three species cited above, gametangial stages have been reported for at least twenty-one other species (see Table 10 and Papenfuss, 1945, 1947). Tetrasporangial phases in these taxa have not been found unequivocally, however, and the complete sexual cycle therefore remains uncertain.

West & Hommersand (1981) have summarized data on other red algae known to produce diploid filamentous, monosiphonous phases of acrochaetioid morphology. In at least one taxon (Codomier, 1973), such a phase has been identified with a described species (*Rhodochorton hauckii*). The gametangial stages in all cases, however, are not of acrochaetioid morphology. Moreover, these algae continue to be classified on the basis of the morphology of the gametan-

gial plants, and the present author feels that taxa with gamete producing stages of non-acrochaetioid morphology should be excluded from the Acrochaetiaceae.

Based on earlier studies (Cabioch & Guiry, 1976; Guiry, 1974, 1975), Guiry (1978a) referred the 'parasitic' genus *Halosacciocolax* to the Acrochaetiaceae. The type species, *H. kjellmanii* Lund, is known from spermatangial as well as tetrasporangial plants (Guiry, 1975; Lund, 1959). Female plants are unknown and Garbary (1979d, p. 488) has excluded the genus from the Acrochaetiaceae. No other 'parasitic' taxa have been referred to the family and until the sexual cycle is known more completely, the taxonomic affinities of *Halosacciocolax* will remain uncertain.

The taxonomic affinities of *Schmitziella* similarly will remain uncertain until all reproductive stages are known and the sexual cycle is determined in culture. Woelkerling & Irvine (1982), who re-examined the generitype specimens and studied other collections, concluded that *Schmitziella* does not belong to the Corallinaceae where it usually has been placed (see Johansen, 1981), and suggested that it should be regarded as a genus *incertae sedis* next to the Acrochaetiaceae. The vegetative thallus and the production of bisporangia are concordant with those in other acrochaetioid algae, but tetrasporangia in *Schmitziella* contain zonately (formed by two successive divisions) rather than cruciately arranged contents. The latter is characteristic of acrochaetioid algae generally, although Stegenga (pers. comm.) notes that in endophytic acrochaetioids, divisions within tetrasporangia sometimes are irregular.

Apomictic cycles elucidated from culture studies will be considered in Section IX below.

Sexual cycles: taxonomy

Two acrochaetioid classification schemes used since 1970 have employed differences in the nature of the sexual cycle to help delineate taxa. In the Feldmann (1962) scheme, haplobiontic taxa are referred to one family (Acrochaetiaceae) and diplobiontic and nonsexual taxa are placed in another family (Audouinellaceae). Stegenga (1979, p. 22) considered this scheme to be '. . . partly obsolete, since there is not enough positive evidence for the existence of haplobiontic life histories in the Acrochaetiaceae'. To date only Lee & Kurogi (1978) have provided firm field evidence in support of haplobionty (in the extended sense of Feldmann, 1962; see also Bold & Wynne, 1978, p. 587) but this requires confirmation in culture. Moreover Dixon (1973, p. 184 *et seq.*) has pointed out clearly that the concepts of haplobionty and diplobionty cannot be applied properly to most red algae and should be discarded.

Stegenga (1979; see also Stegenga & Vroman, 1977) has employed sexual cycle differences in conjunction with other characteristics to delineate a series of genera. In some cases Stegenga regards the sexual cycle as the primary generic criterion but in other cases it is only secondary. Thus all taxa referred by Stegenga to *Chromastrum* presumably have a triphasic trimorphic sexual cycle and have cells which contain stellate chromoplasts with pyrenoids. *Kylinia* is restricted to species with a triphasic trimorphic sexual cycle in which vegetative cells contain 'parietal' chromoplasts with pyrenoids. *Acrochaetium* includes species with a triphasic dimorphic sexual cycle and has cells containing 'parietal' chromoplasts with pyrenoids. *Audouinella,* however, includes both taxa with a triphasic trimorphic sexual cycle and taxa with a triphasic dimorphic sexual cycle; the primary criterion is the occurrence of parietal chromoplasts of irregular or spiral shape without pyrenoids. Finally, *Rhodochorton* includes all taxa with a diphasic dimorphic sexual cycle regardless of chromoplast and pyrenoid attributes and irrespective of the presence or absence of carpotetrasporophytes or of free-living tetrasporangial plants. This scheme has been adopted by West & Hommersand (1981) but has not been subject as yet to critical review by other authors. In this scheme, moreover, the generic placement of many acrochaetioid algae would be uncertain because their sexual cycles are not known.

The generic problem: personal comments

The generic classification of acrochaetioid algae is in a disgraceful state of disarray. There is no clear consensus as to either the number or the circumscription of genera or the relative importance and reliability of the morphological criteria used in generic delineation. Some generic names have been used in so many different ways that it has become difficult to associate the name with a particular concept. In many classification schemes, some or most taxa are placed in genera on 'circumstantial evidence' because data on the primary criteria are not known (e.g. see Stegen-

ga & Van Erp, 1979, p. 426); this can be a very presumptive procedure. In other cases, criteria of questionable reliability continue to be used even though available evidence casts doubt on their suitability for generic delineation. In still other cases, sets of characters are presumed but not demonstrated to be linked (e.g. see Stegenga, 1979, p. 19; Stegenga & Mulder, 1979, p. 305); thus the use of such character sets for generic circumscription remains surrounded by uncertainty.

The root cause of all these problems is the absence of detailed data both from field and lab studies for the vast majority of described species. Sexual cycles, for example, have been documented in culture for less than 5% of the 390 described species and experimental data on the variability in chromoplast morphology and pyrenoid occurrence is available for less than ten species. A similar paucity of data exists for other criteria of presumed generic importance. In the absence of a considerably larger and more trustworthy body of data, it seems scarcely possible to produce any sort of reliable and meaningful 'natural' classification scheme for acrochaetioid algae at present.

One pragmatic solution is to adopt a monogeneric scheme, using the name *Audouinella*. This approach obscures possible evolutionary trends and lumps together some very different taxa (e.g. '*Chromastrum secundatum*' (syn. '*C. virgatulum*'—see Stegenga & Mol, 1980; Woelkerling, 1973b) and '*Rhodochorton purpureum*') which might readily be referred to distinct genera. This approach, however, has the advantage of providing a stable, temporary generic scheme until sufficient data is accumulated on a majority of species to allow for a more meaningful assessment of generic concepts to be made.

One of the most stable attributes among autotrophic plants generally is the *type* of sexual cycle present. For any given species, one and only one type of sexual cycle (i.e. involving karyogamy and meiosis) occurs. In the Rhodophyta, culture studies have led to the discovery of a number of distinctive sexual cycles (see West & Hommersand, 1981) and at least four different sexual cycles are known to occur among acrochaetioid algae. It is possible that these cycles represent distinct lines of evolutionary development and thus could provide an apparently stable basis upon which to delineate genera. The generic scheme of Stegenga (1979) considers the sexual cycle to some extent, but in at least two cases (*Audouinella* and *Rhodochorton*) taxa with different sexual cycles are lumped into the same genus. If the sexual cycle were to become the primary basis of generic delineation, nomenclatural considerations (i.e. knowledge about the nature of the sexual cycle in the type species) would dictate that *Audouinella* (type species: *A. miniata*) be used for triphasic dimorphic taxa, *Acrochaetium* (type species: *A. secundata*) for triphasic trimorphic taxa, and *Rhodochorton* (type species: *R. purpureum*) for diphasic dimorphic taxa (predominant, free-living tetrasporangial phase). A new name would have to be coined for diphasic dimorphic taxa with a carpotetrasporophyte and no free living tetrasporangial phase. Such a scheme could only operate meaningfully, however, if a form genus (i.e. *Colaconema*) were used for the vast majority of taxa for which the type of sexual cycle present remains unknown or uncertain.

In the short term, it seems to me that it is more important to accumulate detailed, trustworthy data on numerous species than to engage in endless manipulation of generic schemes. Use of either of the above two schemes would provide a workable taxonomic framework while new studies are being carried out.

VII. SPECIES LEVEL TAXONOMY

Species concepts

Most species of acrochaetioid algae have been described since 1900; between 1900 and 1949 the number of new taxa nearly tripled from 110 to 329 (Table 6). This occurred during a period when the development and structure of the prostrate system, the type of host organism, and chromoplast morphology were considered to be reliable taxonomic criteria (Woelkerling, 1971, p. 3). By 1968, however, considerable data casting doubt on the reliability of these and other criteria used in species delineation had accumulated, and West (1968, p. 98) concluded that 'It is evident that species concepts in the Acrochaetiaceae are unsatisfactory and must be modified considerably before they reflect a more natural system'. Ten years later (Boney, 1978a, p. 69), the problem of specific concepts was emphasized again.

In recent years there have been relatively few attempts (e.g. Abbott, 1968; Woelkerling, 1971, 1972, 1973a, 1973b) to employ type collection

data in conjunction with field or lab data to help clarify species concepts (see also Stegenga & Borsje, 1976, p. 28; Stegenga & Vroman, 1976, p. 280). Meanwhile, names sometimes continue to be applied to species arbitrarily (e.g. Stegenga & Vroman, 1976, p. 276) or provisionally (e.g. Stegenga & Van Erp, 1979, p. 443) or for the sake of convenience (e.g. Stegenga & Mulder, 1979, p. 300; Stegenga & Van Erp, 1979, p. 442). Moreover, several authors (e.g. Abbott, 1968; Woelkerling, 1973b) have discovered that a number of reported records of species were based on misidentified specimens and that the associated species names and concepts were perpetuated incorrectly in subsequent publications. Circumstances such as these dictate that many descriptions of species must be regarded with great caution, especially in floristic accounts where descriptions are based on information taken from other published sources rather than from original observations. Dixon & Irvine (1977, p. 76) have concluded that species concepts among acrochaetioid algae are the most confused of all the marine Rhodophyta found in the British Isles and West (1978) described the problem of species identification as traumatic. Thus Levin's (1979) view that '. . . plant species are utilitarian mental constructs . . .' certainly appears valid with respect to acrochaetioid algae, and even the mental constructs still seem rather fuzzy in many cases.

How many biological species of acrochaetioid algae there really are remains unknown, but some workers (e.g. Boney, 1980, p. 503, 504; Stegenga, 1979, p. 29; Stegenga & Mulder, 1979, p. 306; White & Boney, 1971, p. 870; Woelkerling, 1971, p. 3) have predicted that substantial synonymizing of described species will take place sooner or later, while others (e.g. Abbott & Hollenberg, 1976; Dixon & Irvine, 1977) have preferred to take a 'conservative approach' and continue to carry large numbers of taxa along 'on the books'. Very few species have been studied intensively while many (perhaps a majority) of specific and infraspecific taxa are known only from the original collections. To date only two taxa (West, 1972a; Garbary & Rueness, 1980) have been described after examination in laboratory culture.

Species studies

West (1968, p. 98) recognized the necessity for quantitative investigation of intraspecific variation in a significant number of species subjected to a range of controlled environments as one means of helping to clarify species concepts, and he (*op. cit.*) also noted that all phases in the life history had to be considered. Subsequent studies using these and other approaches have aimed, directly or indirectly, at examining and evaluating variability in characters thought to be important in species delineation.

One set of studies (Abdel-Rahman & Magne, 1981; Boney, 1972a, 1975, 1978a, 1980a; Garbary, 1979b; Magne, 1977; West, 1979; White & Boney, 1969, 1971) have been concerned with taxa commonly found endophytically or endozoically. Results indicate that many taxa formerly considered host specific (see Woelkerling, 1971, p. 11 for older literature on host specificity as a taxonomic criterion) can grow in culture independently of any host (e.g. Boney, 1972a, 1975, 1978a; West, 1979). At least some species (Garbary, 1979b; White & Boney, 1969) found in particular hosts under field conditions will grow in or on other hosts (both plant and animal) under culture conditions. Reinfection or cross infection of host organisms with endobiotic acrochaetioid algae also has been achieved under culture conditions (Boney, 1978a; White & Boney, 1969). Moreover, some investigators (e.g. Garbary, 1979b; West, 1979) have found that the nature of the substrate can affect the general morphology of the acrochaetioid alga and (e.g. White & Boney, 1971, p. 872) that plants grown free of the host in culture can differ both in general morphology and in the extent of erect system development.

West (1970a, 1979) also found that cell fusions can occur between cells of contiguous prostrate system filaments in some normally endozoic taxa but not in others. Cell fusions between contiguous cells of prostrate filaments have been reported in only two species of acrochaetioid algae (*Rhodochorton concrescens*—see West, 1970a and *R. spetsbergensis*—see Rosenvinge, 1923–24 (as *R. penicilliforme*; see Woelkerling, 1973b for nomenclature). Both these taxa share this feature as well as several other characteristics with certain species currently assigned to *Rhodophysema* (especially *R. feldmannii*—see Cabioch, 1975 and Masuda & Ohta, 1981); further study is needed to determine whether these two 'Rhodochortons' are really acrochaetioid algae or belong elsewhere. Sexual cycles for both species remain unknown.

To date, only Abdel-Rahman & Magne (1981; see also Magne, 1977) have succeeded in com-

pleting an entire sexual cycle of an endophytic species in the lab. Sexual, carposporophyte and tetrasporangial stages apparently are known only from a single endophytic species (*Audouinella liagorae*—see Woelkerling, 1971) under field conditions.

Few firm taxonomic decisions or opinions have emerged so far from these studies of endobiotic taxa although White & Boney (1971) have suggested that a number of taxa are probably conspecific. West (1979, p. 114) has used the presence or absence of cell fusions between prostrate system cells to help delineate species. Boney (1975, p. 478), White & Boney (1969, p. 272) and Woelkerling (1971, p. 11) all have concluded that host specificity is not a good taxonomic criterion and Boney (1975, p. 480) also noted that growth forms cause many taxonomic problems which can be resolved only by culture studies under defined conditions. Boney (1978a, p. 70) and White & Boney (1969) have suggested that reduction of two endobiotic taxa to conspecificity be contingent upon demonstrating that host free plants of the two taxa grown in culture are morphologically concordant and that successful cross-infection of the two acrochaetioid-free hosts with the relevant acrochaetioids can occur. Garbary (1979b, p. 454) feels, however, that such criteria are too rigorous for use in defining species.

A second series of studies has involved the comparative examination of type collections. Abbott (1968) clarified species concepts for three taxa occurring endophytically in *Liagora*. Woelkerling (1970, 1971, 1972, 1973a, 1973b) reduced a number of taxa to synonymy after a comparative analysis of type collections revealed that relevant specimens were morphologically and anatomically concordant and/or represented overlapping regions within a spectrum of continuous variation. Because reduction of species to synonymy involves taxonomic opinion, such actions have not necessarily gained automatic acceptance even though evidence obtained from type collection comparisons appears unequivocal. Thus, for example, Woelkerling (1973a, p. 96) concluded after comparing the relevant types that the acrochaetioid taxa originally described as *Callithamnion daviesii β secundata* Lyngbye (1819) and *C. virgatulum* Harvey (1833) were conspecific, thus concurring with the earlier opinions of Hamel (1927, 1928a) and Rosenvinge (1909). Subsequently, however, some authors (e.g. Dixon & Irvine, 1977; Kornmann & Sahling, 1977) maintained the two as distinct species while other authors (e.g. Rueness, 1977; South & Hooper, 1980; Stegenga & Mol, 1980) regarded them as conspecific. The absence of consensus over issues of taxonomic synonymy at species level also exists in a number of other cases (e.g. compare Woelkerling, 1972; Coppejans & Boudouresque, 1976; and Stegenga & Mulder, 1979), and this is another factor contributing to the current state of confusion over species concepts in this group. It also appears that the relative importance of type collection assessment in resolving problems of taxonomic synonymy requires further study since some authors (e.g. Dixon & Irvine, 1977, p. 115) require a 'detailed investigation of the relationship' of relevant taxa even after type collection comparisons in conjunction with studies of other populations indicates that such taxa are conspecific.

A third series of studies has provided data from culture-grown plants on the morphological variability of certain taxonomic characteristics. Less than 10% of the described species have been investigated in this way and meaningful statistical analyses have been provided in only one paper (Garbary, 1979c). In most cases only the effects for differing temperatures, day lengths, and/or light intensities have been considered.

For many characteristics, responses to given environmental conditions vary both among and within species. With respect to the vegetative thallus, West (1972a) found that frequency of branching in *Acrochaetium proskaueri* increased with higher illuminances (1500 lx) and higher temperatures (15°C) whereas Stegenga & Vroman (1976) reported that branching in *A. densum* was greatest at 8°C, decreased at higher temperatures and appeared to be correlated positively with illuminance only at low temperatures. Stegenga & Borsje (1977) found that branch frequency appeared to be correlated negatively with temperature in tetrasporangial plants of *A. hallandicum* but in sexual plants, it showed no relationship to temperature. Garbary (1979c) reported differing responses in six species examined comparatively, and Stegenga & Van Erp (1979) concluded that branch frequency was not a good taxonomic character. Stegenga & Mulder (1979a) also found that in *Chromastrum moniliforme,* branch frequency decreased as the population density increased.

Branch arrangement also can vary. Based on field studies, Woelkerling (1971) concluded that both branching frequency and arrangement were

of doubtful value as taxonomic characters. Subsequently, experimental data has appeared for several species. Garbary (1979c) reported that branches in *Audouinella secundata* were mostly secund at 8°C and 13°C but became irregular at higher temperatures. In *Acrochaetium densum*, Stegenga & Vroman (1976) discovered that branching in tetrasporangial plants also was secund and independent of temperature and light regimes, but in sexual plants, branch arrangement became multilateral under the combined effects of low temperature (8°C) and high illuminance (3400–5700 lx).

With particular species, cell size may be influenced by the rate of plant growth (West, 1979, p. 379), salinity levels (White & Boney, 1969, p. 258), plant height (Stegenga & Vroman, 1976, p. 268), temperature (Garbary, 1979c; Stegenga & Borsje, 1976, 1977; Stegenga & Vroman, 1976), or illuminance (Stegenga & Borsje, 1977; Stegenga & Vroman, 1976). Responses also can differ between clones (Stegenga & Borsje, 1976) and between sexual plants and tetrasporangial plants of the same species (Stegenga & Borsje, 1977). According to Garbary (1979c, p. 497, 498), however, the recorded variation falls within 'traditional taxonomic understanding', and Stegenga & Van Erp (1979) and Stegenga & Vroman (1976) have concluded that cell dimensions are among the more stable taxonomic characters. Woelkerling (1971) reached similar conclusions based on field studies and a literature survey.

Hair-cell formation in several species (Stegenga & Borsje, 1977; Stegenga & Mulder, 1979; Stegenga & Vroman, 1976; West, 1972a) is promoted by high illuminance (1500 lx or more), but responses to temperature (see Stegenga & Borsje, 1977; Stegenga & Mulder, 1979; Stegenga & Van Wissen, 1979; West, 1972a) vary from species to species. In terms of overall plant size, various species appear to have different optimal temperature requirements. In *Audouinella secundata*, the tallest plants grew in 13°C cultures (Garbary, 1979c); in *Acrochaetium hallandicum* optimal temperature was 20°C (Stegenga & Borsje, 1977); and in *A. densum* optimal temperature was 25°C (Stegenga & Vroman, 1976).

Monosporangial arrangement and size also have been examined for several species. West (1972a) found that in *Acrochaetium proskaueri*, sporangia may be solitary or borne in clusters and that the number of sporangia per cluster increased in bright light (1500 lx) as compared to dim light (150 lx). Stegenga & Vroman (1976) reported that in *A. densum*, sporangial size was not affected by temperature (2–29°C) or illuminance (150–5700 lx). In several other species, however, Garbary (1979c) noted a decrease in sporangial length with increasing temperature. Stegenga & Borsje (1977) discovered that in sexual plants of *Acrochaetium hallandicum*, monosporangial dimensions were not affected by light or temperature but in tetrasporophytes, monosporangial diameter increased under the combined effects of high illuminance and low temperature. Nevertheless Stegenga & Van Erp (1979) and Stegenga & Vroman (1976) regard monosporangial dimensions as useful characters for delineating species and Garbary (1979c) found that variation induced under experimental conditions did not fall outside the ranges reported in field collected plants.

New data on host–epiphyte relationships have been obtained for several species. Stegenga & Borsje (1976) found that in culture, tetraspores of *Acrochaetium dasyae* germinate only in the presence of *Dasya* plants even though (Woelkerling, 1973b) the acrochaetioid occurs on various hosts under field conditions. Similarly, Stegenga & Mulder (1979) noted that in *Chromastrum collopodum* spore germination often was low and plants developed aberrantly in the absence of the usual host, *Chordaria flagelliformis*. Although these authors do not conclude that 'host-specificity' is a reliable species criterion, they suggest that for at least some taxa, 'fairly strong substrate preferences' appear to occur and that this might be considered 'as a possible direction in speciation'.

VIII. FAMILY AND ORDER CLASSIFICATION

Historical data on family and order classification schemes have been summarized by Stegenga (1979) and Woelkerling (1971). In most recent floristic works (e.g. Abbott & Hollenberg, 1976; Dixon & Irvine, 1976; Guiry, 1978a; Kornmann & Sahling, 1977; Lee, 1980; Perestenko, 1980; Rueness, 1976), textbooks and book chapters (e.g. Bold & Wynne, 1978; Christensen, 1980; Kraft, 1981) and morphosystematic studies (e.g. Stegenga, 1979; Woelkerling, 1971, 1973b) all acrochaetioid algae have been placed within a single family in the order Nemalionales. Several other classification schemes also have been proposed although none has gained widespread acceptance. Cordero (1977), for example, recognizes two families: the Chantransiaceae con-

taining *Rhodochorton* and the Acrochaetiaceae containing *Acrochaetium*. The former family is referred to the Bangiophyceae (ordinal affinities not given) while the latter is referred to the Nemalionales (within the Florideophyceae). Humm (1979, p. 71) follows Aziz (1965) and Rosenvinge (1909), both of whom place *Rhodochorton* in the Ceramiales and other acrochaetioid algae in the Nemalionales (see also West, 1972b, p. 229).

Several authors also have placed acrochaetioid algae within a separate order, the Acrochaetiales. Some European workers (e.g. Ardre, 1970; Boudouresque & Perret, 1977; Bourrelly, 1970; Cinelli *et al.*, 1976; Lichtlé, 1973a, 1973b) apparently have followed Feldmann (1962), who recognized two families and eight genera within the order Acrochaetiales. Feldmann (1953, 1962) characterized the Acrochaetiales by the absence of a carpogonial branch and delineated the two families on presumed differences in the sexual cycle and in the number of chromoplasts per cell. Dixon (1961, p. 10) and Papenfuss (1966, p. 247–248), however, have noted that carpogonial branches also may not occur in some other red algae (e.g. *Gelidium*) and both concluded that recognition of the order was not warranted. More recently, however, Garbary (1978a) supported recognition of the order but on different grounds. He included a single monogeneric family and concluded (p. 252) that '. . . if *Audouinella* is to be regarded as the most primitive extant genus in the Florideophycidae (and this is supported by present knowledge of morphology and ultrastructure), then this is sufficient grounds for recognizing *Audouinella* as a distinct order (i.e. the Acrochaetiales)'. He also felt that '. . . the separation of the Acrochaetiales highlights its phylogenetic importance and provides a sounder classificatory framework for discussing relationships between the Florideophyceae and the advanced Bangiophyceae'. Garbary's proposals, however, have not been adopted by subsequent workers (e.g. Kraft, 1981; Stegenga, 1979; Stegenga & Mol, 1980; West & Hommersand, 1981).

IX. OTHER STUDIES

Morphology

A number of studies published since 1970 have provided data of potential taxonomic interest on apomictic reproduction. Apomictic cycles involving tetraspores now have been documented in culture for at least four taxa (Garbary & Rueness, 1980; West, 1970a, 1972a, 1979). Contents of tetrasporangia apparently divide apomeiotically into four more or less cruciately arranged spores. After germination, these tetraspores ultimately give rise to other tetraspore-bearing plants. Sexual stages could not be induced through manipulation of temperature, irradiance or photoperiod, and whether these plants are haploid or diploid or even possess a sexual cycle remains unknown. In *Acrochaetium proskaueri*, West (1972a) induced tetrasporangial formation only in cultures grown at 15°C, 1500 lx and a 16:8 light/dark photoperiod; under all other conditions tested only monosporangia developed, and these germinated to produce new monosporangial plants. In the remaining three species, tetrasporangia are the only known reproductive structures. Umezaki (1977) summarizes data on both apomictic and sexual cycles.

Bisporangia have been recorded in at least ten species including gametangial plants of *Audouinella dictyotae* (Woelkerling, 1971), and multipartite sporangia have been found in at least three species (Boergesen, 1937; Howe, 1914; Klavestad, 1957; Knaggs, 1967a). Both types of spores have yet to be studied cytologically or in culture, and it remains uncertain whether bispores give rise to new bisporangial plants as occurs in the Corallinaceae (see Chamberlain, 1977). Numerous culture studies (see Tables 7, 8 for references) have confirmed that monosporangia germinate to give rise to new plants presumably of the same ploidy level; these may bear monosporangia and/or sexual or tetrasporangial reproductive structures.

A number of other studies contain information on environmental factors which affect or regulate reproduction in acrochaetioid algae. Data are most extensive for *Rhodochorton floridulum* (Knaggs, 1967b; Rueness, 1976; Stegenga, 1978) and *R. purpureum* (Knaggs, 1966; Ohta & Kurogi, 1979; Pearlmutter & Vadas, 1978; Stegenga, 1978; West, 1969, 1970b, 1972b, 1974). Clonal variation is evident for both species. Stegenga (1978) induced tetrasporangia and gametangia in cultures of a Dutch strain of *R. floridulum* grown under 1750 lx in a variety of day length and temperature regimes, but Rueness (1976) found that plants of a Norwegian strain remained sterile under all conditions tested. West (1972b) found that clones of *R. purpureum* from Alaska, California, Chile and Washington responded differently to particular combinations of temperature, photoperiod, illuminance and salinity. Plants from

Chile, for example, produced sporangia in all photoperiods tested while plants of the other clones sporulated only when grown in short (≤12 h) photoperiods.

The effects of different combinations of temperatures, photoperiods, and/or light regimes upon formation of sporangia and gametangia have been reported for about fifteen other species (Abdel-Rahman, 1982; Abdel-Rahman & Magne, 1981; Edwards, 1969; Garbary & Rueness, 1980; Stegenga & Borsje, 1976, 1977; Stegenga & Mulder, 1979; Stegenga & Van Erp, 1979; Stegenga & Van Wissen, 1979; Stegenga & Vroman, 1976; West, 1968, 1970a, 1972a, 1979) but no clear cut or widespread patterns appear evident and different responses occurred even among clones of the same species. In some cases (e.g. Edwards, 1969; Garbary & Rueness, 1980; Stegenga & Van Erp, 1979; West, 1970a, 1979) gametangia could not be induced under any conditions tested.

Because all of the above studies have been based on plants grown in seawater enriched media, the effects of nutrient levels upon reproduction remain almost entirely unknown. Knaggs (1967b) suggested that nitrate and phosphate concentrations may regulate sporangial production in *Rhodochorton floridulum*. Rueness (1976), however, could not induce sporulation in *R. floridulum* by lowering the concentrations of these nutrients. Studies employing chemically defined culture media are needed to help clarify matters.

Physiology–biochemistry

Although physiological–biochemical studies involving acrochaetioid algae are few, some resulting data have been considered from the taxonomic or phylogenetic viewpoints. Mallery & Richardson (1971, 1972) examined the biliproteins and soluble proteins of one species of *Acrochaetium* and of ten other species (each in a different genus) and concluded that *Acrochaetium* was considered generally as the most primitive genus of Florideophycidae and showed some strong biochemical affinities with several taxa of Bangiophycidae. In a subsequent study, Richardson & Mallery (1973) analysed one species of *Rhodochorton* and three species of *Acrochaetium* for soluble proteins, biliproteins and esterase patterns from polyacrylamide discontinuous pH gel electrophoresis data and concluded (p. 1054) that all sexually reproducing acrochaetioid algae should be placed in a single genus.

Boney (1972b) has investigated fluorescent substances in five acrochaetioid algae while Boney & White (1968) have looked at phycoerythrins from four acrochaetioid algae with a view towards taxonomic assessment but these authors did not reach any firm conclusions. Subsequently Boney (1978b, p. 14) emphasized the 'need for a continuing search for suitable biochemical criteria, notably on a presence or absence basis . . .'. Although *Audouinella floridula* has been included in general surveys for the occurrence of phytohaemagglutinins (Blunden *et al.*, 1978) and for anti-influenza virus activity (Blunden *et al.*, 1981), no one apparently has published a taxonomically oriented, broad scale biochemical study involving numerous taxa of acrochaetioid algae. Boney (1978b, p. 14) also discouraged using differences in the amounts of compounds present for making taxonomic distinctions. This view is supported by data from studies of Van Der Velde (1977, 1981) who found that relative pigment contents, protein levels, enzyme activity levels and carbohydrate levels in two species of *Acrochaetium* all were affected by light of different wavelengths (see also Van Der Velde *et al.*, 1975 and Van Der Velde & Hemrika-Wagner, 1978).

Electron microscopy

Transmission electron microscopy studies of acrochaetioid algae apparently have been limited to work on the chromoplasts (Duckett & Peel, 1978; Hara, 1972; Hara & Chihara, 1974; Lichtlé, 1973a, 1973b). Lichtlé (1973a) compared the plastid ultrastructure of *Rhodochorton purpureum* and *Rhodothamniella floridula*. Hara (1972) and Hara & Chihara (1974) examined several acrochaetioid algae as part of broad surveys of red algal chromoplast ultrastructure and reported that the acrochaetioids studied have a '*Nemalion*-type' of chromoplast, which is the dominant type in the subclass Bangiophycidae. The Acrochaetiaceae (Hara & Chihara, 1974, p. 226) however, were kept in the Florideophycidae and placed in the Order Nemalionales.

Garbary (1978b) examined eight species of acrochaetioid algae by means of scanning electron microscopy to elucidate possible species differences in surface characters and to look for new characters against which proposed generic delimitations in the family could be tested. Al-

though some variation in surface structure was reported (the extent to which this variation is artifactual remains unknown), firm taxonomic conclusions were not drawn because (Garbary, 1978b, p. 220) '. . . too few species were examined even to suggest tentative relationships on the basis of surface structure'.

Ecology

Diverse types of ecological studies include data on acrochaetioid algae. Hommeril & Rioult (1962) reported that *Rhodochorton floridulum* played an important role as a sand-binder on sand covered rocks in some areas of France. Knaggs (1968) reviewed available literature on the ecology and distribution of *R. purpureum* and found that this species grew in a wide variety of habitats and that thallus morphology was markedly affected by local environmental conditions. Boney (1980) recorded an unusual growth form of this species (as *Audouinella purpurea*) involving mineral deposition and stratification. Larpent-Gourgaud & Ducher (1977) isolated and examined four bacteria contaminating a culture of an unidentified species of *Acrochaetium*; their results suggested that the bacteria were intimately bound to the cell wall of the alga but precise ecological relationships were uncertain.

Among field based studies, Schneider (1976) included spatial and temporal data on two acrochaetioid (and 150 other) algae from along the continental shelf of North and South Carolina. Plants of *Audouinella hallandica* were found at depths of 17–35 m. Klavestad (1978) examined the distribution of twelve species (eight of *Acrochaetium*, two of *Audouinella*, one of *Kylinia*, one of *Rhodochorton*) in relation to pollution in Oslofjord (Norway) and concluded (p. 92) that *Acrochaetium thuretii* and *A. virgatulum* appear to thrive well under eutrophic conditions. Garbary (1976) established life-form spectra for over 600 species including thirty-one acrochaetioids (twenty-four of *Acrochaetium*, two of *Audouinella*, five of *Rhodochorton*); twenty-six acrochaetioid species were classed as ephemerophytes (present throughout the year, more than one generation per year, spores or zygotes germinating immediately) while the remainder were classed as probable hypnophytes (algae present only during one part of the year and passing the rest of the year in a resting stage or as a microscopic vegetative form).

Phenological data on acrochaetioid algae have been published as parts of larger studies dealing with areas of Greece (Haritonidis, 1978), Newfoundland (South & Hooper, 1980), New Hampshire (Hehre & Mathieson, 1970), Nova Scotia (Bird *et al.*, 1976), Texas (Edwards, 1969; Edwards & Kapraun, 1973) and elsewhere. Edwards (1969) combined field data with culture studies in an attempt to elucidate causal factors for the observed seasonal distributions. Both *Acrochaetium crassipes* and *A. flexuosum* occurred throughout the year in the field; in culture optimal growth occurred under temperatures of 24–29°C and in daylengths of 12–24 h. Monosporangia, the only reproductive structures observed, occurred throughout the year in the field and in all culture conditions tested.

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A TAXONOMIC REASSESSMENT OF *LITHOPHYLLUM* (CORALLINACEAE, RHODOPHYTA) BASED ON STUDIES OF R. A. PHILIPPI'S ORIGINAL COLLECTIONS

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Critical studies of the original collections upon which *Lithophyllum* Philippi (Corallinaceae, Rhodophyta) is based have revealed that only two of the four species included in the initial presentation conform to any modern concept of the genus. Early concepts of *Lithophyllum* based on characters associated with external morphology have given way to more modern concepts based on anatomical features, and since 1943 at least six different concepts have been employed. Of the four species originally included in the genus, Philippi's specimens of *L. decussatum* Philippi are too fragmentary to allow for any firm determination, while lectotype material of *L. expansum* Philippi is considered conspecific with *Mesophyllum lichenoides* (Ellis) Lemoine. The lectotype collection of *Lithophyllum incrustans* Philippi (which also is the generitype specimen of *Lithophyllum*) and the lectotype specimen of *L. lichenoides* Philippi conform to some modern concepts of *Lithophyllum* but not to others. Based on detailed morphological–anatomical studies of Philippi's collections, the six modern concepts of *Lithophyllum* are reassessed in relation to a series of hypotheses concerning thallus ontogeny and hypothallial attributes, but no single concept can be supported unequivocally based on the evidence available currently. Relevant historical data on the genus and on the various species studied also are presented.

Philippi (1837) established the genus *Lithophyllum* (Corallinaceae, Rhodophyta) for rigid calcareous plants consisting of leaf-like expansions. Previously, organisms fitting this description had been included among the nullipores (see Lamarck, 1816, p. 203; 1836, p. 306), and these commonly were classified as animals. Based on collections from the coast of Sicily, Philippi (1837) assigned four species to the genus, three of which (*L. expansum*, *L. incrustans*, *L. lichenoides*) were newly described. For the fourth species [*L. decussatum*], Philippi listed *Millepora decussata* Ellis & Solander (1786, p. 131, pl. 23, fig. 9) as a synonym and also provided a reference to Esper (1796, *Millepora*, pl. 25, fig. 4).

Foslie (1898a) selected *L. incrustans* as lectotype species. Schmitz's (1889, p. 455) choice of "*L. lichenoides* (Ellis & Solander) Philippi" is not tenable since Philippi did not include the Ellis & Solander species [i.e. *Millepora lichenoides* (Ellis) Ellis & Solander] in the initial presentation of *Lithophyllum*. Moreover, it was Hauck (1883, p. 268) who effected the combination "*L. lichenoides* (Ellis & Solander) Rosanoff ex Hauck"; Philippi apparently never placed the "Ellis & Solander taxon" in *Lithophyllum* as suggested by Schmitz (1889) and did not equate his "lịchenoides" with that of Ellis & Solander.

The basionym usually cited (see Farr, Leussink & Staffleu, 1979, p. 1076) for the Ellis & Solander taxon is *Millepora lichenoides* Ellis & Solander (1786, p. 131,

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pl. 23, figs 10–12). The earliest name and thus the correct basionym for this taxon, however, appears to be *Corallium lichenoides* Ellis (1768, p. 407, pl. 17, figs 9–11). The Ellis 1768 illustrations for *C. lichenoides* were reproduced in the Ellis & Solander 1786 account of *Millepora lichenoides*. Thus the latter name represents a new combination [i.e. *Millepora lichenoides* (Ellis) Ellis & Solander] rather than a new species.

The confusion between *L. lichenoides* Philippi and *Millepora lichenoides* (Ellis) Ellis & Solander has persisted ever since Kuetzing (1849, p. 697) regarded the two taxa as conspecific, and this confusion has led to several discussions (Mason, 1953; Adey, 1965) on the proper typification of *Lithophyllum*.

The original concept of *Lithophyllum* has undergone considerable change since 1837, and in more recent botanical publications (e.g. Hamel & Lemoine, 1953; Mason, 1953; Kylin, 1956; Masaki, 1968; Adey, 1970a; Cabioch, 1972; Johansen, 1976, 1981) its generic delineation has been based primarily upon anatomical and reproductive attributes rather than upon thallus form. At present, taxa of Corallinaceae may be referred to *Lithophyllum* as delineated by Adey, Masaki & Akioka (1974, p. 344) and Johansen (1976) if all of the following attributes occur: (1) geniculae absent; (2) tetrasporangial conceptacles uniporate and tetrasporangia lacking apical plugs; (3) cells of contiguous filaments generally interconnected by secondary pits (cell fusions absent or rare); (4) hypothallium devoid of a layer(s) of vertically elongate cells (sometimes termed palisade cells—see Turner & Woelkerling, 1982a); (5) thallus holophytic rather than parasitic.

Since 1837, at least 525 of the 1483 described taxa of nongeniculate Corallinaceae known to this author have been referred to *Lithophyllum* at various times. This includes over 250 taxa which never have been referred to other genera. Thus *Lithophyllum* has become associated with more taxa of non-geniculate Corallinaceae than any other genus except *Lithothamnion* (see Woelkerling, 1983), and both the botanical and the geological literature contain numerous references to *Lithophyllum* and its included species.

The relationships between the various changes in the generic circumscription of *Lithophyllum* and Philippi's original collections never have been determined, and indeed, apparently no one has re-examined or provided further data on any of Philippi's specimens. Thus none of the attributes upon which the genus *Lithophyllum* currently is based are known definitely to occur in any of the collections which Philippi had in hand when he established the genus. Moreover, the location of Philippi's collections apparently had become obscure (see Adey, 1970a, p. 19).

During a visit to the Rijksherbarium (L) in Leiden in May 1980, the present author undertook a special search to determine whether Kuetzing had retained any of the Philippi collections of *Lithothamnion* which he (Kuetzing, 1869, p. 35) reportedly had seen. Concurrent with the rediscovery of Philippi's original *Lithothamnion* collections (Woelkerling, 1983, fig. 2), all of Philippi's original *Lithophyllum* specimens were found together with identification labels in Philippi's script. Three of Philippi's *Lithophyllum* collections (*L. decussatum*, *L. incrustans*, *L. lichenoides*) were found in the same box (L943, 10 . . . 34; see Woelkerling, 1983, fig. 1) as all of Philippi's original *Lithothamnion* specimens. These had been filed among the unnamed collections of Corallinaceae at the Rijksherbarium. The fourth species (*L. expansum*) was found in a separate box

(L943, 7 . . . 84) among the named collections of Corallinaceae at the Rijksherbarium.

The rediscovery of these collections has provided the first opportunity to examine these plants critically and to determine whether the specimens in each collection possess the attributes associated with the present day concepts of *Lithophyllum*. This paper presents the results of these examinations and considers in detail the taxonomic implications of the findings. Brief historical accounts of the genus and of the four species also are included.

MATERIALS AND METHODS

Data were obtained from the type specimens which currently are housed at **L** (Rijksherbarium, Leiden, Netherlands). Microtechnique procedures follow Woelkerling (1980a) and a representative set of permanent slides from all collections examined has been retained at **LTB** (Department of Botany, La Trobe University, Bundoora, Victoria, Australia). Cellular measurements quoted include the decalcified cell walls as in most cases the protoplasts of the dried specimens were distorted. Wherever cell measurements are given in the text, "*L*" denotes cell length, "*D*" denotes cell diameter and "*L*/*D*" denotes the ratio of cell length to cell diameter. Scanning electron microscopy procedures are outlined by Woelkerling (1978) and herbarium abbreviations are taken from Holmgren, Keuken & Schofield (1981). Identification of hand writing was effected by comparison with samples on herbarium specimens in **L** and **MEL** (National Herbarium of Victoria, Royal Botanic Gardens, Melbourne, Victoria, Australia), with correspondence lodged at **L** and **MEL**, and with data in Koster (1948).

HISTORICAL BACKGROUND

Prior to 1866, most authors (except Zanardini, 1843) did not recognize *Lithophyllum* Philippi (1837) as a distinct genus. Kuetzing (1841, pp. 29–30) at first noted the similarity in thallus form between *Lithophyllum*, *Agardhia* Meneghini (1838), and *Melobesia* Lamouroux (1812). Afterwards, however, Kuetzing (1843, 1845, 1849) consistently listed *Lithophyllum* as a subgenus of *Spongites* even though he did describe *L. laeve* (Kuetzing, 1847, p. 33) which he later (Kuetzing, 1849) placed in *Mastophora*.

Decaisne (1842a, p. 126; 1842b, p. 114), Endlicher (1843, p. 49), Lindley (1846, p. 25), Montagne (1846, p. 137) and Harvey (1847, pl. 73), in contrast, all relegated *Lithophyllum* to the synonomy of *Melobesia*, based on apparent similarity in thallus form. Areschoug (1852, p. 515), however, described *Lithophyllum* as a distinct subgenus of *Melobesia*, and restricted it to taxa which: (1) produced more or less imbricate lobes, (2) had a surface layer of subhexagonal cells and (3) had the lower cell layers arranged in regular, superimposed transverse rows. Subsequently, Rosanoff (1866) resurrected *Lithophyllum* as a distinct genus, based primarily on Areschoug's criteria. Rosanoff (1866, pp. 79, 82) also emphasized that fronds of *Lithophyllum* were considerably thicker than those of *Melobesia* but not as thick as those of *Lithothamnion* and noted that *Lithophyllum* never produced cells analogous to the trichocytes of *Melobesia*. Philippi (1837) did not mention anatomical characters in the generic protologue for *Lithophyllum*, and since neither Areschoug nor Rosanoff examined Philippi's original collections, the attributes mentioned by Areschoug and Rosanoff were presumed but not demonstrated to occur in the taxa Philippi assigned to *Lithophyllum*.

The second major refinement to the generic concept occurred when Heydrich (1897b) restricted *Lithophyllum* to taxa which produce tetrasporangia within

uniporate conceptacles (Heydrich concurrently placed taxa with multiporate tetrasporangial conceptacles into *Lithothamnion*—see Woelkerling, 1983). Previously, reproductive features were not used to delimit *Lithophyllum* as a genus (e.g. see Rosanoff, 1866; Hauck, 1883; Schmitz & Hauptfleisch, 1897), and even though Solms-Laubach (1881, pp. 63, 64) recognized differences in the sporangial conceptacles, he included both multiporate and uniporate taxa within *Lithophyllum*. Foslie (1898b, 1900), who previously (Foslie, 1895) regarded *Lithophyllum* as a subgenus of *Lithothamnion*, accepted Heydrich's proposal and further restricted *Lithophyllum* to taxa in which the tetrasporangia were arranged around the periphery of the uniporate conceptacle chamber floor. Lemoine (1909, 1910, 1911) noted anatomical differences between *Lithophyllum* and *Lithothamnion* but still accepted the Heydrich–Foslie criteria for purposes of generic delineation. Philippi (1837) did not mention reproductive structures in his generic diagnosis or species protologues, and neither Heydrich nor Foslie nor Lemoine re-examined Philippi's collections to confirm the presence of characters they used to delimit *Lithophyllum*.

A third major refinement to the generic concept came when Rosenvinge (1917) restricted *Lithophyllum* to taxa with uniporate tetrasporangial conceptacles in which vegetative cells of contiguous perithallial filaments were interconnected by secondary pits. The use of secondary pit occurrence to delineate *Lithophyllum* was supported independently by Pilger (1919), was emphasized subsequently by Suneson (1937, 1943), and has formed part of all modern concepts of the genus. No one, however, has confirmed that secondary pits occur in any of the collections upon which Philippi originally based *Lithophyllum*.

Suneson's (1943, p. 59) concept of *Lithophyllum* effectively encompassed all taxa of non-geniculate Corallinaceae possessing uniporate tetrasporangial conceptacles and secondary pits between cells of contiguous perithallial filaments. Since then, at least seven other generic names have been employed for taxa (Table I) possessing uniporate tetrasporangial conceptacles and secondary pits, and this has affected the generic circumscription of *Lithophyllum* in various ways.

TABLE I. Generic names used since 1943 for non-geniculate Corallinaceae possessing uniporate tetrasporangial conceptacles and secondary pit connections

Crodelia Heydrich, 1911
Dermatolithon Foslie, 1898a
Ezo Adey, Masaki & Akioka, 1974
Goniolithon Foslie, 1898a
Lithophyllum Philippi, 1837
Metamastophora Setchell, 1943
Pseudolithophyllum Lemoine, 1913
Tenarea Bory, 1832

Only taxa which include non-fossil species are listed.

Hamel & Lemoine (1953, pp. 27, 45–46) restricted *Lithophyllum* to taxa in which perithallial cells were arranged, at least in part, in rows and in which the hypothallium was either multistratose and coaxial (i.e. having cells arranged in more or less arching, decumbent tiers) or unistratose and composed of small, more or less isodiametric cells. Hamel & Lemoine (1953) recognized three re-

lated genera: *Dermatolithon* Foslie (1898b) for taxa with perithallial cells arranged in rows and with a unistratose hypothallium composed of vertically elongate, palisade-like cells (sometimes termed a palisade hypothallium); *Tenarea* Bory (1832) for taxa with perithallial cells arranged in irregular rows and a multistratose non-coaxial hypothallium; and *Pseudolithophyllum* Lemoine (1913) for taxa with cells apparently not arranged in rows and with a unistratose hypothallium composed of small, regular, non-palisade cells. [Adey (1970a, 1970b) subsequently found that the type species of *Pseudolithophyllum* lacks secondary-pits and is not closely related to *Lithophyllum*; consequently the name *Pseudolithophyllum* cannot be used for the genus possessing characters outlined by Hamel & Lemoine (1953) and by Cabioch (1972)].

Mason (1953) restricted *Lithophyllum* to taxa with a multistratose hypothallium composed of horizontally elongate cells and recognized *Dermatolithon* for taxa with a uni- or di-stratose palisade hypothallium.

Kylin (1956) limited *Lithophyllum* to taxa with a multistratose coaxial hypothallium. Kylin also recognized *Dermatolithon* and *Tenarea* sensu Hamel & Lemoine (1953) but subsumed *Pseudolithophyllum* Lemoine (1913) [sensu Hamel & Lemoine, 1953] into *Crodelia* Heydrich (1911) and included within *Crodelia* all taxa with a unistratose non-palisade hypothallium.

Masaki (1968) used *Lithophyllum* for taxa with either a unistratose non-palisade hypothallium or a multistratose hypothallium and used *Dermatolithon* in the same sense as Mason (1953).

Cabioch (1972) limited *Lithophyllum* to taxa with a unistratose, non-palisade primary hypothallium and a secondary hypothallium ("faux hypothalle"—see Johansen, 1981, p. 42) which arises from perithallial tissue. Cabioch recognized four additional genera: *Goniolithon* (sensu Foslie, 1898a, non Foslie, 1900—see Setchell & Mason, 1943 and Cabioch, 1970) for taxa with a multistratose hypothallium and a perithallium composed largely of palisade-like cells; *Dermatolithon* for encrusting taxa which possess a unistratose palisade hypothallium; *Tenarea* for more or less upright taxa which possess a unistratose palisade hypothallium; and *Pseudolithophyllum* for taxa which possess a unistratose, non-palisade, primary hypothallium and which lack a secondary hypothallium.

Adey (1965, 1970a, 1970b) examined generic concepts among *Lithophyllum*-like taxa several times; most recently (Adey et al., 1974), three genera were recognized: *Lithophyllum* for taxa which are non-parasitic, lack haustoria, and have a non-palisade hypothallium; *Tenarea* for non-parasitic taxa lacking haustoria but possessing a palisade hypothallium; and *Ezo* Adey, Masaki, & Akioka for parasitic taxa with haustoria but devoid of a palisade hypothallium.

Johansen (1976) at first followed the concepts of Adey et al. (1974), but subsequently (Johansen, 1981, pp. 41–44) recognized six *Lithophyllum*-like genera: *Lithophyllum* (sensu Masaki, 1968), *Dermatolithon*, *Goniolithon*, and *Tenarea* (all sensu Cabioch, 1972), *Ezo* (sensu Adey et al., 1974), and *Metamastophora* (sensu Woelkerling, 1980a, 1980b). *Metamastophora* is unique among *Lithophyllum*-like plants in its erect, tentaculate habit and in possessing numerous cell fusions; secondary pit connections occur only in older perithallial tissues.

Thus since Suneson (1937, 1943), a series of authors have proposed a number of concepts for *Lithophyllum*; these differ from one another primarily in attri-

butes associated with the hypothallium (Table II). Although the presence of uniporate tetrasporangial conceptacles and the occurrence of secondary pit connections are common to all modern concepts of *Lithophyllum*, there is at present no consensus as to which of the six concepts should be employed. Moreover, none of these modern concepts hitherto has been evaluated in relation to Philippi's original collections, and consequently all proposals concerning *Lithophyllum* are attended by nomenclatural uncertainties and by assumptions regarding the type collections.

TABLE II. A summary of differences in the concepts of *Lithophyllum* which involve hypothallial attributes

Reference	Hypothallial attributes
Suneson (1943)	Unistratose or multistratose; palisade cells present or absent
Masaki (1968)/Johansen (1981)	Unistratose or multistratose; palisade cells absent
Adey (1970a)/Hamel & Lemoine (1953)	Unistratose or multistratose and coaxial; palisade cells absent
Mason (1953)	Multistratose; palisade cells absent
Kylin (1956)	Multistratose and coaxial; palisade cells absent
Cabioch (1972)	Unistratose, but also producing a secondary coaxial hypothallium ("faux hypothalle"); palisade cells absent

In the present account, the concept of *Lithophyllum* presented by Masaki (1968; see also Adey et al., 1974) and adopted by Johansen (1976, 1981) will be used as a framework for discussion, recognizing, of course, that the choice is subjective.

THE PHILIPPI COLLECTIONS

"**Lithophyllum decussatum** Philippi"

NOMENCLATURAL HISTORY

Philippi (1837, p. 389) applied the name *L. decussatum* to plants in hand from Sicily which were composed of lamellae which were thick, suborbiculate, decussate, variously crowded together and had entire margins. Philippi (1837, pl. 9, figs 4a–e) also provided some illustrations, listed *Millepora decussata* Ellis & Solander (1786, p. 131, pl. 23, fig. 9) as a "synonym" and gave Esper (1796, p. 137, *Millepora* pl. 25, fig. 4) as a second reference. The Esper figure was reprinted from Ellis & Solander. As a consequence, Philippi effected the nomenclatural combination *L. decussatum* (Ellis & Solander) Philippi.

Whether the Philippi specimens are conspecific with those upon which the Ellis & Solander taxon is based is uncertain. Philippi did not examine any of Ellis' material. Moreover, the Ellis collections are considered to have been lost (Dixon, 1960), thus precluding any possible direct comparisons of material at present. In addition, the written accounts of both Philippi (1837) and of Ellis &

Solander (1786) are superficial and do not provide enough data upon which to decide the question of conspecificity in a modern context. Their accompanying illustrations provide no help either; those of Philippi (1837) show some anatomical features while that of Ellis & Solander (1786) is a habit sketch.

Although the Ellis & Solander collections apparently never have been re-examined, most twentieth-century authors (e.g. De Toni, 1905, 1924; Foslie, 1909; Lemoine, 1911; Hamel & Lemoine, 1953; Bressan, 1974) have presumed that the Philippi and the Ellis & Solander collections are conspecific and have considered the taxon to be a species of *Lithophyllum*. *Millepora decussata* Ellis & Solander also has been treated as a distinct species within the genera *Melobesia* Lamouroux (e.g. Endlicher, 1843; Areschoug, 1852), *Sphaeranthera* Heydrich (Heydrich, 1900, 1901b) and *Spongites* Kuetzing (Kuetzing, 1849), and it has been regarded as a variety of *Lithophyllum expansum* Philippi [Heydrich, 1901a, p. 192; also listed as *Hyperantherella expansa* (Philippi) Heydrich (Heydrich, 1901a, p. 192) and *Stereophyllum expansum* (Philippi) Heydrich (1907, p. 224)], of *Lithophyllum incrustans* Philippi (Heydrich, 1911, p. 17, as *Crodelia*), and of *Lithothamnion agariciforme* (Pallas) Foslie (Foslie, 1897, p. 5). Specimens referred to *L. decussatum* by Solms-Laubach (1881) subsequently have been treated as a separate species (*Lithothamnion philippii* Foslie—see Hamel & Lemoine, 1953, p. 83).

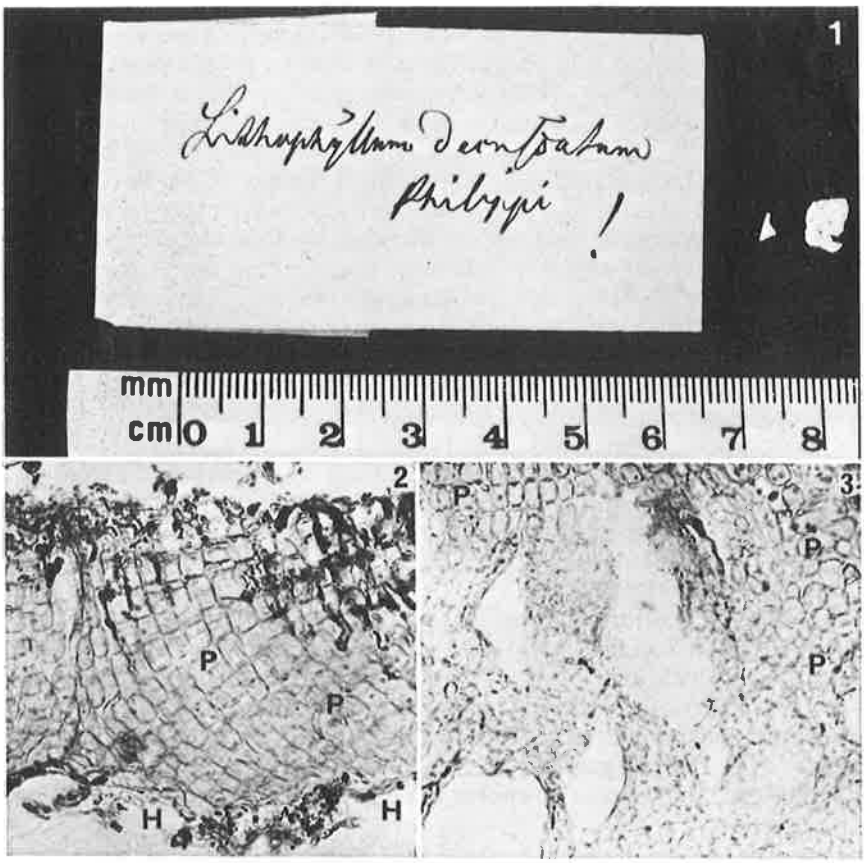
THE PHILIPPI COLLECTION

The Philippi collection of *L. decussatum* survives as two fragments less than 6·5 mm in greatest dimension (Fig. 1). Both fragments contain at least two layers of individuals, one apparently epiphytic on the other. Neither fragment, however, agrees closely with Philippi's (1837, p. 389) published description or with the original account of Ellis & Solander (1786), thus creating further uncertainty as to the conspecificity of the Philippi and the Ellis & Solander material. Philippi's fragments also appear to be sterile and generally in a poor state of preservation.

Some anatomical details were elucidated from sections of the smaller fragment, but many data are missing due to the imperfect condition of the specimens. Thus in the lower layer or host plant (Fig. 3), the epithallium is completely destroyed while in the upper layer or epiphytic plant (Fig. 2), only a few isolated epithallial (?) cells could be found. These cells (*L*, 3–4 μm; *D*, 8–9 μm; *L*/*D*, 0·3–0·5) appear to have distally rounded or compressed cell walls rather than angular walls but so few cells were seen that firm statements are not possible.

The perithallial tissue of the epiphytic plant is generally eight to 12 cells thick and is reasonably well preserved except for severe damage to the meristem (Fig. 2). In both longitudinal and transverse sections, cells are more or less square to rectangular in outline (*L*, 8–25 μm; *D*, 7–14 μm; *L*/*D*, 1–3). Cells of contiguous filaments are interconnected by secondary pits; cell fusions and trichocytes were not observed. The hypothallium appears to be composed of a single layer of more or less isodiametric to somewhat elongate cells [*L*, 11–19 μm; *D*, 8–11 μm; *L*/*D*, 1–2(–2·5)].

Except for small areas, the perithallial tissue of the host plant (Fig. 3) is barely recognizable and the meristem no longer exists. Where discernible, cells are more or less square to rectangular to elliptical in outline (*L*, 6–27 μm; *D*, 6–11 μm; *L*/*D*, 1–3) and cells of contiguous filaments are interconnected by secondary



FIGS 1–3. "*Lithophyllum decussatum*". FIG. 1. The Philippi collection (part of L943, 10 . . . 34). Note two fragments (far right) and the packet with label in Kuetzing's script. FIG. 2. Section through a fragment of the epiphyte. Note perithallial tissue (P) and position of the hypothallium (H) (×262). FIG. 3. Section through part of the host plant showing some intact perithallial tissue (P) (×268).

pits. Cell fusions and trichocytes were not observed, and a distinct hypothallium could not be identified.

Conceptacles were not found in either plant.

TAXONOMIC DISPOSITION

Plants in the Philippi collections cannot be identified confidently at generic or species level. The occurrence of secondary pit connections means that Philippi's specimens could fall within the broadest concept of *Lithophyllum* (i.e. Suneson, 1937, 1943), but in the absence of reproductive data and of firm data on epithallial cell wall shape, the possibility of these plants belonging to *Sporolithon* cannot be precluded. Similarly the relationship of Philippi's plants to those described by Ellis & Solander (1786) remains unresolved, and whether more modern concepts (e.g. Printz, 1929; Hamel & Lemoine, 1953; Bressan, 1974) of

L. decussatum conform to either the Philippi material or to the specimens of Ellis & Solander cannot be determined at present.

"**Lithophyllum expansum** Philippi"

NOMENCLATURAL HISTORY

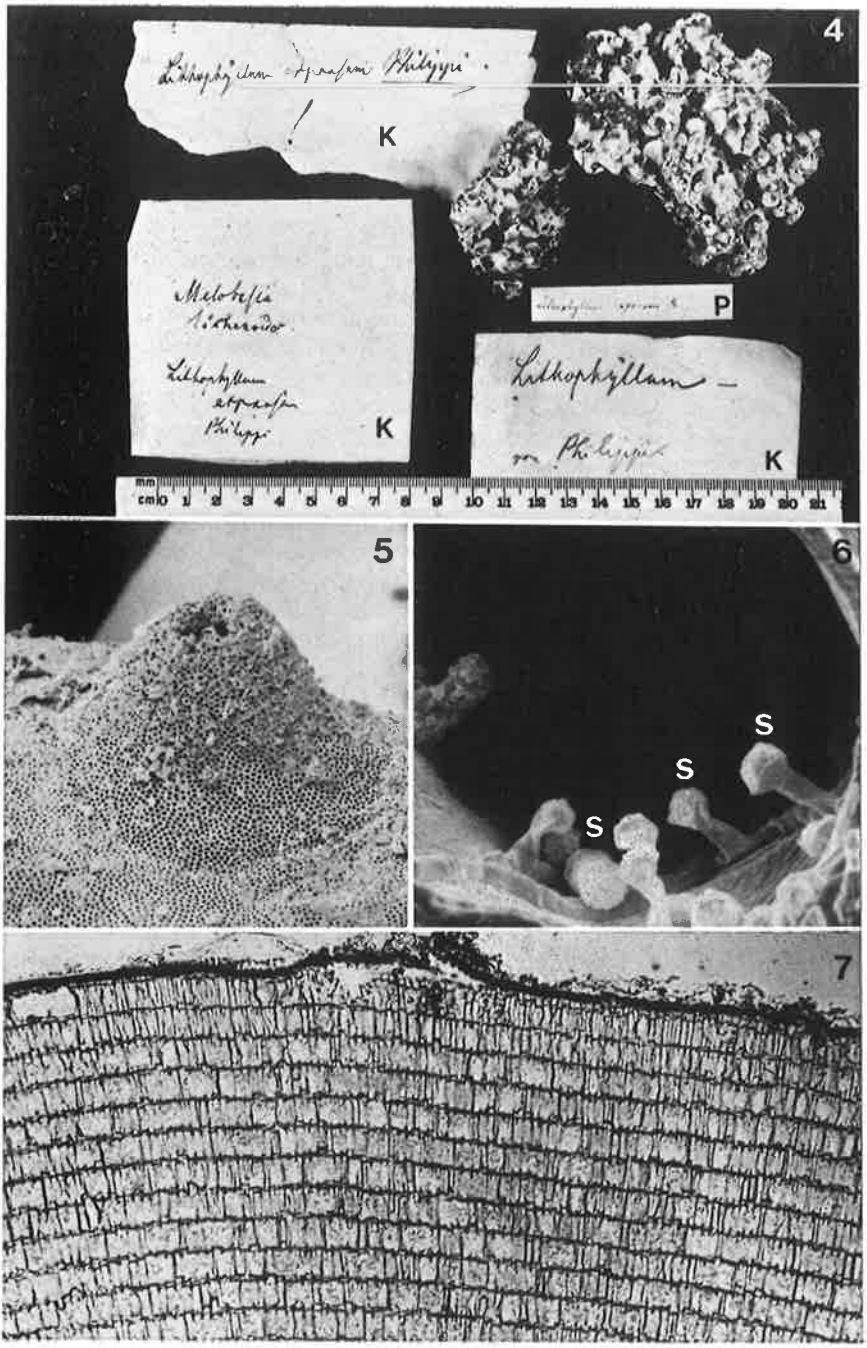
Philippi (1837, p. 389) established *L. expansum* for plants composed of extremely large, horizontally expanded, circular, overlapping lamellae with obtusely lobed and entire margins. In addition, he stated that his plants were pale, discoloured white beneath and that his largest specimen was 11·4 cm long and 7·6 cm broad. Philippi also questioned whether the *specimens* mentioned by Ehrenberg [1834, p. 353 (p. 129 of reprint)] under *Pocillopora agariciformis* (Pallas) Ehrenberg were conspecific with *L. expansum*.

Since 1837, *L. expansum* Philippi has been considered conspecific with *Melobesia agariciformis* (Pallas) Harvey (e.g. Harvey, 1847), has been regarded as a species inquirendae (e.g. Areschoug, 1852, p. 519), has been treated as a variety of *L. incrustans* Philippi (e.g. Heydrich, 1911, p. 13, as *Crodelia*) and has been recognized as a distinct species within the genera *Crodelia* Heydrich (e.g. Kylin, 1956; Levring, 1974), *Hyperantherella* Heydrich (Heydrich, 1901a, p. 192), *Lithophyllum* Philippi (e.g. Solms-Laubach, 1881; Hauck, 1883; Funk, 1927; Suneson, 1937), *Lithothamnium* Philippi (Foslie, 1895, p. 205), *Melobesia* (Endlicher, 1843), *Pseudolithophyllum* Lemoine sensu Lemoine (e.g. Hamel & Lemoine, 1953; Cabioch, 1972; Bressan, 1974; Lemoine, 1978), *Stereophyllum* Heydrich (Heydrich, 1904) and *Tenarea* Bory (Kuntze, 1898). Philippi's taxon is lectotype species of *Stereophyllum* Heydrich, 1904 (non *Stereophyllum* Mitten, 1859, nec *Stereophyllum* Karsten, 1889), and incorrectly has been used to lectotypify *Crodelia* (Kylin, 1956).

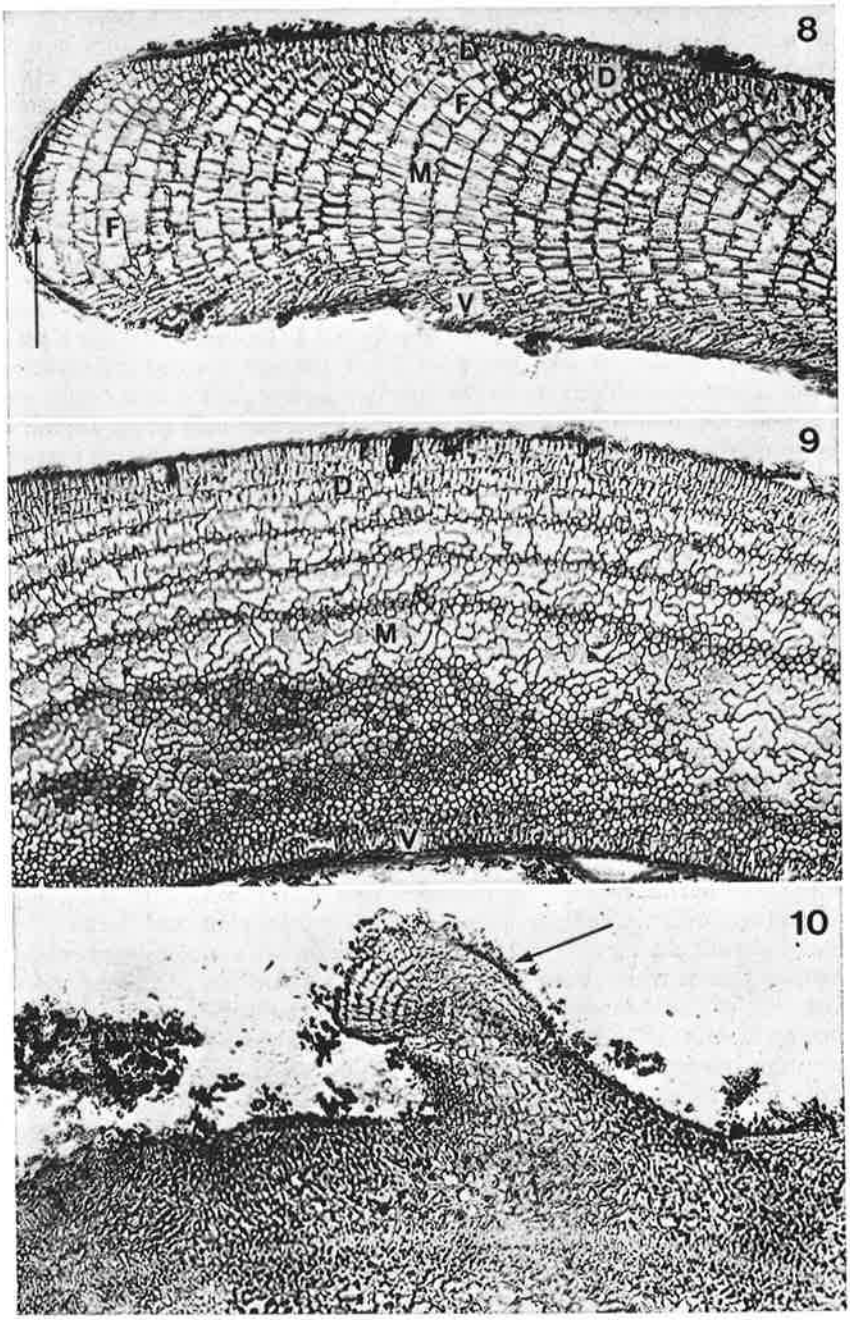
LECTOTYPE COLLECTION

The original collection of *L. expansum* Philippi (Fig. 4), designated here as the lectotype element, consists of two pieces of thallus each composed of more or less undulate, overlapping sometimes interlocking, horizontally oriented to ascending, irregularly lobate lamellae and of numerous additional small fragments. The largest thallus piece is up to 9·2 cm long, 6·25 cm broad and 2·3 cm thick. The other intact piece measures 4·5 cm long, 3·3 cm broad and 2·3 cm thick and at some stage probably was part of the larger piece. Four more or less conoidal, uniporate conceptacles were found—one on the smaller of the two intact pieces and three on fragments (Fig. 5). Based on SEM examination, these appear to be male conceptacles since the remains of apparent spermatangia occurred in the ostiole of one of them (Fig. 6). Conceptacle roofs protrude up to 300 μm above the thallus surface.

All vegetative tissues (Figs 7–9) are derived from a primary, internal, unistratose meristem situated just beneath a single layer of epithallial tissue. Within paradermal and longitudinal sections of lamellae, individual filaments are more or less readily discernible. The proximal portions of most filaments collectively form a multiaxial core in which the long axes of cells [L, 30–60 μm; D, 8–11 (–14) μm; L/D, 3–5] lie in planes more or less parallel to the lamellar surface and the lamellar apex. Laterally adjacent cells of contiguous filaments



FIGS 4–7. Lectotype of *Lithophyllum expansum* Philippi. FIG. 4. Lectotype collection (L943, 7 . . . 84) with accompanying labels in Kuetzing's (K) and Philippi's (P) script. FIG. 5. SEM of probable male conceptacle (×90). FIG. 6. SEM of conceptacle ostiole showing remains of apparent spermatangia (S) (×2000). FIG. 7. Paradermal section of thallus margin. Note arching tiers of medullary cells and numerous fusions between adjacent cells of contiguous filaments (×98).



FIGS 8–10. Lectotype of *Lithophyllum expansum* Philippi. FIG. 8. L.S. of lamella showing arching tiers of medullary cells (M) (a so called coaxial hypothallium), a dorsal (D) and a ventral (V) cortex, fusions (F) between cells of contiguous filaments, and a primary meristem (arrow) just beneath the surface (×112). FIG. 9. T.S. of lamella; labels as for Fig. 8 (×104). FIG. 10. View of a new lobose lamella (arrow) arising from dorsal surface of older lamella (×117).

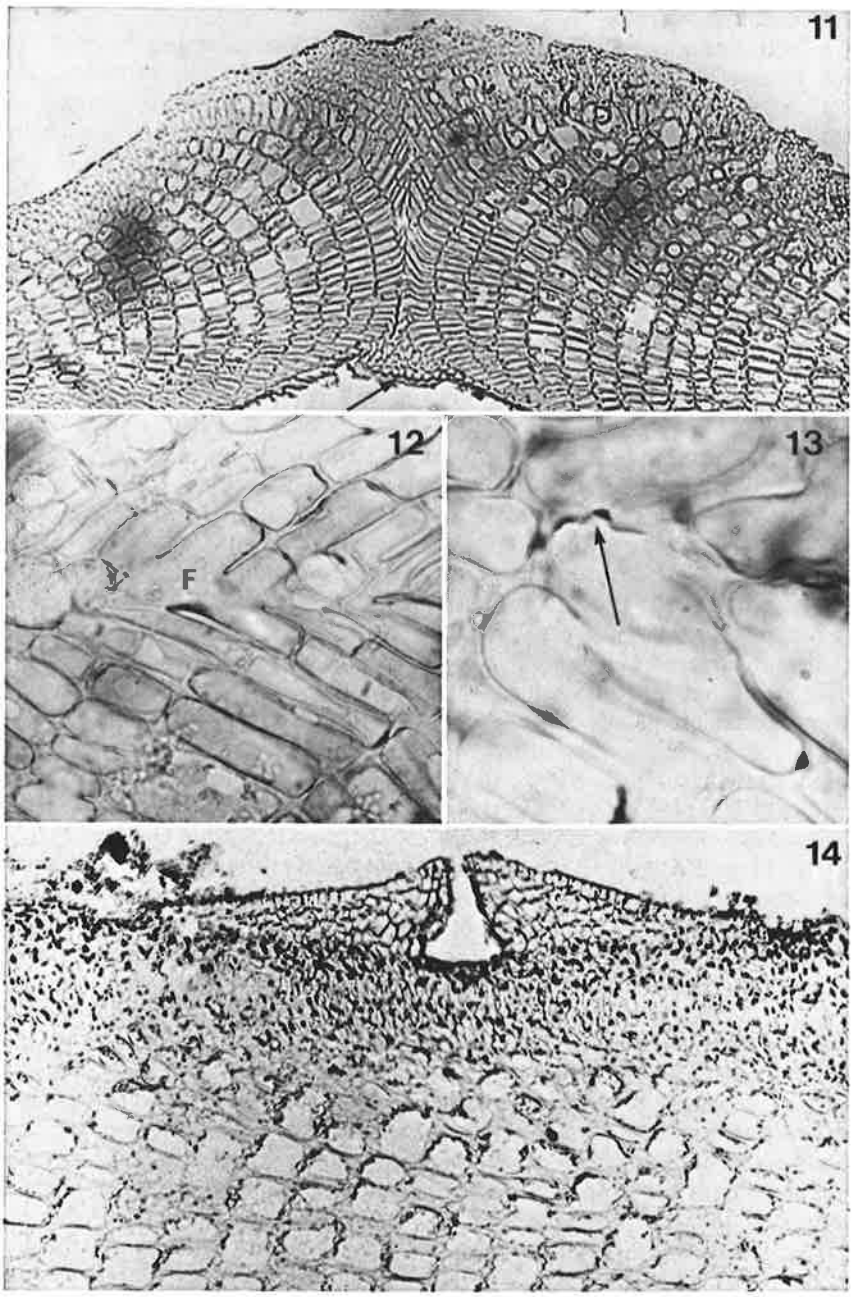
appear to form a tissue composed of arching, decumbent tiers of cells (Figs 7, 8). Some authors (e.g. Adey, 1970a; Adey & MacIntyre, 1973; Gordon, Masaki & Akioka, 1976; Johansen, 1976, 1981) have referred to such a tissue as a coaxial hypothallium, but since only a single meristem is involved (for discussion on meristem and tissue terminology, see Woelkerling, 1978, 1980a; Turner & Woelkerling, 1982a), the tissue more properly should be considered as a medulla analogous to that found in *Mastophoropsis* (Woelkerling, 1978) and most geniculate Corallinaceae (Johansen, 1976, 1981). Within tiers, cells of adjacent filaments commonly are interconnected by means of cell fusions (Figs 7, 8).

Except near the apices of lamellae, distal portions of most filaments arch outwards to varying degrees towards the thallus surface (Figs 8, 9). These outward arching portions of filaments collectively form a cortex in which the long axes of cells (L, 11–30 μm; D, 6–10 μm; L/D, 1·4–4) become oriented more and more towards a plane perpendicular to the lamellar surface. The dorsal cortex generally is more clearly defined than the ventral cortex, and cells in the former tend to be somewhat shorter than cells in the latter. Each cortical filament terminates in an epithallial cell (L, 4–8 μm; D, 8–11 (–14) μm; L/D, 0·5–0·8) beneath which the meristem cell is situated. Fusions also occur between cells of adjacent cortical filaments.

Most new cells arise near the apex or beneath the dorsal surface of lamellae. Although meristematic activity appears to be more or less uniform beneath the dorsal lamellar surface, certain localized groups of meristem cells may become exceptionally active and give rise to numerous basipetal derivatives. This results ultimately in the production of a new lobose lamella which grows out over, and becomes more or less superimposed upon, the underlying progenitor lamella (Figs 4, 10). The mode of formation of new lobose branches (lamellae) from the dorsal surface of lamellae in *L. expansum* contrasts markedly with that in *Lithoporella melobesioides* (Foslie) Foslie and *Mastophora rosea* (C. Agardh) Setchell (see Turner & Woelkerling, 1982a). In *Lithophyllum expansum* only a single primary meristem is involved and the direction of filament growth does not change in an abrupt manner. In the other two taxa, branch formation initially involves the production of two distinct secondary meristems, and the direction of filament growth changes abruptly. Moreover, branches are composed entirely of secondary tissues while those in *L. expansum* are composed of primary tissues.

Lamellae of *L. expansum* may become joined secondarily to other lamellae and opposing margins of the same lamella also may join secondarily (Fig. 11). In the latter case, opposing margin cells become deflected and most meristematic activity appears to cease. Adjunctive cell fusions may occur between cells of opposing filaments (Fig. 12) and in at least one instance two cells of opposing filaments have become joined by a secondary pit connection (Fig. 13). Similar adjunctive cell fusions were described for *Lithoporella melobesioides* and *Mastophora rosea* (Turner & Woelkerling, 1982a).

The single, small uniporate conceptacle examined anatomically (Fig. 14) contained an empty, more or less pyriform chamber 63 μm in diameter and an elongated ostiole ca. 50 μm long surrounded by a roof up to seven cell layers deep.



FIGS 11–14. Lectotype of *Lithophyllum expansum* Philippi. FIG. 11. L.S. of opposing margins of a lamella which have become joined (arrow) secondarily (×125). FIG. 12. Adjunctive cell fusions (F) between cells of opposing marginal filaments of two lamellae which have become joined secondarily ×(544). FIG. 13. A secondary pit connection (arrow) between cells of two adjacent filaments (×3200). FIG. 14. Small, uniporate conceptacle with empty chamber along dorsal surface of lamella (×145).

TAXONOMIC IMPLICATIONS

The lectotype material of *L. expansum* Philippi almost certainly belongs to the genus *Mesophyllum* Lemoine (1928) as currently delineated by Johansen (1976, 1981) and Cabioch (1972). Lectotype plants are non-geniculate, possess a so-called "coaxial hypothallium", have fusions (not secondary pits) between cells of contiguous filaments, have rounded epithallial cells, and appear to have simple (not dendroid) spermatangia. All of these features characterize the genus *Mesophyllum* (see Johansen, 1976; Lebednik, 1978; Townsend, 1979). Multiporate tetrasporangial conceptacles, also characteristic of *Mesophyllum*, were not observed in Philippi's specimens, but uniporate sexual conceptacles were. Because of the other anatomical features and because of the distinctive foliose habit of Philippi's specimens, however, there is no doubt as to the generic affinity with *Mesophyllum*.

At least 132 taxa have been referred to *Mesophyllum* since its establishment by Lemoine (1928). As noted by Johansen (1981, p. 126), however, only *M. lichenoides* (Ellis) Lemoine [Basionym: *Corallium lichenoides* Ellis 1768, pp. 407, 419, pl. 17, figs 9–11, later described as *Millepora lichenoides* (Ellis) Ellis & Solander, 1786, p. 131, pl. 23, figs 10–12], the lectotype species of *Mesophyllum*, extends north of 35°N latitude in the Atlantic Ocean, and Philippi's specimens certainly conform to modern concepts (e.g. Hamel & Lemoine, 1953; Cabioch, 1972; Adey & Adey, 1973; Bressan, 1974; Cabioch & Giraud, 1978) of that species. Like many other taxa of non-geniculate Corallinaceae, the relationships between the current concept of *Mesophyllum lichenoides* (Ellis) Lemoine and the type specimens of that taxon have not been determined, and because the Ellis collections are considered lost (Dixon, 1960), it has not been possible to compare type material of *M. lichenoides* with type material of *L. expansum*. However, the original drawings of Ellis (1768, pl. 17, figs 9–11), later reproduced by Ellis & Solander (1786, pl. 23, figs 10–12), show the distinctive habit of this species and the markedly protruding conceptacles on the dorsal thallus surface; Adey & Adey (1973, p. 364) note that these characters readily differentiate *M. lichenoides* from other non-geniculate corallines in the British Isles (from which Ellis's specimens originated). Ellis's drawings, moreover, agree closely with the appearance of Philippi's specimens of *L. expansum*. Thus, circumstantial evidence indicates that the two taxa probably are conspecific, and in the absence of contrary data, *L. expansum* Philippi is considered here to be a heterotypic synonym of *Mesophyllum lichenoides* (Ellis) Lemoine.

Since at least 1908, Philippi's epithet "expansum" has been widely misapplied to a species with quite different anatomical characters from those evident in the type specimens of *L. expansum*. Pilger (1908, text fig. 4, pl. 14, fig. h, pl. 15, fig. a) showed secondary pit connections rather than cell fusions between cells of contiguous filaments in specimens he referred to *L. expansum*. This concept was accepted by Lemoine (1911, 1915) and most subsequent authors (e.g. Suneson, 1937; Feldman, 1939; Hamel & Lemoine, 1953; Lemoine, 1965; Cabioch, 1972; Bressan, 1974; Levring, 1974), and in this context, Philippi's taxon has been referred to the genera *Crodelia*, *Lithophyllum* and *Pseudolithophyllum* (sensu Lemoine, 1913). Results from this study, however, indicate clearly that the modern concept of Philippi's "expansum" (as exemplified in the account of Suneson, 1937) in no way agrees with the type specimens of *L. expansum*

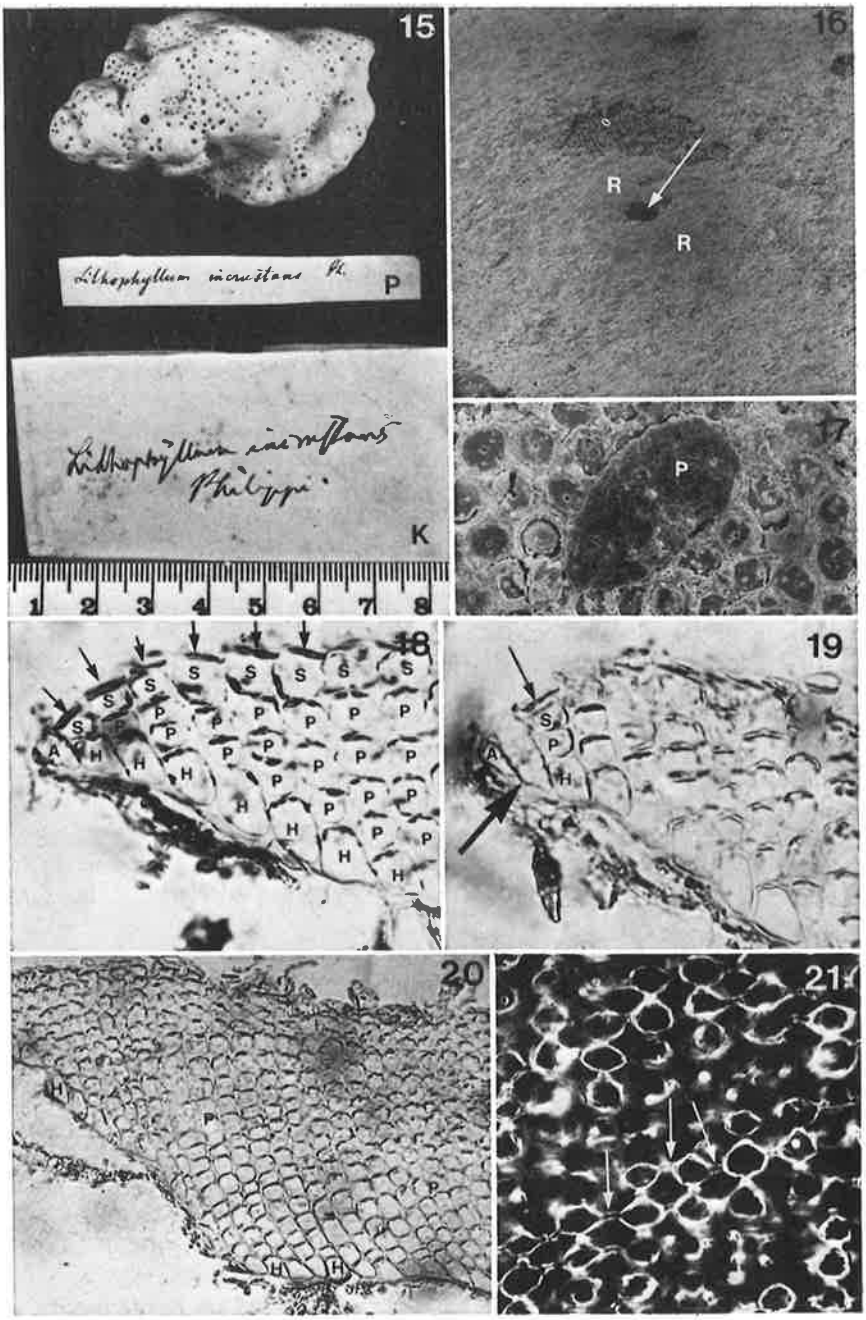
Philippi. Rather, the modern concept of "expansum" conforms to the type specimens of *L. incrustans* Philippi, as noted elsewhere in this paper. Thus, considerable confusion exists in the use of both of these names; in most modern accounts they are misapplied and caution must be exercised when referring to published records of these taxa.

"**Lithophyllum incrustans** Philippi"

NOMENCLATURAL HISTORY

Philippi (1837, p. 388) established *L. incrustans* for plants with thick reddish-white crusts, with simple scarcely lobate margins, and which were encrusted on a foreign body. He also referred to two illustrations (namely pl. 27, figs 2d, D) in the 1767 German edition of Ellis's 1755 book which depict the organism Ellis (1755, p. 76) described under the polynomial *Corallium cretaceum lichenoides.* (The plates in the 1767 German and 1755 English editions are identical.) Philippi, unlike Ellis (1768, p. 407), did not equate *Corallium cretaceum lichenoides* with *Corallium lichenoides* Ellis (1768, p. 407, pl. 17, figs 9–11); the two taxa are based on completely independent sets of illustrations (compare Ellis, 1755, pl. 27, figs 2d, D with Ellis, 1768, pl. 17, figs 9–11) which depict plants so different from one another that they are almost certainly distinct species. Since Ellis's collections are considered to be lost (Dixon, 1960), it has been impossible to examine any of the relevant specimens. Subsequently (Ellis & Solander, 1786, p. 131, pl. 23, figs 10–12; Lamouroux, 1821, p. 46, pl. 23, figs 10–12), the Ellis, 1768 set of figures of *C. lichenoides* were used to depict *Millepora lichenoides* (Ellis) Ellis & Solander, which now is known as *Mesophyllum lichenoides* (Ellis) Lemoine. The Ellis 1755/1767 set of figures cited by Philippi (1837), in contrast, were not used in Ellis & Solander (1786), and until mentioned by Philippi (who had access to Ellis & Solander—see Philippi, 1837, p. 388), the 1755/1767 figures remained obscure. Thus, in the absence of contrary evidence, *Corallium cretaceum lichenoides* and *Corallium lichenoides* are regarded here as distinct entities and only the former is considered linked in any way with *L. incrustans* Philippi.

Since 1837, *L. incrustans* Philippi has been treated as a species inquirendae (e.g. Areschoug, 1852), has been considered conspecific with *Lithothamnion polymorphum* (Linneaus) Areschoug (e.g. Hauck, 1883, p. 272), has been treated as a distinct variety of *L. polymorphum* (Vinassa, 1892), and has been recognized as a distinct species within the genera *Crodelia* Heydrich (see Heydrich, 1911, p. 12), *Hyperantherella* Heydrich (see Heydrich, 1900, p. 316), *Lithophyllum* Philippi (Zanardini, 1843 and most authors since 1898), *Lithothamnium* Philippi (e.g. Foslie, 1895, p. 122; Heydrich, 1897a, p. 58; Collins, 1901, p. 260; Boergesen, 1943, p. 16), *Melobesia* Lamouroux (see Endlicher, 1843, p. 49) and *Spongites* Kuetzing (see Kuetzing, 1849, p. 698). Foslie (1898a, p. 6) lectotypified *Lithophyllum* with *L. incrustans* Philippi (see Mason, 1953 for further discussion) and Papenfuss (1967, p. 98) showed that *Hyperantherella* Heydrich, *Stereophyllum* Heydrich, and *Crodelia* Heydrich, all of which are based on *L. incrustans*, are homotypic synonyms of *Lithophyllum* Philippi.



FIGS 15–21. Lectotype of *Lithophyllum incrustans* Philippi. FIG. 15. Lectotype collection (part of L943, 10 . . . 34) with accompanying labels in Kuetzing's (K) and Philippi's (P) script. FIG. 16. SEM of uniporate tetrasporangial conceptacle showing a flattened

LECTOTYPE COLLECTION

The original collection of *L. incrustans* Philippi (Fig. 15), designated here as the lectotype specimen, consists of a single, smooth-surfaced, excrescence-free crust covering a 62 mm long, 36 mm broad, 25 mm high (max. dimensions) snail shell. The crust is perforated by numerous holes 0·4–1·1 mm in diameter, probably produced by boring animals. Uniporate conceptacles (Fig. 16) occur over most of the thallus surface; conceptacle roofs are more or less flush with the thallus and during early development, the ostioles appear to be blocked by some sort of plug-like material which is not directly associated with the sporangia (Fig. 17).

The vegetative tissues appear to be derived from two distinct meristems—one primary and superficial and one secondary and internal (Figs 18, 19; meristem terminology follows Turner & Woelkerling, 1982a). Cells of the primary meristem are terminal and are situated around the thallus margin. These cells divide in an anticlinal, transaxial manner to produce hypothallial cells basipetally. Soon afterwards the newly formed hypothallial cells undergo single periclinal coaxial divisions. The basipetal products remain non-meristematic and form part of the unistratose hypothallium. The acropetal products remain meristematic and collectively constitute a new secondary meristem whose cells are not connected by primary pits to cells of the primary meristem. Subsequently, cells of the secondary meristem undergo periclinal transaxial divisions to form perithallial cells basipetally. A single layer of epithallial cells also is formed acropetally and as a result the secondary meristem becomes situated in an intercalary position just beneath the epithallium. Cabioch (1972, p. 183 et seq. fig. 16–1) describes a similar mode of development in plants she identified as *Pseudolithophyllum expansum* (Philippi) Lemoine (see also Suneson, 1937, p. 21, figs 11a–c).

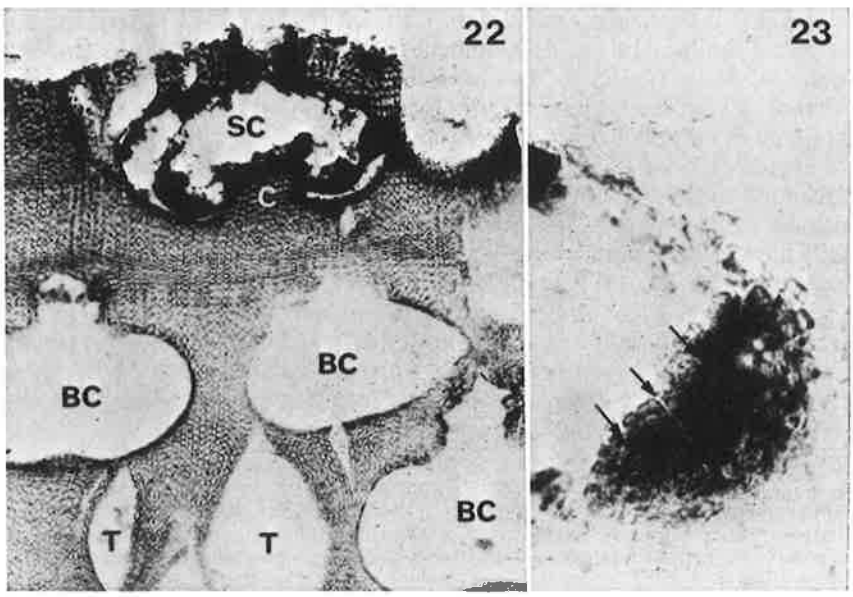
Thallus structure appears similar in longitudinal and transverse sections. The hypothallium (Fig. 20) is unistratose and composed of cells (*L*, 8–21 μm; *D*, 5–14 μm; *L*/*D*, 0·6–2·5) which are neither extremely elongate nor palisade-like. Attachment to the substratum occurs by cellular adhesion; neither rhizoids nor haustoria were observed. The perithallium (Figs 20, 22) consists of numerous, readily identifiable, laterally conjoined, more or less vertically oriented filaments whose cells [*L*, 5–14(–19) μm; *D*, 8–11 μm; *L*/*D*, 0·6–1·5(–1·9)] may be broader than long, more or less isodiametric, or somewhat longer than broad. Cells of adjacent filaments usually are not aligned into distinct tiers or rows but are interconnected by secondary pits (Fig. 21). Larger perithallial cells (*L*, 14–24 μm; *D*, 11–14 μm; *L*/*D*, 1·1–2·3) occur in several localized regions, usually just above

conceptacle roof (R) and the ostiole (arrow) (×67). FIG. 17. Plug-like material (P) blocking the ostiole of a young uniporate conceptacle (×532). FIG. 18. Thallus margin showing primary apical meristem (A), hypothallial cells (H), cells of the secondary meristem (S) beneath the dorsal epithallium; remains of epithallial cells (arrows) and perithallial cells (P) (×560). FIG. 19. Another portion of the thallus margin showing a primary apical cell (A), the first basipetally produced hypothallial cell (large arrow) and the next formed row showing cells of the hypothallium (H), perithallium (P), secondary meristem (S) and remains of the epithallium (small arrow) (×540). FIG. 20. Older portion of thallus showing a unistratose hypothallium (H) at the bottom and numerous layers of perithallial tissue (P). Most epithallial cells have been destroyed (×215). FIG. 21. Secondary pit connections (arrows) between cells of contiguous perithallial filaments (×514).

the hypothallial layer. The epithallium is not completely intact but appears to be unistratose and made up of more or less compressed to narrowly elliptical cells (L, 3–6 μm; D, 8–11 μm; L/D, 0·3–0·8) whose walls are rounded rather than angular.

Tissue gaps appear to occur commonly within the perithallium (Fig. 22). These may be lenticular, ovoid, rounded or irregular in outline and in at least some cases are in open connection with the thallus surface. Their origin and function are unknown; perhaps such gaps are created as a result of grazing or boring activities of animals or as a result of localized tissue degeneration. These tissue gaps are readily differentiated from buried conceptacles (Fig. 22); the latter usually are subtended by several layers of vertically very compressed cells whereas tissue gaps are not.

Conceptacles (Fig. 22) presumably arise from subsurface perithallial tissue, possess more or less ovoid chambers up to 380 μm in diameter and 175 μm in height and are uniporate. The conceptacle roof consists of up to ten layers of perithallial cells which are interconnected by secondary pits. Ostioles up to 76 μm across and 98 μm long are present. In some conceptacles a central columella is clearly evident (Fig. 22) but in others no columella is apparent (Fig. 22). Tetrasporangia (Fig. 23) are poorly preserved and thus accurate measurements have not been possible. With age, conceptacles are overgrown by perithallial tissue and become buried within the thallus.



FIGS 22–23. Lectotype of *Lithophyllum incrustans* Philippi. FIG. 22. T.S. through mature tissues showing a uniporate conceptacle (SC) at the thallus surface with remains of a columella (C), portions of several empty conceptacles (BC) which have become buried in the perithallium, and tissue gaps (T) in the perithallium (×94). FIG. 23. Remains of a tetrasporangium in one conceptacle. Note lines of division (arrows) in sporangium (×440).

TAXONOMIC IMPLICATIONS

The lectotype specimen of *L. incrustans* Philippi falls within the concept of *Lithophyllum* as delineated by Masaki (1968; see also Adey et al., 1974) and adopted by Johansen (1981). Philippi's specimens are non-geniculate, possess uniporate tetrasporangial conceptacles, are not parasitic, lack a palisade hypothallium, and have cells of contiguous filaments interconnected by secondary pits. Collectively these characters delineate *Lithophyllum* from other genera of Corallinaceae, if the Masaki (1968)/Johansen (1981) concept of the genus is adopted. At least six concepts of *Lithophyllum* (see Historical Background and Table II) have been put forth since 1943, however, and there is no consensus at present as to which most accurately reflects the true biological situation. The circumscription of *Lithophyllum* in relation to *L. incrustans* as lectotype species is considered further in the discussion.

A number of accounts (e.g. Heydrich, 1911; Lemoine, 1911; Bauch, 1937; Feldman, 1939; Hamel & Lemoine, 1953; Cabioch, 1969, 1972; Adey & Adey, 1973; Bressan, 1974) of plants referred to *L. incrustans* have been published, but none of these accounts have included comparison of specimens in hand with the lectotype specimens of Philippi. Moreover, the concepts of *L. incrustans* have varied considerably from one presentation to another. Thus, for example, *L. incrustans* sensu Hamel & Lemoine (1953) and sensu Bressan (1974) includes only plants with a multistratose hypothallium; *L. incrustans* sensu Cabioch (1972) includes only plants which produce a unistratose hypothallium and with a "faux hypothalle" which develops secondarily from perithallial tissue; and *L. incrustans* sensu Adey & Adey (1973) contains plants which may have a unistratose or possibly a multistratose coaxial hypothallium. Accounts of *L. incrustans* also vary with respect to other characteristics, and short of re-examining all relevant specimens and comparing them with the Philippi type, it is not possible to say with certainty which authors are really dealing with *L. incrustans* and which authors are not. It does seem certain, however, that the name *L. incrustans* has been misapplied in a number of cases, and that all published records of this species must be treated with caution. Moreover, as noted earlier, a number of published records for *Pseudolithophyllum expansum* (Philippi) Lemoine (e.g. Bressan, 1974; Cabioch, 1972; Hamel & Lemoine, 1953; Suneson, 1937) [as *Lithophyllum*] involve plants which almost certainly belong to *L. incrustans* [i.e. data in the published descriptions agree with Philippi's type specimen of *L. incrustans*]. Until this confusion is resolved by careful restudy of all specimens involved, published records for both taxa must be regarded with suspicion.

"**Lithophyllum lichenoides** Philippi"

NOMENCLATURAL HISTORY

Philippi (1837, p. 389) established *L. lichenoides* (with a query) for plants with lamellae that are subsemicircular, thin, and variously and densely crowded together; and with margins that are wavy and incised–lobate. He also stated that this species produces coherent masses "several inches" thick which often are more than 30 cm long and are proportionately as broad. Philippi questioned whether this taxon was a rough form of plants discussed by Esper (1796, p. 137, *Millepora* pl. 25, figs 1, 2, 3) under the name *Millepora decussata* var., and

Philippi listed a Berlin Museum specimen under the herbarium (?) name of *Millepora squamosa*.

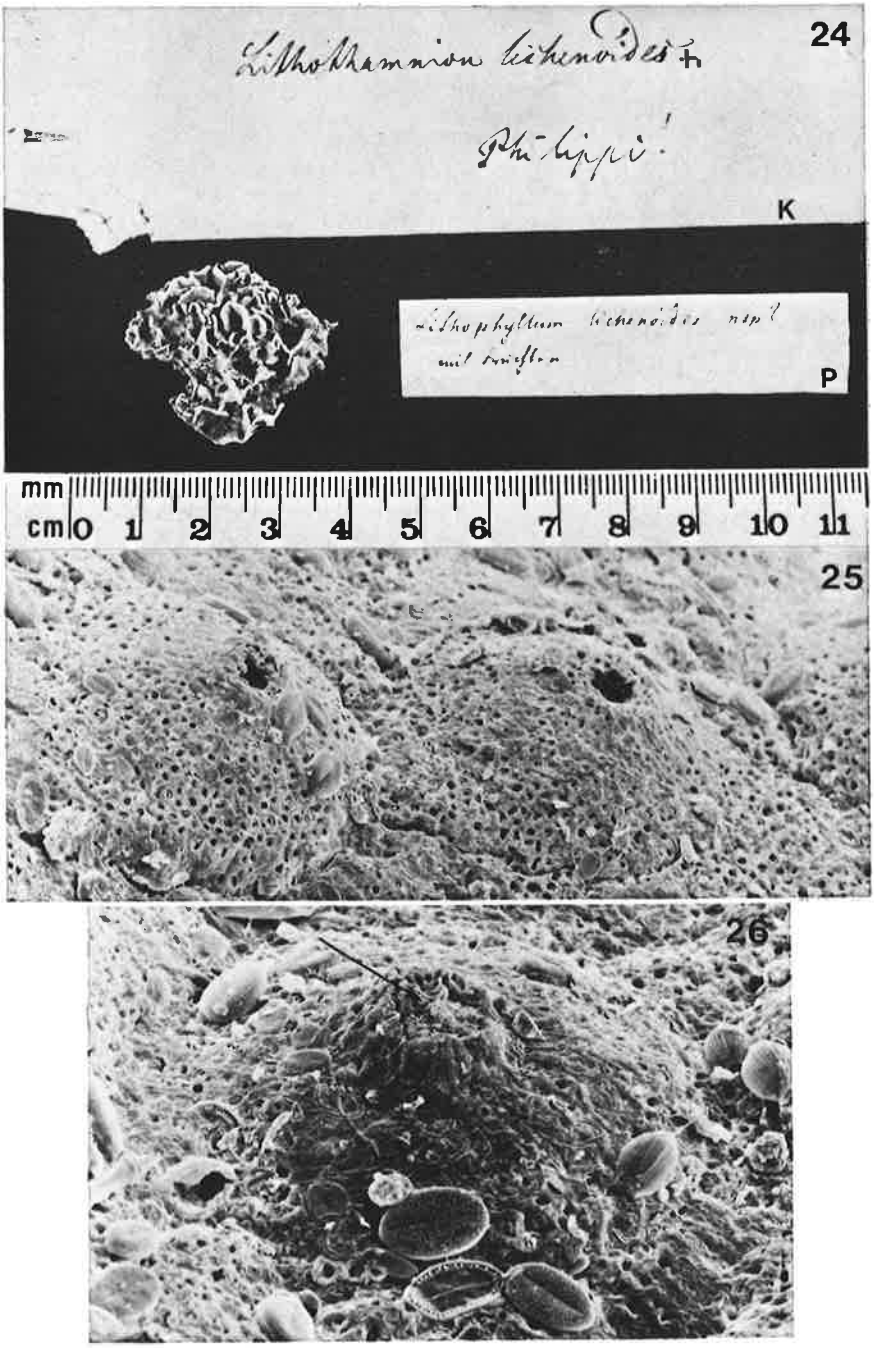
The post-1837 nomenclatural history of *L. lichenoides* is complex and follows two distinct courses: one involving the name *L. lichenoides* Philippi and one in which *L. lichenoides* Philippi became confused with and equated to *L. lichenoides* (Ellis) Rosanoff ex Hauck (Basionym: *Corallium lichenoides* Ellis, 1768, p. 407). Endlicher (1843) transferred *L. lichenoides* Philippi to the genus *Melobesia* [as *M. lichenoides* (Philippi) Endlicher]. After 1843, Philippi's taxon was not recognized as a distinct species until Rosanoff (1866, p. 91) provided a detailed account of specimens he identified as *L. lichenoides* Philippi. Rosanoff's plants had, among other features, tetrasporangia with distinct apical plugs borne within multiporate conceptacles (Rosanoff, 1866, pl. 5, figs 2, 4, 5, 6). Rosanoff, however, did not confirm that multiporate tetrasporangial conceptacles also occurred in the plants upon which Philippi based the species originally. Lemoine (1911, p. 169) later listed *L. lichenoides* Philippi as a taxonomic synonym of *Tenarea tortuosa* (Esper) Lemoine; more recently Bressan (1974) followed suit using the binomial *L. tortuosum* (Esper) Foslie.

The confusion between Philippi's taxon and that of Ellis first arose when Kuetzing (1849, p. 697), apparently misled by the similarity of names (see also Setchell, 1943, p. 128), united the two taxa under the binomial *Mastophora lichenoides* "Kuetzing". Areschoug (1852, p. 515) transferred both to *Melobesia lichenoides* (Ellis) Areschoug. Later Hauck (1883, p. 268) questioned whether the two names really applied to the same taxon, but Schmitz (1889, p. 455) believing the two taxa to be nomenclatural synonyms, erroneously linked the two authors using the combination "*L. lichenoides* (Ellis & Solander) Philippi ex Schmitz", and designated it as type species of *Lithophyllum*. Although Philippi never made such a combination and never linked his taxon to that of Ellis (thus Schmitz's choice of a type in *Lithophyllum* is not tenable), most modern authors have regarded the two to be synonymous and have listed the taxon as *Mesophyllum lichenoides* (Ellis) Lemoine. *M. lichenoides* (Ellis) Lemoine is the lectotype species of *Mesophyllum*.

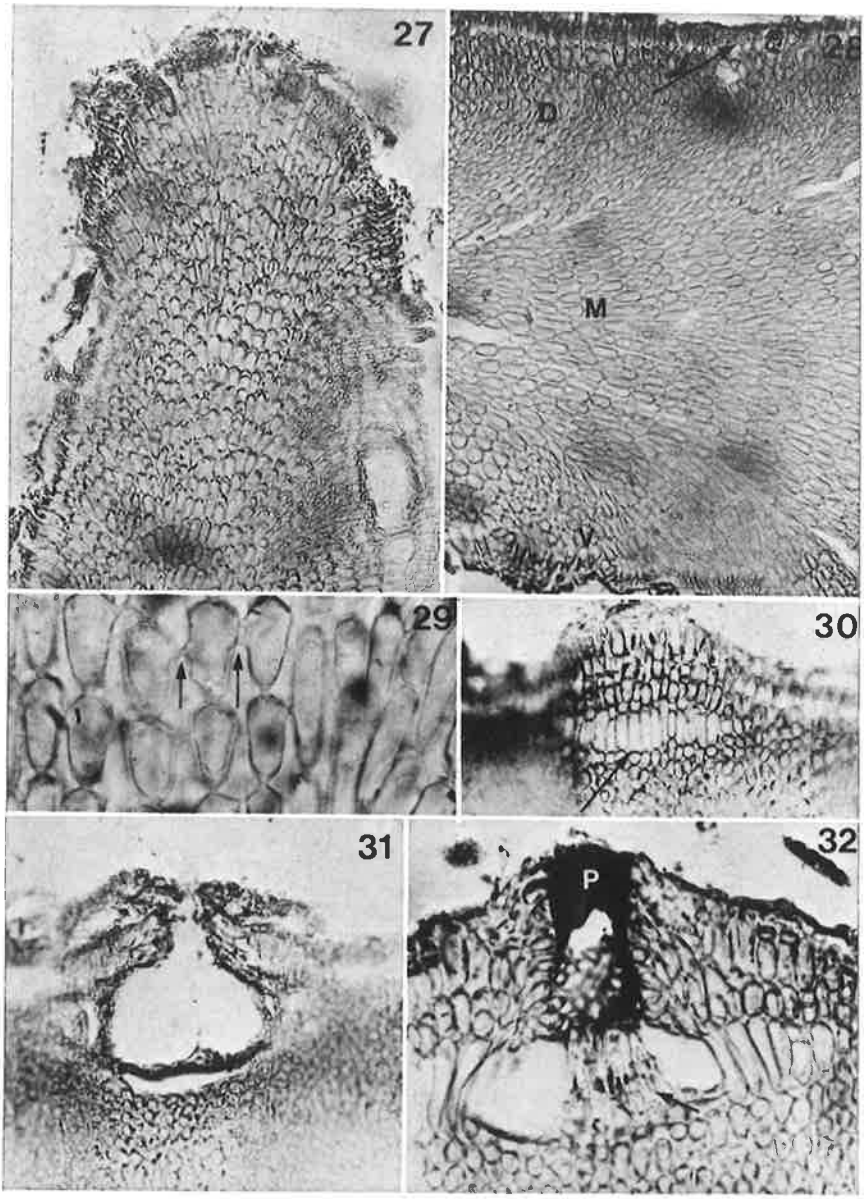
LECTOTYPE COLLECTION

The original collection of *L. lichenoides* Phillipi (Fig. 24), designated here as lectotype specimen, contains a single fragment up to 30 mm long, 20 mm broad, and 26 mm high, which, based on comments of Philippi (1837, p. 389), probably formed part of a larger colony. The specimen is composed of a number of more or less vertically oriented lamellae which are variously lobed and contorted and interlocked to form a coherent honeycombed mass. Most lamellae possess numerous uniporate conceptacles on one surface (Figs 25, 26). Conceptacle roofs protrude up to 75 μm above the lamellar surface, are more or less domoid and often possess a slightly protruding ostiole, which, prior to sporangium release, appears to be blocked by some sort of plug (Fig. 26).

All vegetative tissues are derived from a single primary meristem (Fig. 27) in a manner analogous to that in *Mastophoropsis* (Woelkerling, 1978), and within lamellae individual filaments are readily discernible. The proximal portions of most filaments collectively form a multiaxial core or medulla (Figs 27, 28) in which the long axes of cells (L, 11–25 μm; D, 6–9 μm; L/D, 1–3·5) lie in planes



FIGS 24–26. Lectotype of *Lithophyllum lichenoides* Philippi. FIG. 24. Lectotype collection (part of L943, 10 . . . 34) with accompanying labels in Kuetzing's (K) and Philippi's (P) script. FIG. 25. SEM of mature conceptacles on dorsal lamellar surface (×268). FIG. 26. SEM of young conceptacle with ostiole (arrow) blocked by plug-like material (×416).



FIGS 27–32. Lectotype of *Lithophyllum lichenoides* Philippi. FIG. 27. L.S. through apex of lamella showing multiaxial development (×217). FIG. 28. Longitudinal section through lamella showing central medulla (M), the dorsal (D) and ventral (V) cortices, and meristem cells (arrow) beneath the remains of the dorsal epithallium (×214). FIG. 29. Secondary pits (arrows) between cells of contiguous medullary filaments (×900). FIG. 30. Conceptacle meristem (arrow) situated in the dorsal cortex (×224). FIG. 31. Section through a mature, empty conceptacle along dorsal surface of lamella (×234). FIG. 32. Section through a young conceptacle showing a columella-like structure (arrow) and an ostiole blocked by a plug (P) (×373).

more or less parallel to the lamellar surface and the lamellar apex. Except at the very apices of lamellae, distal portions of most filaments arch outwards to varying degrees towards the thallus surface (Fig. 28). These filaments collectively form a cortex in which the long axes of cells [*L*, 11–19(–28) μm; *D*, 5–9 μm; *L*/*D*, 1·4–2·5(–3·0)] become oriented more and more in a plane perpendicular to the lamellar surface. Because the arching is more pronounced beneath the dorsal surface, the dorsal cortex is much more clearly defined than the ventral cortex. The cortex is overlain by an epithallium composed of the terminal, non-meristematic cells (*L*, 3–9 μm; *D*, 3–9 μm; *L*/*D*, 0·4–1·2) of filaments. With rare exceptions, a single epithallial cell terminates each filament and thus the epithallium is unistratose. Each epithallial cell is subtended by a meristematic cell (collectively these form the primary meristem) which gives rise to new cells basipetally. Cellular elongation appears to be progressive behind the meristem. Most new cells arise near the apex or beneath the dorsal surface of the lamellae. Cortical and medullary cells of contiguous filaments are interconnected by secondary pits (Fig. 29); cell fusions were not observed.

Conceptacles (Figs 30–32) occur only along the dorsal surface; conceptacle primordia (Fig. 30) appear to arise adventitiously in the outer cortex where localized groups of cortical cells become extremely elongate and produce a new meristem. Mature conceptacles with chambers up to 111 μm in diameter and 82 μm high (excluding the pore canal) were observed. A central columella-like structure composed of a group of very elongate cells occurred in one younger conceptacle (Fig. 32) but not in any of the more mature conceptacles (Fig. 31). Whether the conceptacles are gametic or tetrasporic remains uncertain since the chambers contain no recognizable contents.

TAXONOMIC IMPLICATIONS

The lectotype specimen of *L. lichenoides* Philippi belongs to the genus *Lithophyllum* as circumscribed by *Masaki* (1968; see also Adey et al., 1974) and used by Johansen (1981). This concept of *Lithophyllum* is among the broadest of the six concepts (Table II) currently in use. Structurally and developmentally, however, *L. lichenoides* and *L. incrustans* (the lectotype species of *Lithophyllum*) show marked differences. In *L. lichenoides* the vegetative thallus develops almost entirely from a single meristem and tissues are organized into distinct medullary, cortical, and epithallial regions.

In *L. incrustans*, vegetative thallus development involves two distinct meristems: one meristem gives rise to a unistratose hypothallium and another meristem gives rise to perithallial tissue basipetally and epithallial tissue acropetally. Although both taxa possess other characters in common (e.g. uniporate tetrasporangial conceptacles, secondary pit connections between cells of contiguous filaments, no geniculae, no palisade hypothallial tissue, non-parasitic) which link them to *Lithophyllum* sensu Masaki (1968) and Johansen (1981), the marked developmental and structural differences may warrant segregating *L. lichenoides* generically from *L. incrustans*. Further comments on this appear in the general discussion.

In more recent times, *L. lichenoides* Philippi has been regarded as conspecific either with *Mesophyllum lichenoides* (Ellis) Lemoine [see Hamel & Lemoine, 1953, p. 77] or with *L. tortuosum* (Esper) Foslie [see Bressan, 1974, p. 93].

Results from this study of Philippi's type indicate clearly that *L. lichenoides* cannot be placed in *Mesophyllum* (whose taxa have multiporate tetrasporangial conceptacles and in which fusions occur between cells of contiguous filaments). Whether *L. lichenoides* is conspecific with *L. tortuosum* (Esper) Foslie as suggested by Bressan [1974; see also Lemoine, 1911, p. 169; 1915, p. 12 (both as *Tenarea*)] is uncertain. Philippi's specimens appear to share many morphological and anatomical features with plants Bressan referred to *L. tortuosum* (see also Ardré, 1970, p. 86; Masaki, 1968, p. 40) and may be conspecific with them. The relationships between the modern concepts of *L. tortuosum* and Esper's original specimens, however, still need to be determined. Similarly Philippi's plants of *L. lichenoides* resemble plants referred to *L. dentatum* (Kuetzing) Foslie by Bressan (1974, p. 90) and by Hamel & Lemoine (1953, p. 50), but comparisons of the types of these two taxa have yet to be made. Once relevant type specimens have been compared, the taxonomic status of *L. lichenoides* Philippi can be determined more confidently.

DISCUSSION

Based on this study of Philippi's collections, only two of the four taxa originally included within *Lithophyllum* Philippi (1837) match any of the six concepts of the genus employed since 1943 (Table III). *L. lichenoides* falls within five of the six concepts while the lectotype species, *L. incrustans*, conforms to only three. Which of these three concepts most accurately reflects the delineation of *Lithophyllum* as a genus remains unresolved, and this in turn may have implications for the generic classification of the Lithophylloideae (sensu Johansen, 1981).

TABLE III. A summary of relationships between Philippi's collections and various modern concepts of *Lithophyllum*

Concept/reference	*L. decussatum*	*L. expansum*	*L. incrustans*	*L. lichenoides*
Suneson (1943)	?	—	+	+
Mason (1953)	?	—	—	+
Hamel & Lemoine (1953)/Adey (1970a)	?	—	+	+
Kylin (1956)	?	—	—	+
Masaki (1968)/Johansen (1981)	?	—	+	+
Cabioch (1972)	?	—	—	—

Collections which fall within particular concepts are designated with a plus (+) sign and those which do not with a minus (—) sign.

The circumscription *Lithophyllum* and the generic classification of the Lithophylloideae rest in part upon which of the following hypotheses concerning hypothallial attributes are accepted or rejected:

(1) Hypothallial attributes are of no significance in circumscribing or classifying genera of Lithophylloideae;
(2) Taxa with a palisade hypothallium (or perithallium) are distinct generically from those which lack palisade tissues;
(3) Taxa with a unistratose hypothallium are distinct generically from those with a multistratose hypothallium;
(4) Taxa with a unistratose hypothallium but which produce a secondary

hypothallium ("faux hypothalle", Cabioch, 1972) are distinct generically from those which do not;

(5) Taxa with a coaxial multistratose hypothallium are distinct generically from those with a non-coaxial multistratose hypothallium.

To date, acceptance or rejection of these hypotheses (Table IV) has been based largely on limited data obtained from mature plants; developmental data based on field-collected plants are few (see Cabioch, 1972), and data from culture-grown plants are extremely scant (see Suneson, 1982).

At present, there appears to be a general consensus among authors cited in Table IV to reject the first hypothesis and accept the second. The Suneson (1943) concept of *Lithophyllum*, which implies acceptance of hypothesis 1 and rejection of the others, has fallen into disfavour and Suneson (1982) himself has abandoned this concept. Johansen (1981, p. 41), who rejects the first but accepts the second hypothesis, divides the Lithophylloideae into two groups: the *Lithophyllum* series for genera with non-palisade tissues, and the *Dermatolithon* series for genera with palisade tissues. The generitype specimen of *Lithophyllum* (i.e. the Philippi collection of *L. incrustans*) possesses non-palisade tissues and thus fits into the Johansen scheme.

TABLE IV. Relationship of hypotheses concerning hypothallial attributes and the modern concepts of *Lithophyllum*

Reference	Hypothesis (see text) 1	2	3	4	5
Suneson (1943)	A	R	R	R	R
Mason (1953)	R	A	A(?)	N	R
Hamel & Lemoine (1953)/Adey (1970a)	R	A	R	R	?
Kylin (1956)	R	A	A	N	A
Masaki (1968)/Johansen (1981)	R	A	R	R	R
Cabioch (1972)	R	A	A(?)	A	?

A, accept; R, reject; N, not considered.

There is no consensus over acceptance or rejection of the third hypothesis. The concepts of *Lithophyllum* presented by Mason (1953), Kylin (1956) and Cabioch (1972) accept explicitly or implicitly that taxa with unistratose hypothallia are generically distinct from taxa with multistratose hypothallia, while the concepts of *Lithophyllum* presented by Hamel & Lemoine (1953) and Adey (1970a) on the one hand and by Masaki (1968) and Johansen (1981) on the other hand encompass both types of hypothallia. Mason (1953) and Kylin (1956), moreover, limit *Lithophyllum* to taxa with a multistratose hypothallium, and Cabioch (1972) limits *Lithophyllum* to taxa which produce a unistratose primary hypothallium but which also produce a multistratose secondary hypothallium (i.e. a "faux hypothalle"). Thus Cabioch also explicitly accepts the fourth hypothesis. The production of secondary hypothallia were not considered by Hamel & Lemoine (1953), Masaki (1968) or Adey (1970a), but Adey & Adey (1973) reported that secondary hypothallia may or may not occur in plants they referred to *L. incrustans*, and this led Johansen (1981, p. 42) to reject any generic segregation based on the occurrence of a secondary hypothallium.

The generitype specimen of *Lithophyllum* possesses a unistratose hypothallium

and does not show any evidence of secondary hypothallial development. Consequently, the concepts of *Lithophyllum* presented by Mason (1953), Kylin (1956) and Cabioch (1972) do not conform to characteristics present in the generitype specimen and must, therefore, be rejected. Thus, among the existing concepts of *Lithophyllum*, the choice is between that of Hamel & Lemoine (1953) and Adey (1970a), and that of Masaki (1968) and Johansen (1981). Among taxa with a multistratose hypothallium, the Hamel & Lemoine/Adey concept of *Lithophyllum* specifies that the hypothallium be coaxial (see hypothesis 5), while the Masaki/Johansen concept does not. Both concepts reject generic segregation of taxa with unistratose and multistratose hypothallia (hypothesis 3).

There is no firm evidence from studies of Lithophylloideae to favour or reject a generic segregation based on a unistratose vs a multistratose hypothallium or on a coaxial vs a non-coaxial hypothallium. Thorough field and culture studies are needed to test these hypotheses. Based on studies of four other genera of non-geniculate Corallinaceae (*Lithoporella* and *Mastophora* [Turner & Woelkerling, 1982a, 1982b], *Mastophoropsis* [Woelkerling, 1978] and *Metamastophora* [Woelkerling, 1980a, 1980b]), however, it seems likely that the ontogeny of taxa with a unistratose hypothallium may be fundamentally different from that of taxa with a multistratose (either coaxial or non-coaxial) hypothallium, and such a difference could provide a sound basis for generic delineation. This would mean that the genus *Lithophyllum*, based on *L. incrustans*, would include only taxa with a primary unistratose hypothallium and a different generic name would have to be used for taxa with a multistratose hypothallium.

In the absence of firm evidence favouring acceptance of hypotheses 3 and/or 5, it seems best, for the present, to reserve judgement and to subscribe to the Masaki/Johansen concept of *Lithophyllum*, to which Philippi's generitype collection (of *L. incrustans*) conforms.

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A TAXONOMIC REASSESSMENT OF *LITHOTHAMNIUM* (CORALLINACEAE, RHODOPHYTA) BASED ON STUDIES OF R. A. PHILIPPI'S ORIGINAL COLLECTIONS

By Wm. J. Woelkerling

On page 178, line 9 and page 181, line 22, *Lithothamnium* should read *Lithophyllum*.

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STUDIES ON SELECTED CORALLINACEAE (RHODOPHYTA) AND OTHER ALGAE IN A DEFINED MARINE CULTURE MEDIUM

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Abstract: A marine culture medium (MCM) has been developed and shown to have the unique ability to support the growth of several coralline algae. The results of experiments designed to determine the effects of varying certain ionic concentrations and buffers are presented for this defined medium. Optima of 5 mM Ca^{2+}, 1 mM SO_4^{2-} and 1 μM BO_3^{3-} (lower than the respective sea-water levels) were found for growth or oxygen evolution in *Corallina*. No organic buffer was needed for growth of Corallinaceae, but growth stimulation was observed for a strain of *Callithamnion* (Ceramiaceae) when Tris–(hydroxymethyl)aminomethane buffer was added. This stimulation could not be duplicated with other similar buffers. Results of growth studies with a diverse selection of marine macrophytes have indicated that MCM generally supports growth better than sea water alone but often not as well as enriched sea water. The best MCM growth results were observed with members of the Rhodophyceae and certain Chlorophyceae.

INTRODUCTION

Although an almost bewildering array of defined culture media have been developed for marine organisms (see reviews by Provasoli *et al.*, 1957; Droop, 1969; McLachlan, 1973; Kinne, 1976; Ukeles, 1976), many remain untested on macroscopic algae, and apparently none has been used successfully for growing taxa of Corallinaceae (Rhodophyta). Previous culture-based studies of Corallinaceae (e.g., Von Stosch, 1964, 1969; Jones & Moorjani, 1973; Chihara, 1973, 1974; Johansen & Colthart, 1975; Notoya, 1976; Brown *et al.*, 1977; Chamberlain, 1977,1978; Smith & Roth, 1979) all employed undefined, natural sea-water based media. In a number of cases plants became necrotic, developed abnormally, or grew very slowly. The only two published accounts of culture work on coralline life histories (Von Stosch, 1969; Chamberlain, 1977) involved undefined media. West & Hommersand (1981) have stated that before more extensive culture work on coralline life histories can be undertaken, much more needs to be known about the nutritional physiology of these algae and more suitable culture media need to be developed. Thus, as a prelude to work on experimental assessment of variation in morphological–anatomical attributes of potential taxonomic significance and on sexual and apomictic cycles in the Corallinaceae, it seemed highly desirable to develop a

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chemically defined culture medium which would support normal growth, calcification and reproduction of plants raised from spores.

Preliminary examinations of the chemical composition of a variety of extant defined media and comparisons with natural sea water revealed that most of these media possess a number of potentially undesirable characteristics. First, the concentrations of some ions (notably phosphate and a number of micronutrients – see Table IV and McLachlan, 1973) are substantially greater in the defined media than in natural sea water, but the general necessity for such high concentrations apparently has not been demonstrated. Secondly, the concentrations of some other ions (notably calcium, sulfate and borate), while generally similar to those in sea water, appear to be both high compared to concentrations used in freshwater media (Nichols, 1973) and totally unnecessary for ensuring stability of the medium. Thirdly, a number of extant defined media employ organic buffers which are directly or indirectly metabolizable (e.g., glycylglycine – see McLachlan, 1973; Tris – see Hanisak, 1979, p. 321) and/or which have demonstrated negative effects (e.g., Tris – see Smith & Foy, 1974; Van Steveninck, 1975) and/or whose effects on marine macroscopic algae are unknown. Finally some media also contain organic salts (e.g., sodium glycerophosphate – see McLachlan, 1973) which promote bacterial growth, and many media use a single salt (e.g., magnesium sulfate) as the source of two nutrients, thereby making manipulation of individual nutrient levels more difficult for experimental purposes. It was decided, therefore, to design empirically a stable, chemically defined marine culture medium (MCM) and to preliminarily assess its suitability for growing Corallinaceae and other macroscopic marine algae. Design goals included using a separate salt for each nutrient, employing inorganic compounds insofar as possible, determining whether Tris (widely used as a buffer in marine media) or another organic buffer was a necessary ingredient, and determining whether the high levels of certain nutrients found in other marine media and natural sea water are necessary. This report summarizes results of three series of experiments: one designed to determine suitable concentrations for a number of nutrients; one designed to examine the need for and role of Tris and several other buffers; and one designed to test the suitability of MCM relative to Provasoli's enriched sea water (PES – see McLachlan, 1973) and to natural sea water for growing selected taxa of Corallinaceae from spores and for maintaining other macroscopic algae in closed-system cultures. Because available data (see Johansen, 1981) suggest that the growth rates of most coralline algae are slow, clones of *Callithamnion byssoides* which grow comparatively fast (Spencer, unpubl. data), were used to test algal response to specific changes in the medium. The medium most suitable for growth of *Callithamnion* and the Corallinaceae was then tested on a variety of marine macrophytes.

Materials and Methods

The physical and chemical conditions employed during the various experiments are summarized in Tables I and II respectively. Provasoli's enriched sea water (PES, see

McLachlan, 1973 for recipe) was utilized for treatments involving enriched sea water. MCM was prepared by adding the ingredient stocks listed in Table III sequentially to the NaCl stock. Tris was not used in some experiments and Na_2SO_4 and $NaHCO_3$ were added directly as salts rather than stock solutions when producing final concentrations > 1.0 mM Na_2SO_4 or 5.0 mM $NaHCO_3$. Details of individual stock preparations are as follows. (1) $CaCl_2$ and $MgCl_2$ are difficult to weigh accurately because of deliquescence. See McLachlan (1973, p. 35) for method of preparing stock solutions of high accuracy. (2) Micronutrient mix contains 6.6 mM Na_2EDTA, 1 mM $FeCl_3$, 1 mM $MnCl_2$, 1 mM $ZnCl_2$, 1 mM Na_2MoO_4, 1 mM H_3BO_3, 0.3 mM $CuCl_2$ and 0.2 mM $CoCl_2$. To prepare, dissolve salts sequentially in 800 ml H_2O and bring the final volume to 1 liter. MCM concentrations are 0.001 of stock concentrations. (3) Vitamin mix contains 1.48 mM thiamine, 4.04 μM biotin and 0.74 μM cyanocobalamin. Prepare in 3 steps: (a) dissolve 10 mg biotin and 10 mg cyanocobalamin in 80 ml H_2O and bring final volume to 100 ml, (b) separately dissolve 500 mg thiamine–HCl in $\approx$800 ml H_2O, (c) add 10 ml of solution A to solution B then bring volume to 1 liter with H_2O and use as a stock solution. Solution should be stored frozen. MCM concentrations are 0.001 of vitamin stock concentrations. (4) $NaHCO_3$ stock solutions should be prepared in ice cold water and used immediately. (5) The Tris stock is 8.0 g of Tris–(hydroxymethyl)-aminomethane in 800 ml H_2O; bring volume to 1000 ml. Prepare new stock every 30 days.

Field samples used directly in experiments or employed as a source of spores were transported to the laboratory in plastic bags, stored in an ice-filled chest and then transferred to a 40-l aerated sea-water holding tank at 10–15 °C for 12–48 h prior to use. For certain experiments, portions from one or several *Corallina* plants with a total drip-free wet wt of 950–1000 mg were inoculated into 80 × 100 mm Pyrex deep storage dishes containing 250 ml of medium. For spore-initiated coralline experiments, plant fragments bearing tetrasporangial conceptacles were placed in 20–25 ml of sterilized sea water in 95 × 15 mm Petri dishes and the conceptacles were broken open. Within 30–60 s, the spore tetrads within mature, excised tetrasporangia separate and the

TABLE I

Experimental physical conditions.

Parameter	Organism		
	Corallinaceae	*Callithamnion*	Other algae
Dish diameter (mm)	180 90	70	70
Dish depth (mm)	80 50	50	50
Medium volume (ml)	250 100	50	100–1000
Photoperiod (L : $\overline{D}$)	16 : $\overline{8}$	16 : $\overline{8}$	16 : $\overline{8}$
Photon flux density (μmol · m^{-2} · s^{-1})	10–20	5–7	10–25
Temperature (°C)	15	20	15–24
Agitation	none	115 rpm	none

individual spores are released. These spores were transferred in capillary pipettes to 35 × 10 mm Petri dishes containing 5 ml of the appropriate medium, and the Petri plates then were placed within 90 × 50 mm crystallization dishes and left undisturbed to allow spore adhesion to the bottom of the Petri plate. After 72–96 h, counts of living (i.e., pigmented) and dead (i.e., non-pigmented) spores were taken and the dishes were then flooded with an additional 95 ml of medium.

For experiments involving *Callithamnion byssoides* Arnott ex Harvey in Hooker (from Georgia, JAW 685) the inoculum was prepared from stock culture plants by chopping filaments with a razor blade, placing the resulting fragments in a funnel fitted with a

TABLE II

Summary of test media used for various experiments during the developmental phase of MCM.

Compound	Test medium:	Nutrient concentration A	B	C
$MgCl_2$		20 mM	20 mM	40 mM
KCl		10 mM	10 mM	10 mM
$CaCl_2$		10 mM	10 mM	2.5 mM
$NaNO_3$		1 mM	1 mM	1 mM
Na_2SO_4		20 mM	20 mM	1 mM
Na_2HPO_4		30 μM	30 μM	30 μM
$FeCl_3$		1 μM	1 μM	1 μM
H_3BO_3		40 μM	1 μM	1 μM
Na_2HCO_3		10 mM	5 mM	5 mM

In addition all formulations contained the following substances in the stated concentrations: 450 mM NaCl, 1 μM $MnCl_2$, 1 μM $ZnCl_2$, 1 μM Na_2MoO_4, 0.3 μM $CuCl_2$, 0.2 μM $CoCl_2$, 1.5 μM thiamine HCl, 4 nM biotin, 0.74 nM cyanocobalamin, 1.2 × total micronutrient concentration Na_2EDTA.

TABLE III

Preparation of MCM.

Ingredient	Concentration in stock	Amount of stock per l (ml)	Final concentration
NaCl	600 mM	750	450 mM
$MgCl_2$	4 M	10	40 mM
KCl	1 M	10	10 mM
$CaCl_2$	500 mM	10	5 mM
$NaNO_3$	100 mM	10	1 mM
Na_2SO_4	100 mM	10	1 mM
Na_2HPO_4	30 mM	1	30 μM
Micronutrients	–	1	–
Vitamins	–	1	–
$NaHCO_3$	50 mM	50	2.5 mM
Tris	660 mM	1	0.66 mM
H_2O	–	147	–

For details of individual stock preparations see p. 63.

20 μm Nitex screen and rinsing with culture medium. The rinsed material was finally resuspended in ≈20 ml of culture medium. Uniformly suspended inoculum was then transferred into dishes using a wide-mouth pipette. The inocula for other algae consisted of visually equal amounts of vegetative material obtained form pre-existing cultures (California) or from field-collected samples (Australia).

TABLE IV

Comparison of MCM, PES, sea water, and ASP-6.

Component	MCM	PES[a]	Sea water[b]	ASP-6[c]
Salinity	32‰	30.7‰	34.3‰	–
Cl^-	505 mM	489 mM	548 mM	424 mM
Na^+	457 mM	471 mM	470 mM	415 mM
Mg^{2+}	40 mM	48 mM	54 mM	33 mM
K^+	10 mM	8.9 mM	10 mM	9.4 mM
Ca^{2+}	5 mM	9.2 mM	10 mM	10 mM
HCO_3^-	2.5 mM[d]	2.3 mM[d]	2.3 mM[d]	–
NO_3^-	1 mM	660–709 μM	0.7–50 μM	3.5 mM
SO_4^-	1 mM	25 mM	28 mM	33 mM
PO_4^{3-}	30 μM	26–59 μM	0.03–33 μM	317 μM
Fe^{3+}	1 μM	10.2–15.4 μM	0.02–5.2 μM	35.8 μM
Mn^{2+}	1 μM	2.8–3.0 μM	0.02–0.18 μM	18 μM
Zn^{2+}	1 μM	0.38–51 μM	0.08–0.21 μM	7.7 μM
MoO_4^{2-}	1 μM	0.003–17 μM	0.003–0.17 μM	5.2 μM
BO_3^{3-}	1 μM	457 μM	430 μM	185 μM
Cu^{2+}	0.3 μM	0.16–0.38 μM	0.16–0.38 μM	0.32 μM
Co^{2+}	0.2 μM	0.070–0.076 μM	0.002–0.008 μM	0.17 μM
Thiamine	1.48 μM	0.237 μM	0–0.000059 μM	5.9 μM
Biotin	4.0 nM	3.3 nM	–	20.5 nM
Cyanocobalamin	0.74 nM	1.18 nM	0–0.0036 nM	0.69 nM
Tris	660 μM	506 μM	0	8.25 mM
EDTA	6.6 μM	10 μM	0	0

[a] Calculated estimates using data from Barnes (1954), Collier (1970), and McLachlan (1973).
[b] Determined from data given by Collier (1970, Tables 1–5, 1–6, and 1–7).
[c] Values based on data given by McLachlan (1973).
[d] Varies depending on pH.

Rates of oxygen evolution were determined from polarographic data generated using a Clark type O_2 electrode (see Delieu & Walker, 1972). Samples of *Corallina* were finely chopped with a razor blade prior to introduction into the electrode chamber. Each sample subsequently was recovered from the chamber, placed in 90% acetone and pulverized; chlorophyll extraction was allowed to take place for 24 h in the dark at 2 °C and subsequent determinations were made using formula 1 of Jensen (1978, p. 62). For the other algae, plants were removed from culture vessels by filtration through a funnel fitted with 20 μm Nitex (Tetco, Inc.) screening (0.45-μm Millipore filters in the case of *Prymnesium*), washed briefly with 10 mM phosphate buffer (pH 7.0), and then frozen overnight. Thawed plants were extracted with 90% acetone in an ice bath for 1 h and

chlorophyll *a* determinations were made using the formula in Jensen (1978).

Kjeldahl digestion (according to Steyermark, 1961) was followed by ammonia nitrogen determination using the indanetrione hydrate (ninhydrin) spectrophotometric method of Jacobs (1960). Interference of cations in the assays was avoided by the use of EDTA (Meyer & Riklis, 1953). Digestion was carried out on the complete sample following chlorophyll determinations. Samples were heated in 18 × 150 mm test tubes in a 70 °C water bath for 1 h to evaporate the acetone. Five hundred microliters of concentrated H_2SO_4 were then added followed by 320 mg K_2SO_4 and 8 mg HgO. Capped with a glass vial, the tubes were heated for 4 h in a sand bath on a hot plate so that gently refuxing of H_2SO_4 went 3 cm up the tube after all water was gone. Some of the acid in the cooled tubes was neutralized by the addition of ≈ 9 ml of 2 M NaOH in 0.4 M Na-acetate. The volume was brought to 10 or 20 ml before the assay.

For the spectrophotometric nitrogen assay 200 to 500 µl of diluted digest were added to a test tube along with enough acetate buffer (0.2 M acetate pH 5.3 with 0.2% EDTA) to make a final volume of 2.0 ml. Indanetrione hydrate reagent was prepared by mixing equal volumes of a 4% stock of indanetrione hydrate in ethylene glycol monomethyl ether (Fisher certified) and the same pH 5.3 acetate buffer. This working stock was made 0.4% with respect to sodium hydrosulfite (reducing agent) immediately before use. After addition of 2.0 ml of this reagent the sample tubes were immediately placed in a boiling water bath for 20 min. Upon cooling the volume of each was brought to 10 ml with 50% ethanol and the A_{570} was determined. Standards of NH_4Cl were run with each determination; accurate results were obtained when the assay tube contained 1 to 7 µg N.

All experiments involving Australian algae were undertaken at La Trobe University; all other work was done in the Department of Botany, the University of California, Berkeley.

Results

Experiments associated with MCM development

The MCM formulation (Table III) used in later experiments was derived in part from data obtained during an initial sequence of tests designed to elucidate whether particular concentrations of various nutrients were suited for maintaining coralline red algae in culture. The results, based on experiments involving vegetative branches from field collected plants of *Corallina officinalis* L. (Australia) and *C. vancouveriensis* Yendo (California) as well as on spores and germlings of the latter species subjected to various test media (Table II), indicated that the concentrations of Ca^{2+}, Mg^{2+}, SO_4^{2-}, and BO_3^{3-} could be reduced relative to those of sea water without adverse effects. Thus results from one series of experiments showed that the rates of oxygen evolution (Table V) from vegetative tissues of *C. officianalis* incubated for 7, 11, or 14 days (in a series of trials using sea water and variations of test medium A) were consistently higher

in treatments with 1 μM BO_3^{3-} than in treatments with 10 μM or 40 μM BO_3^{3-} or in sea water controls containing $\approx$430 μM BO_3^{3-}.

TABLE V

Oxygen evolution rates (μmol O_2 · mg Chl a^{-1} · h^{-1}) in plants of *Corallina officinalis* grown in test medium A with various concentrations of BO_3^{3-}: means and SD are based on three trials.

Treatment	BO_3^{3-} conc.	Incubation time (days)		
		7	11	14
Sea water control	$\approx$430 μM	240 ± 5	147 ± 8	149 ± 6
1	40 μM	217 ± 4	159 ± 10	137 ± 9
2	10 μM	175 ± 6	175 ± 7	120 ± 6
3	1 μM	283 ± 8	225 ± 5	198 ± 5
4	0	265 ± 5	145 ± 14	180 ± 7

TABLE VI

Rates of oxygen evolution (μmol O_2 · mg Chl a^{-1} · h^{-1}) in vegetative branches of *Corallina vancouveriensis* grown in various media for 4 days and for 7 days: means and SD are based on five trials.

Medium	Treatment	Rates of oxygen evolution after	
		4 days	7 days
Sea water	–	268 ± 6	243 ± 4
Test medium B	–	215 ± 2	188 ± 9
Test medium B	2 mM NO_3^-	248 ± 5	223 ± 7
Test medium B	0.5 mM NO_3^-	lost	233 ± 7
Test medium B	20 mM K^+	234 ± 9	145 ± 6
Test medium B	5 mM K^+	278 ± 11	147 ± 9
Test medium B	60 μM PO_4^{3-}	200 ± 7	190 ± 8
Test medium B	15 μM PO_4^{3-}	258 ± 7	186 ± 7
Test medium B	40 mM SO_4^-	238 ± 4	100 ± 6
Test medium B	10 mM SO_4^-	305 ± 6	184 ± 9
Test medium B	40 mM Mg^{2+}	337 ± 8	254 ± 4
Test medium B	10 mM Mg^{2+}	219 ± 7	220 ± 6
Test medium B	5 mM Ca^{2+}	421 ± 8	196 ± 10
Test medium B	2.5 mM Ca^{2+}	473 ± 6	320 ± 8

In another series of treatments, vegetative tissues of *C. vancouveriensis* were placed in natural sea water or in test medium B or in variations of test medium B in which the concentrations of six macronutrients were independently doubled and/or halved and/or quartered, and rates of oxygen evolution were compared after incubation periods of 4 and 7 days (Table VI). Responses in media containing 2.5 or 5 mM Ca^{2+} or 10 mM SO_4^{2-} were markedly better than responses in test medium B (10 mM Ca^{2+}; 20 mM SO_4^{2-}) or in natural sea water ($\approx$ 10 mM Ca^{2+}; $\approx$28 mM SO_4^{2-}). Responses in 40 mM

Mg^{2+} were better than in 10 mM Mg^{2+} or in test medium B (20 mM Mg^{2+}) or in sea water ($\approx$ 54 mM Mg^{2+}). These data led to the conclusions that reduced concentrations of Ca^{2+}, Mg^{2+}, and SO_4^{2-} relative to sea water probably do not adversely affect the species tested. This contrasts with results obtained in the trials involving K^+, where after 7 days, plants grown in 20 mM or in 5 mM K^+ showed markedly lower oxygen evolution rates than in test medium B or in natural sea water, both containing 10 mM K^+. Responses to the concentrations of NO_3^- and PO_4^{3-} tested were similar to those for test medium B and for sea water, suggesting that levels in these ranges probably are not critical.

TABLE VII

Germination responses of *Corallina vancouveriensis* spores after 38 days to test medium B, with varying levels of indicated nutrients: each culture was inoculated with 20–25 spores; results represent range values for triplicate cultures in each treatment.

Treatment	Ion concentration				% Spore germination and development
	Ca^{2+} (mM)	Mg^{2+} (mM)	PO_4^{3-} (μM)	NO_3^- (mM)	
1	10	40	30	1.0	0
2	10	40	30	0.5	0
3	10	40	15	1.0	0–8
4	10	40	15	0.5	0
5	10	20	30	1.0	0
6	10	20	30	0.5	0–14
7	10	20	15	1.0	0
8	10	20	15	0.5	0
9	2.5	40	30	1.0	100
10	2.5	40	30	0.5	100[a]
11	2.5	40	15	1.0	100[a]
12	2.5	40	15	0.5	83–100[a]
13	2.5	20	30	1.0	5–36
14	2.5	20	30	0.5	63–92
15	2.5	20	15	1.0	68–100
16	2.5	20	15	0.5	0
Sea water	–	–	–	–	0

[a] Geniculae present on several crusts.

Spore viability and germination responses in relation to different nutrient regimes also were examined in two series of treatments. In one set of trials responses were examined in a 38-day experiment using test medium B with all possible combinations of 2.5 and 10 mM Ca^{2+}, 20 and 40 mM Mg^{2+}, 15 and 30 μM PO_4^{3-} and 0.5 and 1.0 mM NO_3^-. Complete survival of inoculated spores of *C. vancouveriensis* occurred only in media containing both 2.5 mM Ca^{2+} and 40 mM Mg^{2+} (Table VII). Very low survival rates or total death occurred in all cultures containing 10 mM Ca^{2+}. Distinct trends with respect to NO_3^- and PO_4^{3-} concentrations were not evident. These data were similar to those obtained with vegetative tissues; the data also suggested that Ca^{2+} concen-

tration may be critical for the survival and development of spores and sporelings. Consequently a further experiment using test medium C was conducted to determine spore survival and germination rates of *C. vancouveriensis* in relation to Ca^{2+} concentration. The results (Table VIII) indicated clearly that 5 mM Ca^{2+} is optimal for spore

TABLE VIII

Germination responses of *Corallina vancouveriensis* to test medium C, with different concentrations of Ca^{2+}: data are presented as percent germination of inoculum; results represent range values for triplicate cultures inoculated with 100–250 spores; ungerminated but viable spores were not included.

No.	Treatment	Ca^{2+} (mM)	Bodega population (days)			Cypress Pt. population (days)		
			4	7	14	4	7	14
1	Sea water	≈10	40–73	34–61	26–46	22–58	16–58	12–48
2	PES	≈10	35–95	35–86	35–86	28–58	41–63	40–59
3	Test med. C	0.001	0	0	0	0	0	0
4	Test med. C	0.01	0	0	0	0	0	0
5	Test med. C	0.1	0	0	0	0	0	0
6	Test med. C	1.0	0	0	0	0	0	0
7	Test med. C	2.5	12–45	6–41	0–27	20–45	9–36	9–19
8	Test med. C	5.0	63–87	54–74	33–65	74–88	72–91	53–79
9	Test med. C	10	0–2	0	0	0–6	0	0
10	Test med. C	25	2–13	0	0	0–2	0	0

development. No spores survived when Ca^{2+} levels were increased to 10 mM or more or were reduced to 1 mM or less. Results from this experiment also suggest that spores would germinate and develop successfully in a 5 mM Ca^{2+} medium containing 40 mM Mg^{2+} and 1 mM SO_4^{2-} (compare test media B and C, Table II). Data from separate experiments (see below) provide evidence that a spectrum of other algae also can survive in a medium containing 1 mM SO_4^{2-} (which is much lower than that of natural sea water or other media – see Table IV).

Based on results from the above series of experiments and discussions between the first author and Prof. G. C. Gerloff (University of Wisconsin, Madison) on general algal nutrition, the MCM formulation was derived from modifications to test media B and C and then used in subsequent experiments.

BUFFERING

Because of their more rapid growth, cultures of *Callithamnion byssoides* were used to examine buffer effects on growth. In a preliminary experiment the growth responses of *C. byssoides* in sea water, PES and MCM were compared. Responses in both PES and MCM were substantially better than in natural sea water (Table IX) and, based on doubling time, *C. byssoides* grew nearly as well in MCM as in PES. These data suggested that the MCM formulation derived from experiments on Corallinaceae potentially were acceptable for growing non-corallinaceous algae.

Results form experiment A (Table X) confirm that growth in MCM is nearly as rapid as in PES (compare treatments 1 and 2; also see treatments 6 and 8) and demonstrate that when both HCO_3^- and Tris are omitted, growth in MCM is reduced markedly (compare treatments 2 and 3). The addition of only bicarbonate has considerable effect in increasing the growth rate (compare treatments 3 and 4) while the addition of only Tris increases growth even more (compare treatments 3, 4 and 5). The addition of bicarbonate (treatment 4) or Tris (treatment 5) appear to have a similar effect on the pH. The presence of both results in a higher pH but does not result in greater growth

TABLE IX

Growth responses of *Callithamnion byssoides* to selected nutrient regimes: MCM is from Table III chlorophyll *a* and total organic nitrogen were determined after 28 days; the inoculum contained 9.4 μg N; doubling times were determined from nitrogen determinations; data are from three replicates.

No.	Medium	pH[a]	μg Chl *a*	μg N	Average doubling time (days)
1	Sea water	8.15	0.1 ± 0.09	27 ± 2.8	18
2	PES	8.28	18.5 ± 2.4	430 ± 28	5.1
3	MCM	8.63	8.3 ± 1.7	251 ± 21	5.9

[a] pH measured at the midpoint of the light cycle after 7 days.

TABLE X

The effect of added bicarbonate and added buffers on the growth of *Callithamnion byssoides*: the procedure is the same as in Table IX except for inoculum size; the organic buffers are Tris–(hydroxymethyl)amino-methane, *N*-Tris(hydroxymethyl)methyl glycine (tricine) and 4-(2-hydroxyethyl)-1-piperazine-propane sulfonic acid (HEPPS).

Treatment	Medium	Variation	pH[a]	μg Chl *a*	μg N	Doubling time (days)
Experiment A	(inoculum contained 14.7 μg total N)					
1	PES	none	8.20	42 ± 5.0	520 ± 65	5.4
2	MCM[c]	none	8.40	38 ± 11	410 ± 65	5.8
3	MCM[b]	no HCO_3^-, no Tris	6.78	0.60 ± 0.25	32 ± 14	25
4	MCM	no Tris	8.29	16 ± 3.0	170 ± 13	7.9
5	MCM[b,c]	no HCO_3^-	8.22	45 ± 4.2	450 ± 14	5.7
Experiment B	(inoculum contained 17.3 μg total N)					
6	PES	none	8.21	22 ± 4.3	338 ± 125	6.5
7	PES	no Tris	8.20	9.3 ± 3.6	173 ± 76	8.4
8	MCM[b]	no Tris	8.26	7.2 ± 1.4	105 ± 15	11
9	MCM	none	8.36	16 ± 5.5	334 ± 180	6.6
10	MCM[b]	2.0 mM tricine	7.89	5.6 ± 2.7	147 ± 36	9.1
11	MCM[b]	2.0 mM HEPPS	7.88	9.1 ± 4.9	104 ± 2	11

[a] pH determined at the midpoint of the light cycle just before harvest in A and in the final light cycle in B.

[b] Titrated to pH 7.7 with NaOH initially.

[c] Addition of Tris caused a flocculent precipitate during growth.

relative to medium containing only Tris (compare treatments 2 and 5). Thus, it would appear that Tris not only acts as a buffer, but also stimulates growth.

TABLE XI

The effect of varying Tris concentration on the growth of *C. byssoides*: procedures are as in Table IX; data are final total μg of chlorophyll; initial pH adjusted to 7.7.

Tris conc. (mM)	MCM	PES
0.66	43 ± 8.1	14 ± 14.7
0.2	35 ± 7.3	25 ± 3.4
0.1	31 ± 11	22 ± 6.6
0.01	33 ± 8.7	21 ± 4.1
0	35 ± 8.6	22 ± 3.7

Results from Treatment 3 (Table X) confirm that Tris acts as a growth stimulator. Omission of Tris from either PES (compare treatments 6 and 7) or MCM (compare treatments 8 and 9) results in reduced growth. Reduced growth in MCM also occurs when other organic buffers with comparable buffering ranges are substituted for Tris (compare treatment 8 with treatments 10 and 11). These results suggest that stimulation of growth by Tris is not due to its buffering effect alone. Table XI shows that the level of Tris in PES (0.66 mM) is required for the stimulation and may be suboptimal.

As indicated in Table XIII, stimulation by Tris was not observed with all algae tested and often does not account for the improved growth in PES. Preliminary results with the Corallinaceae indicate no effect of Tris addition to MCM upon their growth.

THE GROWTH OF DIVERSE ALGAE ON MCM

Results from studies of germination and development responses (Table VIII) of spores of *Corallina vancouveriensis* to natural sea water, PES and MCM (without Tris) suggest that survival and germination in MCM (treatment 8, Table VIII) is similar to or better than in PES and that both MCM and PES are better than sea water. After 40 days, many of the sporelings growing in MCM had produced upright branches with one to four intergeniculae whereas sporelings in PES and sea water had produced basal crusts only. Preliminary work (Bramwell & Woelkerling, unpubl. data) on several species of the *Heteroderma–Fosliella* complex (Corallinaceae, Rhodophyta) indicates that in culture tetraspores of these nongeniculate taxa germinate and produce crusts in MCM and PES but not in natural sea water. Further studies are now in progress. Data on growth responses of *Callithamnion byssoides* (Tables IX, X) also indicate that growth in MCM is nearly as rapid as in PES and far better than in natural sea water.

The suitability of MCM as a general culture medium was also examined in three additional experiments. In the first, growth of a variety of marine algae in MCM, PES, and natural sea water was compared. The results (Table XII) indicate that while the

TABLE XII

Growth of diverse algae in MCM, PES and natural sea water (from three replicates).

Alga and source	Days in culture	μg Chl *a*[a]		
		PES	MCM	Sea water
Rhodophyta				
Audouinella saviana (Meneghini) Woelk., JAW 1553, Tunisia	44	28 ± 4.7	17 ± 6.0	0.7 ± 0.4
Branchioglossum woodii (J. Ag.) Kylin, JAW 653, Mexico	47	22 ± 9.4	2.5 ± 1.0	< 0.05
Caloglossa leprieurii (Mont.) J. Ag., JAW 686, Georgia	66	2.3 ± 0.5	4.2 ± 1.8	< 0.05
Champia parvula (C. Ag.) Harv., JAW 2310, Rhode Island	47	37 ± 22	9.1 ± 3.6	< 0.05
Erythrocladia sp., JAW 645, Mexico	44	16 ± 3.6	17 ± 3.4	< 0.05
Spyridia filamentosa (Wulf.) Harv., JAW 677, Hawaii	49	22 ± 4.5	12 ± 1.5	1.6 ± 0.7
Phaeophyta				
Dictyota dichotoma (Huds.) Lam., UTEX 1676-1677	59	22 ± 3.4	12 ± 1.4	5.0 ± 1.6
Giffordia oviger (Harv.) Hollenberg & Abbott, JAW 640, Calif.	35	20 ± 5.8	< 0.05	0.13 ± 0.12
Sphacelaria furcigera Kütz., JAW 2192, Mexico	47	153 ± 45	0.3 ± 0.2	2.6 ± 1.2
Chlorophyta				
Cladophora sp., JAW 2237, Philippines	66	75 ± 33	6.6 ± 1.3	0.7 ± 0.12
Microdictyon boergesenii Setchell, JAW 1555, Bahamas	59	106 ± 45	2.3 ± 0.8	0.7 ± 0.24
Percursaria percursa (C. Ag.) J. Ag., UTEX 1423	42	359 ± 57	9.2 ± 5.1	6.0 ± 2.3
Rhizoclonium riparium (Roth) Harv., JAW 474, Wash.	42	156	48 ± 6.1	7.3 ± 2.3
Valonia ventricosa J. Ag., JAW 1569, Florida	59	41 ± 24	62 ± 18	3.1 ± 3.7
Chrysophyta				
Prymnesium parvum H. Carter, UTEX 995	35	155 ± 44	56 ± 10	8.8 ± 1.5

[a] Values not corrected for spectral overlap when other chlorophylls present.

TABLE XIII

Growth of various algae in sea water (SW), MCM without Tris, MCM with Tris and PES: data are presented as average chlorophyll *a* of three cultures; isolates are the same as in Table XII.

Alga	Chlorophyll *a* (μg)			
	SW	MCM	MCM + Tris	PES
Branchioglossum	4.2 ± 0.7	77 ± 2.0	81 ± 2.4	18.5 ± 5.6
Audouinella	3.3 ± 0.5	19 ± 14	44 ± 20	11.9 ± 5.4
Dictyota	5.7 ± 0.4	10.3 ± 4.6	24.6 ± 23	65 ± 48
Sphacelaria	1.9 ± 1.4	18.7 ± 4.0	18.8 ± 3.1	71 ± 6
Microdictyon	3.9 ± 0.2	3.9 ± 1.4	12 ± 4.1	49.5 ± 12
Percursaria	5.4 ± 1.1	12 ± 5.1	13 ± 6	122 ± 13

TABLE XIV

Representative taxa from Australia which have grown successfully in MCM for periods of at least 5 months at 15 °C, 16 h light–8 h dark cycle.

Chlorophyta
- *Bryopsis gemellipara* J. Agardh
- *Caulerpa cactoides* (Turner) C. Agardh
- *C. flexilis* Lamouroux
- *C. geminata* Harvey
- *C. hedleyi* Weber van Bosse
- *C. longifolia* C. Agardh
- *C. scalpelliformis* (R. Brown in Turner) C. Agardh
- *C. simpliciuscula* (Turner) C. Agardh
- *C. trifaria* Harvey
- *Chaetomorpha aerea* (Dillwyn) Kützing
- *C. darwinii* (Hooker) Kützing
- *Codium australicum* Silva
- *C. pomoides* J. Agardh
- *Dictyosphaerea sericia* Harvey

Rhodophyta
- *Audouinella daviesii* (Dillwyn) Woelkerling
- *Audouinella* sp.
- *Bostrychia radicans* (Montagne) Montagne
- *Botryocladia obovata* (Sonder) Kylin
- *Caloglossa leprieurii* (Montagne) J. Agardh
- *Ceramium* sp.
- *Epymenia wilsonis* Sonder
- *Griffithsia monilis* Harvey
- *Heteroderma* sp.
- *Jania* sp.
- *Lomentaria* sp.
- *Peyssonnelia* sp.
- *Polysiphonia* sp.

growth of all Chlorophyta, Chrysophyta and Rhodophyta tested were substantially greater in both MCM and PES than in natural sea water, most taxa grew better in PES than in MCM. The three Phaeophyta tested grew poorly both in MCM and sea water compared to PES. In a related experiment the growth of six taxa was compared in sea water, PES, MCM with Tris and MCM without Tris. The results (Table XIII) show that with the exception of *Sphacelaria*, growth in MCM with Tris was greater than growth in MCM without Tris. In all cases the poorest growth occurred in natural sea water.

Results from both of the above experiments suggest that a variety of red and green algae can be maintained in MCM although most tend to grow more slowly than in PES. In a third experiment, vegetative fragments or spores of a series of red and green algae (Table XIV) were inoculated into MCM without Tris and grown for more extended periods of time. After 5 months, these taxa retained normal morphology, and all produced new tissue. Although comparative growth rate data were not obtained, species of *Caulerpa* appear to grow particularly well in MCM, possibly because of the low concentration of sulfate. O'Kelley (1974) notes that some coenocytic green algae may exclude sulfate, and this suggests that sulfate levels in sea water may not be optimal for such algae. Attempts, however, to grow *Ulva*, *Plocamium*, and seedlings of the seagrass *Amphibolis* in MCM failed; after several weeks the plants became necrotic and eventually they died. In additional experiments tetrasporophytes of *Cumagloia andersonii* (Farlow) Setchell and Gardner were successfully cultured in MCM (DeCew & Zupan, unpubl. data). Tetrasporangia developed and released viable spores in MCM but not in other media (PES and sea water).

Discussion

West & Hommersand (1981) have indicated that two prerequisites to undertaking more extensive laboratory-based experimental studies involving the Corallinaceae were the development of more suitable culture media and a better understanding of the nutritional physiology of these algae. Results from the present study hopefully contribute to the attainment of both goals. MCM ostensibly is the first chemically defined marine culture medium in which taxa of Corallinaceae have been grown from spores and which has been optimized specifically for culturing these plants. Based on results from studies of *Corallina*, it appears that calcium concentrations can influence markedly the viability rate of spores (Tables VII, VIII) and that 5 mM Ca^{2+} is nearly optimal. This is approximately half the concentration of Ca^{2+} found in PES, sea water, or some other media (Table IV). It also appears that taxa of Corallinaceae may grow better under chemically defined conditions when the concentration of BO_3^{3-} is reduced by a factor of 430 (Table V) and when the concentration of SO_4^{2-} is reduced by a factor of 28 (Tables IV, VI) as compared (Table IV) to sea water. In contrast, 10 mM K^+ (the level found in sea water – see Table IV) appears more optimal than other levels tested (Table VI), based on 7-day trials.

MCM has been designed so that each nutrient is supplied independently as a sodium or chloride salt and so that, except for vitamins, only inorganic compounds are used as nutrient sources. This contrasts with most other defined media (see McLachlan, 1973) where multinutrient and/or organic compounds are employed. Tris has been included as an optional ingredient because of its apparent effect as a growth stimulator (Tables X, XI, XIII). Tris does not appear to be essential for the survival of *Corallina* or of other algae tested (Table XIII) since the results reported in Tables VI–VIII were based on media devoid of Tris. In some previous sea-water media preparations Tris has been shown to be detrimental to algal growth (Harrison *et al.*, 1980) or to calcification (Smith & Roth, 1979). Results from this study (Table X) also show that Tris is not essential for buffering purposes and that the addition of 2.5 mM bicarbonate serves as an effective buffer in MCM as it does in sea water (see Moberg *et al.*, 1934).

The reason for the stimulatory effect of Tris upon *Callithamnion* growth is unknown. The phenomenon could be related to the precipitation that occurs during growth of cells in the presence of Tris. Specific ion concentrations could be affected. Additional possible side effects include alteration of membrane permeability to certain ions (Van Steveninck *et al.*, 1973) or an enhancement of bacterial growth. Since the precipitate resulting from Tris is laden with bacteria and the level of growth stimulation is variable, an indirect bacterial effect may be the most likely explanation. Ogata (1966) explored the stimulatory effect of Tris upon *Porphyra* photosynthesis and concluded that its buffering increased the effective CO_2 concentration. While such an effect is not precluded by the results of the present study, the inability of other organic buffers to similarly stimulate *Callithamnion* growth makes an additional explanation necessary.

MCM appears to have potential as a defined culture medium for Corallinaceae and also for at least some other macroscopic algae, but additional studies are needed to test MCM further. Results presented here have involved only four taxa of Corallinaceae – two species of *Corallina* and one species each of *Jania* and *Heteroderma*. To date only plants of the last taxon have been grown from spores to reproductive maturity (Bramwell & Woelkerling, unpubl. data), and additional coralline taxa need to be tested. Limited attempts to grow several other coralline taxa from spores have failed, but this may be due to the nonviability of spores during certain seasons of the year rather than to any shortcomings of MCM. Ducker (pers. comm.) also has found that spores of certain Corallinaceae appear to be viable only at certain times of the year.

For most other algae tested (Tables XII, XIII) MCM does not support growth as well as PES, but MCM has the advantage of being chemically defined whereas PES is not. MCM appears to be most suited for various red algae and, in its present form, largely unsuited for brown algae. Among green algae, coenocytic forms such as species of *Caulerpa* and *Valonia* grow exceptionally well whereas mixed results were obtained for multicellular taxa. The suitability for planktonic algae remains generally untested, but some modifications (e.g., addition of a silicate salt) would probably be necessary. Reasons for the varying success and failure of MCM for non-coralline algae have not been examined in this study, but results published by Fries (1966) and Pedersen (1969)

suggest that investigating the potential effects of added bromide and/or iodide to MCM could prove productive.

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Studies on the Distribution of *Pneophyllum–Fosliella* Plants (Corallinaceae, Rhodophyta) on Leaves of the Seagrass *Amphibolis antarctica* (Cymodoceaceae)

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Abstract

The distribution of encrusting *Pneophyllum–Fosliella* plants (Corallinaceae, Rhodophyta) on leaves of the seagrass *Amphibolis antarctica* was examined in terms of density, cover and relative fertility of the epiphytes on host plants from a sublittoral and a eulittoral environment. Significantly greater epiphyte cover, density and (in most cases) relative fertility occurred on sublittoral hosts. In both environments epiphyte cover, density and (usually) relative fertility were significantly greater on outer leaves in an *Amphibolis* cluster than on inner leaves. Cover, density and relative fertility also were significantly greater on distal segments of *Amphibolis* leaves as compared to proximal segments. No significant differences in any parameter, however, occurred between adaxial and abaxial surfaces of particular sets of leaves. The data are discussed in relation to the potentially adverse effects of epiphytes on the host plants.

Introduction

During the course of various studies on seagrass epiphytes, a number of authors (Humm 1964; van der Ben 1969; Taylor and Lewis 1970; Hall and Eiseman 1981; Battiato *et al.* 1982) recorded dense populations of taxa belonging to the *Pneophyllum* (syn. *Heteroderma*)–*Fosliella* complex (Corallinaceae, Rhodophyta). The two genera are closely related members of the subfamily Mastophoroideae which produce 'thin' crusts and often grow intermixed in the same habitats. *Pneophyllum* differs from *Fosliella* in possessing an eight-celled rather than a four-celled central element in the germination disc and in producing intercalary rather than terminal trichocytes (Chamberlain 1983; Jones and Woelkerling 1984). Van den Ende and Haage (1963) found that in Brittany (France) such epiphytes of *Zostera marina* L., including *Pneophyllum lejolisii* (Rosanoff) Chamberlain (as *Melobesia*), showed different patterns of distribution on young and mature leaves and on leaves growing in sheltered and in more exposed situations. In Australia, Ducker *et al.* (1977) concluded that *Fosliella cymodocea* (Foslie) Jones & Woelkerling (as *Heteroderma*) was one of the two most characteristic epiphytes of the endemic seagrass *Amphibolis* [comprising *A. antarctica* (Labillardière) Sonder & Ascherson ex Ascherson and *A. griffithii* (J. M. Black) den Hartog], that plants of the epiphyte always were more numerous in the larger and deeper rock pools and that the coralline epiphyte favoured the adaxial side of the leaf but commonly covered both leaf surfaces completely. Neither Ducker *et al.* (1977) nor van den Ende and Haage (1963), however, provided any numerical data relating to the differential distribution of coralline epiphytes on seagrass leaves.

While collecting populations of the *Pneophyllum–Fosliella* complex for detailed morphological and taxonomic studies, we observed that the distribution of individuals of *Pneophyllum* and *Fosliella* on the leaves of *Amphibolis antarctica* might be influenced by a variety of factors, e.g. the nature of the habitat, the position of particular leaves within

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an *Amphibolis* leaf cluster, the orientation of the leaf surface (adaxial or abaxial) and the segment of a leaf surface (distal, mid, proximal). We therefore decided to examine this matter further and determine how results from such studies might relate to conclusions reached by Ducker *et al.* (1977) and van den Ende and Haage (1963). Our study provides comparative data on two populations of the *Pneophyllum–Fosliella* complex epiphytic on leaves of *Amphibolis antarctica* and has been designed to determine the extent to which the density, cover and fertility of particular coralline epiphytes can vary in relation to the environmental and substrate factors enumerated above.

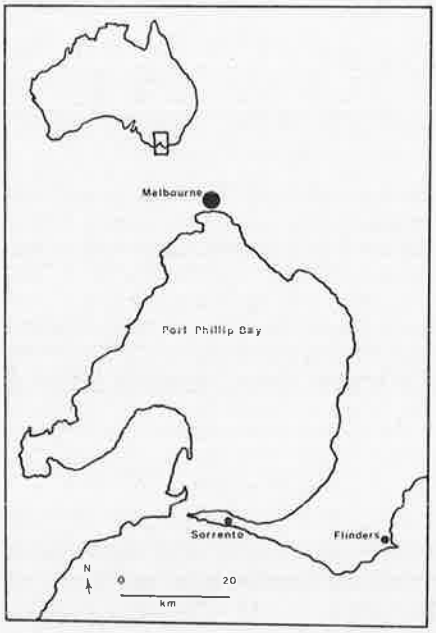

Fig. 1. Map showing localities from which material was collected.

Materials and Methods

Study Sites

Plants of *Amphibolis antarctica* supporting epiphytic populations of the *Pneophyllum–Fosliella* complex were obtained during March 1981 from a mid-eulittoral tide pool at Sorrento, Vic. and a sublittoral community at Flinders, Vic. (Fig. 1). The mid-eulittoral tide pool was 13 m long, 7·3 m across and up to 0·8 m deep, and contained a permanently submerged population of *Amphibolis antarctica* that occupied about 75% of the available bottom substratum. The pool is isolated from the surrounding sea for 4–6 h during each of two daily tidal cycles and surface water temperatures within the pool in March may fluctuate as much as 10°C during a single tidal cycle. The sublittoral *Amphibolis* community at Flinders forms part of an extensive meadow which covers an area of 20·6 km^2 along the south-western shore of Western Port (Bulthuis 1981). Plants used in this study were obtained from depths of 3–4 m at low tide. March sea temperatures were 12–13°C and temperature fluctuations during tidal cycles were negligible.

Data Collection and Analysis

At each locality, 15 upright *Amphibolis* stems, each bearing at least six mature clusters of leaves (Fig. 2), were collected from random coordinates along a 7 m transect line. Stems were preserved in a 10 : 1 sea water : commercial formalin solution and returned to the lab., where 15 clusters of leaves from both the eulittoral pool population and the sublittoral meadow population were chosen randomly for study. Voucher specimens have been deposited in LTB (Department of Botany, La Trobe University). Within each leaf cluster (which usually contained 10–12 leaves, see Ducker *et al.* 1977),

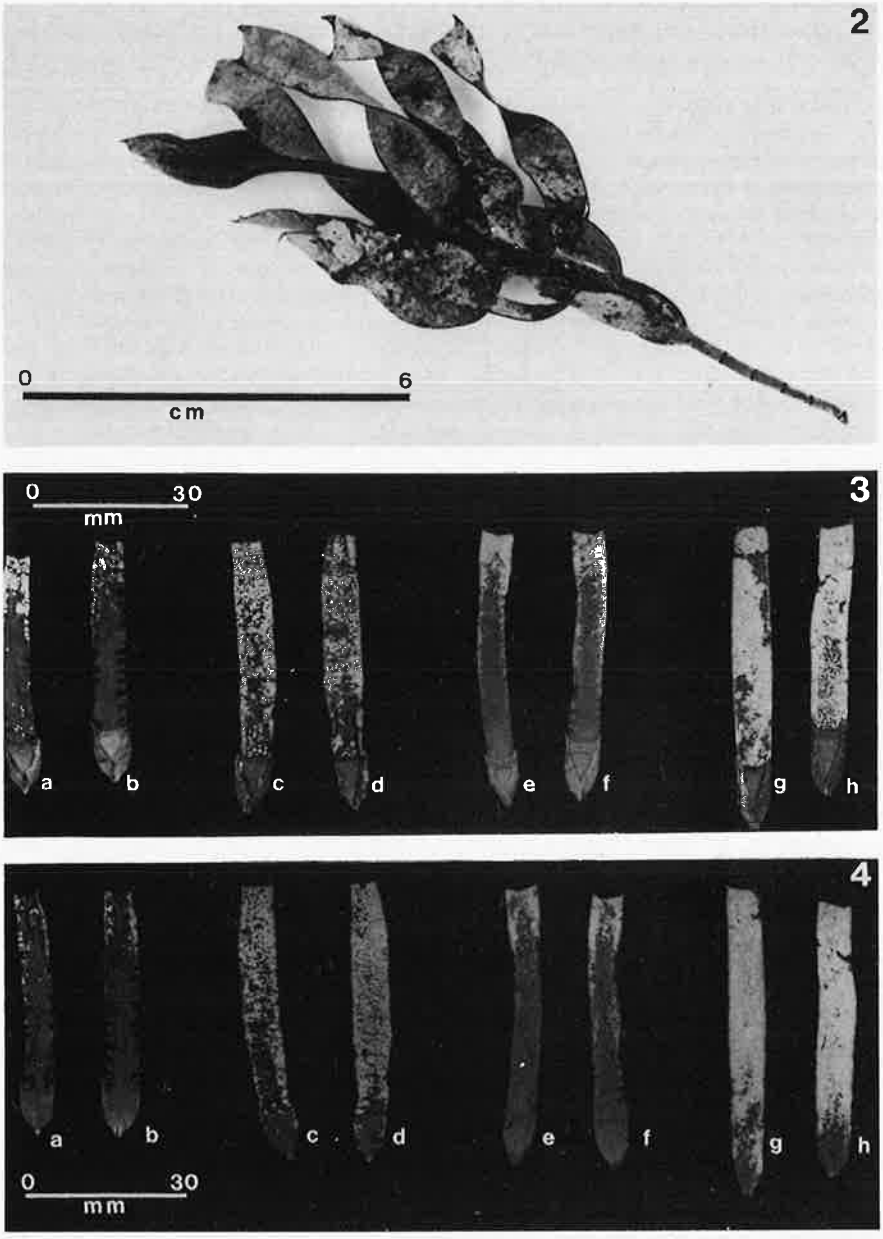

Fig. 2. Portion of *Amphibolis antarctica* showing a terminal cluster of leaves epiphytized by *Pneophyllum–Fosliella* plants.

Fig. 3. Representative *Amphibolis* leaves from eulittoral rock pool (*a–d*) and sublittoral meadow (*e–h*), showing the distribution of *Pneophyllum–Fosliella* plants on the *adaxial* leaf surface. *a*, *b*, *e*, *f* are third innermost leaves; *c*, *d*, *g*, *h* are second outermost leaves.

Fig. 4. *Abaxial* surface of the same leaves shown in Fig. 3; legend as in Fig. 3.

the second outermost and the third innermost leaves were selected for detailed analyses (Figs 3 and 4). The outermost leaves were not chosen because many appeared senescent or dead, and the innermost two leaves were relatively immature or small.

The adaxial (Fig. 3) and abaxial (Fig. 4) surfaces of all leaves chosen were divided arbitrarily into distal, mid and proximal segments of equal size (generally 6–8 mm broad and 10–14 mm long). Within each segment, three 2·5 × 2·5 mm quadrats were located using paired random coordinates and a square ocular grid fitted to an Olympus JM stereo-microscope; in this way 20–30% of the segment surface was able to be sampled. Within each quadrat, the cover, density and relative fertility (i.e. the percentage of plants bearing conceptacles) of the *Pneophyllum–Fosliella* epiphytes were determined. No overlapping of plants was included in cover estimates; raw density data were converted so that final values are given as numbers of individuals per 10 mm^2.

Three species of crustose coralline epiphytes occurred: *Fosliella cruciata* Bressan, *F. cymodoceae* (Foslie) Jones & Woelkerling and *Pneophyllum zonale* (Crouan & Crouan) Chamberlain. [Nomenclature follows Chamberlain (1983) and Jones and Woelkerling (1984).] Because plants of the three species grew mixed together on *Amphibolis* and because species identifications of all individuals could not be made confidently at the magnifications used to obtain numeric data, the three taxa have been treated as a single ecotype, and results have been reported only for the combined cover, density and relative fertility of all three taxa. Statistical comparisons were made using Mann-Whitney U tests (Snedecor and Cochran 1973).

Table 1. Numerical data on cover of *Pneophyllum–Fosliella* plants on *Amphibolis antarctica* leaves
Data reported as mean percentage of cover per leaf segment (n = 45)

Position	Leaf Surface	Segment	Eulittoral pool Mean	Eulittoral pool s.d.	Sublittoral meadow Mean	Sublittoral meadow s.d.
Outer	Abaxial	Distal	9·7	14·2	70·2	22·5
		Mid	8·5	11·8	55·5	26·3
		Proximal	7·2	18·0	40·8	26·8
	Adaxial	Distal	9·6	10·1	67·2	22·4
		Mid	12·2	17·1	61·0	27·1
		Proximal	3·5	8·7	31·4	29·5
Inner	Abaxial	Distal	4·1	9·1	30·1	25·5
		Mid	0·8	3·8	27·7	27·3
		Proximal	0·2	1·5	11·1	28·1
	Adaxial	Distal	2·0	4·2	16·8	12·0
		Mid	0·5	1·7	7·2	13·8
		Proximal	0·2	1·0	1·2	2·9

Results and Discussion

Cover and Density

The data on cover (Table 1) and density (Table 2) provide clear evidence that the sublittoral environment at Flinders is more conducive to the development of *Pneophyllum–Fosliella* plants than is the rock pool environment at Sorrento. Significantly greater (P<0·01) cover and density of these epiphytes occurred on all sublittoral *Amphibolis* leaf segments except for the proximal, adaxial, inner leaf segment where the lowest levels of epiphytes were recorded and no significant differences occurred between habitats. Moreover, when data from entire leaf surfaces, entire leaves and all leaves sampled were compared for the two environments, significantly greater (P<0·01) cover and density of *Pneophyllum–Fosliella* crusts always occurred on sublittoral plants of *Amphibolis* (Figs 3 and 4). This difference may be due in part to smaller diurnal fluctuations in temperature and other abiotic parameters in the sublittoral environment.

Within both environments, similar patterns of epiphyte distribution on host leaves were evident (Tables 1 and 2). Thus along all leaf surfaces examined, whether adaxial or abaxial, significant decreases (P<0·05) in epiphyte cover and density occurred from the distal to

the proximal segments. This may be due partly to the relatively greater levels of illumination at the distal ends of leaf surfaces and partly to the fact that the distal parts of leaves are the oldest.

Significant differences ($P<0\cdot05$) in epiphyte cover and density did not occur between the adaxial and abaxial surfaces of leaves except on the inner leaves of leaf clusters on sublittoral plants; here, cover and density of *Pneophyllum–Fosliella* plants were significantly greater on the abaxial surface. Similar results were obtained when proximal, mid and distal segments of various adaxial and abaxial leaf surfaces were compared. These data do not support the general conclusion of Ducker *et al.* (1977) that *Pneophyllum–Fosliella* epiphytes favour the adaxial leaf surface.

In both the sublittoral and the rock pool environments, the cover and density of *Pneophyllum–Fosliella* plants were significantly greater ($P<0\cdot01$) on the second outermost leaf than on the third innermost leaf. This was true in comparisons of particular leaf segments, entire leaf surfaces and entire leaves. This distribution may result partly from relatively greater levels of illumination on the outer leaves and partly from relatively greater water and nutrient flow past the outer leaves.

Table 2. Numerical data on density of *Pneophyllum–Fosliella* plants on *Amphibolis antarctica* leaves

Data reported as mean number ($n = 45$) of individuals per 10 mm^{-2} host leaf surface

Position	Leaf Surface	Segment	Eulittoral pool Mean	Eulittoral pool s.d.	Sublittoral meadow Mean	Sublittoral meadow s.d.
Outer	Abaxial	Distal	8·2	10·6	34·7	11·7
		Mid	3·7	6·1	32·0	10·4
		Proximal	1·9	6·8	26·6	11·2
	Adaxial	Distal	6·2	6·8	32·3	10·9
		Mid	5·6	7·8	29·4	11·8
		Proximal	2·6	6·1	23·0	17·1
Inner	Abaxial	Distal	3·5	3·7	27·4	14·2
		Mid	0·8	0·9	22·2	15·5
		Proximal	0·8	0·7	10·0	12·4
	Adaxial	Distal	2·6	6·4	17·6	13·6
		Mid	1·0	0·3	11·0	14·2
		Proximal	0·3	1·7	1·4	4·5

Relative Fertility

The data on relative fertility (Table 3) are somewhat less clear-cut than those on cover and density, although several patterns are evident. Thus, when comparisons are made for entire sets of leaves (outer or inner), for abaxial leaf surfaces (from outer or inner leaves) or for adaxial surfaces of outer leaves, significantly greater ($P<0\cdot05$) levels of relative fertility occur in sublittoral populations of *Pneophyllum–Fosliella* than in rock pool populations. Significant differences ($P<0\cdot05$), however, do not occur between populations for adaxial surfaces of inner leaves (where cover and density are lowest), and no clear pattern emerges from comparisons of particular segments of leaf surfaces of sublittoral and rock pool plants as it did for cover and density.

Within both environments, the patterns for relative fertility generally parallel those for cover and density. Thus, along all leaf surfaces examined, significant decreases ($P<0\cdot05$) in relative fertility always occurred from the distal to the proximal leaf segments. Significant differences did not occur, however, between the adaxial and abaxial surfaces of leaves except on inner leaves of leaf clusters of sublittoral plants where significantly higher relative fertility occurred abaxially.

In both the sublittoral and the rock pool environments, relative fertility always was significantly higher ($P<0.05$) on outer leaves of a cluster than on inner leaves. This was true for comparisons of particular leaf segments, particular leaf surfaces and entire sets of leaves.

Table 3. Numerical data on relative fertility of *Pneophyllum–Fosliella* plants on *Amphibolis antarctica* leaves

Data reported as means of 45 measurements

Position	Leaf Surface	Segment	Eulittoral pool Mean	Eulittoral pool s.d.	Sublittoral meadow Mean	Sublittoral meadow s.d.
Outer	Abaxial	Distal	26·8	36	24·2	18·7
		Mid	16·1	32	20·1	20·4
		Proximal	12·6	30	12·0	15·9
	Adaxial	Distal	22·4	32·3	25·2	19·1
		Mid	11·9	25	23·8	22·3
		Proximal	6·3	20·3	7·8	19·2
Inner	Abaxial	Distal	8·4	22·8	9·9	19·1
		Mid	2·2	14·9	3·8	6·2
		Proximal	0·7	1·9	0·4	0·2
	Adaxial	Distal	10·4	20·8	1·9	6·1
		Mid	0	—	0·4	14·9
		Proximal	0	—	0	—

General Discussion

Overall, the results lead to the conclusion that plants of *Pneophyllum–Fosliella* are better adapted to grow on sublittoral plants of *Amphibolis antarctica* than on rock pool plants of this seagrass. Not only do the coralline epiphytes occur with higher densities (4·2–27·5 times greater than in rock pools; see Table 2) and cover more of the leaf surfaces (Table 1) but also a greater proportion of the plants produces conceptacles (Table 3). It also appears that within a leaf cluster the best growth sites for *Pneophyllum–Fosliella* plants are the distal segments of the outer leaves. Almost without exception, the greatest density, cover and relative fertility levels were recorded at these loci (Tables 1–3). The poorest growth sites appear to be the proximal segments of inner leaves. These conclusions apply both to sublittoral and rock pool plants of *Amphibolis* (Figs 3 and 4). Finally, the data provide evidence that plants of *Pneophyllum–Fosliella* can grow and produce conceptacles equally well on the adaxial and the abaxial leaf surfaces.

In a study of biomass accumulation and shading effects of epiphytes on the leaves of southern Australian populations of the seagrass *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog, Bulthuis and Woelkerling (1983*a*) found that coralline algae (i.e. taxa of *Pneophyllum* and *Fosliella*) were more prominent on sublittoral plants than on lower eulittoral plants of the seagrass, a result analogous to findings of the present investigation. Bulthuis and Woelkerling (1983*a*) also concluded that epiphyte biomass (including plants of *Pneophyllum* and *Fosliella*) can accumulate fast enough to reduce the time in which positive net photosynthesis of the leaf blade is possible to less than one half of the leaf life span. Taxa of *Pneophyllum* and *Fosliella* as well as other epiphytes occur ubiquitously on seagrasses, and various authors (e.g. Sand-Jensen 1977; Cambridge 1979; Borum and Wium-Andersen 1980) have suggested that the effects of epiphytes may be deleterious because of shading, lowering of the bicarbonate concentration at the leaf surface or competition for water-borne nutrients. The extent to which populations of *Pneophyllum* and *Fosliella* can adversely affect plants of *Amphibolis* cannot be determined until detailed data on standing crop, density and leaf growth rate comparable with that

for *Heterozostera tasmanica* (see Bulthuis and Woelkerling 1983*b*), are available for *Amphibolis antarctica* and *A. griffithii*. It would appear, however, that because plants of *Pneophyllum* and *Fosliella* commonly develop in abundance wherever *Amphibolis* is found (Ducker *et al.* 1977), these epiphytes may have adverse effects on the seagrass host which need to be identified and determined more precisely.

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An analysis of trichocyte and spore germination attributes as taxonomic characters in the *Pneophyllum–Fosliella* complex (Corallinaceae, Rhodophyta)

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P.L. JONES AND WM. J. WOELKERLING (1984) An analysis of trichocyte and spore germination attributes as taxonomic characters in the *Pneophyllum–Fosliella* complex (Corallinaceae, Rhodophyta). *Phycologia* **23:** 183–194.

Quantitative studies on field populations of five species and on cultured populations of two species of the *Pneophyllum* (syn. *Heteroderma*)–*Fosliella* complex (Corallinaceae, Rhodophyta) have led to the conclusions that trichocyte presence/absence and trichocyte arrangment are influenced by light and temperature and/or vary within field populations to the extent that they are not reliable characters for use in generic delineation. Trichocyte position, in contrast, was constant within hypothallial filaments in all field populations and was not affected by various combinations of light and temperature. In field populations, spore germination resulted in discs with segmentation patterns that were constant within each species; each disc contained either a four-celled or an eight-celled central element. Some variation in spore germination pattern occurred in all culture populations, but in no case did a species with a four-celled central element produce eight-celled variants or vice versa. These results support Chamberlain's conclusion that two genera should be recognized: *Pneophyllum* for taxa with intercalary hypothallial trichocytes and eight-celled central elements, and *Fosliella* for taxa with terminal hypothallial trichocytes and four-celled central elements.

INTRODUCTION

The number, circumscription, and naming of genera within the *Pneophyllum–Fosliella* complex (Corallinaceae, Rhodophyta) have been attended by uncertainty, and at various times at least eight generic names (*Fosliella* Howe 1920; *Guerinea* Picquenard 1912; *Hapalidium* Kuetzing 1843; *Heteroderma* Foslie 1909 [non *Heterodermia* Trevisan 1868]; *Lithocystis* Allman in Harvey 1848; *Melobesia* Lamouroux 1812; *Plectoderma* Reinsch 1874–1875; *Pneophyllum* Kuetzing 1843) have been employed for these algae. Chamberlain (1982, 1983) and Mason (1953) have summarized the associated historical aspects, and accounts of the basic morphology and anatomy of these algae are provided by Chamberlain (1983) and Johansen (1981).

Since 1950, some authors have referred all taxa in the complex to a single genus, variously using the names *Fosliella* (e.g. Bressan 1974; Cabioch 1972; Dawes 1974; Parke & Dixon 1976; Perestenko 1980; Taylor 1957, 1960), *Heteroderma* (e.g. Adey 1970; Adey & MacIntyre 1973), or *Melobesia* (e.g. Ardré 1970; Hamel & Lemoine 1953; Kylin 1956; Pujals 1963). Other authors (e.g. Dawson 1960; Johansen 1976, 1981; Masaki 1968; Mason 1953), in contrast, have recognized two genera—*Fosliella* for taxa possessing trichocytes (see Johansen 1981, pp. 33–36) and *Heteroderma* for taxa which apparently lack trichocytes. The origins of this last scheme, first clarified by Mason (1953, p. 335), lie in the publications of Foslie (1905, p. 96, 102; 1908; 1909, p. 56; see also Setchell & Mason 1943, p. 96). A number of investigators (e.g. Cabioch 1972; Chamberlain 1977a, 1977b, 1978; Ganesan 1963, 1971; Rosenvinge 1917), however, have criticized the use of trichocyte presence or absence for delineating taxa because trichocyte occurrence reportedly can vary within particular taxa and may be influenced by environmental factors such as light and temperature.

In a monographic study of species occurring in Great Britain, Chamberlain (1983) rejected both the one-genus scheme and the two-genus scheme based on trichocyte occurrence and instead divided the complex into two genera based on differences in hypothallial trichocyte position and spore germination pattern. Taxa in which hypothallial trichocytes terminate filaments and in which spore germination involves production

of a four-celled central element are referred by Chamberlain to *Fosliella*, whereas taxa in which hypothallial trichocytes are intercalary within filaments and in which sporogenesis involves production of an eight-celled central element are placed in *Pneophyllum*. Chamberlain confirmed that these trichocyte characteristics were evident in the relevant generitype specimens and similarly found that *Heteroderma* was congeneric with *Pneophyllum*. Neither trichocyte position nor spore segmentation patterns have been used previously to delineate genera in this complex, and because Chamberlain's proposals have just been published, they have yet to be tested by other workers.

The present investigation arose from extensive correspondence between Chamberlain and the second author and was designed firstly to evaluate various attributes associated with trichocytes and spore germination for use in delineating genera within the complex, and secondly to serve as a prelude to monographic studies of the southern Australian representatives of the complex. Emphasis has been placed on assessing the variation present within and among field populations and culture populations of selected taxa, and specific aims were:

(1) to determine the frequency of trichocyte occurrence among individuals of particular populations;

(2) to assess the extent to which trichocyte occurrence, position and arrangement vary within and among populations and to consider if differences in photon flux density and temperature can influence such variability; and

(3) to elucidate whether spore segmentation patterns vary within field populations or in populations grown in culture under differing photon flux densities and temperatures.

The taxonomic implications of the resulting data are considered in relation to the various generic classification schemes currently employed for the complex.

MATERIALS AND METHODS

Field populations

Field samples containing epiphytic populations of five species (Table 1) of the *Pneophyllum–Fosliella* complex were fixed in 1 : 10, commercial formalin : seawater, returned to the laboratory, and stored in 7 : 2 : 1, ethanol : water : glycerine until used. Taxa were identified by comparison with data provided by Bressan *et al* (1977) and Chamberlain (1982, 1983) and where possible by direct comparison with type specimens. Nomenclature follows Chamberlain (1983); this has necessitated making two new name combinations which are considered further in the discussion.

Within each population, two groups of plants, each containing randomly selected individuals, were chosen for analysis. One group was chosen from a series of permanent whole mount slides prepared by decalcifying the plants (still attached to portions of host material) in 0.6 M HNO_3 for 1–2 h, staining with 5% aqueous aniline blue for

Table 1. Collection data on field populations used in this study. Voucher specimens are held in LTB (Department of Botany, La Trobe University, Bundoora, Victoria, Australia)

Fosliella cruciata Bressan in Bressan, Miniati-Radin & Smundin (1977) LTB 12528. Sorrento, Victoria, 0.5 m deep on *Amphibolis antarctica* (Labillardière) Sonder & Ascherson ex Ascherson in a midlittoral rockpool, 5 April 1982.

LTB 10756. Armstrong Point, Rottnest Island, W. Australia, reef pools on *Amphibolis antarctica*, 12 Feb. 1978. (Photographs only.)

Fosliella cymodocea (Foslie) Jones & Woelkerling (see Table 5) LTB 12526. The Gap, Phillip Island, Victoria, 2 m deep on *Amphibolis antarctica*, 13 March 1982.

LTB 13400 A. Green's Beach, Tasmania, 0.5 m deep on *Amphibolis antarctica*, 2 March 1983. (Photographs only.)

Pneophyllum caulerpae (Foslie) Jones & Woelkerling (see Table 5) LTB 12529. Point Lonsdale, Victoria, 1.0 m deep on *Caulerpa cactoides* (Turner) C. Agardh in lower littoral rockpool, 25 Aug. 1978.

Pneophyllum lejolisii (Rosanoff) Y. Chamberlain (1983). LTB 12531. Sorrento, Victoria, 2 m deep on *Zonaria turneriana* J. Agardh off reef edge, 23 March 1982.

LTB 13400 B. Green's Beach, Tasmania, 0.5 m deep on *Amphibolis antarctica*, 2 March 1983. (Photographs only.)

Pneophyllum zonale (P. Crouan & H. Crouan) Y. Chamberlain (1983). LTB 12527. The Gap, Phillip Island, Victoria, 2 m deep on *Amphibolis antarctica*, 13 March 1982.

3–4 min, rinsing off excess stain with water, and mounting in 20% aqueous "Karo" dextrose with 2% phenol added to prevent fungal growth. Data were obtained from 100 plants observed in surface view.

Data on the second group of individuals were obtained from cross sections of entire thalli containing mature conceptacles. Permanent slides were prepared from material which had been completely decalcified in 0.6 M HNO_3 (1–2 h), stained in 5% aqueous $KMnO_4$ for 4–6 min, dehydrated through 30, 60, 90 and 100% ethanol at 10 min intervals, transferred into epoxy propane for 90 min and then embedded under vacuum in Spurr's resin (vinylcyclohexane dioxide, 5 g; diglycidyl ether of polyprophylene glycol, 3.5 g; nonenyl succinic anhydride, 13 g; dimethylaminoethanol, 0.2 g) according to the following schedule:

(1) 1:1, epoxy propane:Spurr's resin—1 h;
(2) Spurr's resin—1 h;
(3) Fresh Spurr's resin—1 h.

Material of suitable size then was placed in 'boats' and fresh Spurr's resin was added and allowed to harden at 70°C for 12–24 h. Sections 6–12 μm thick were cut with a steel knife, placed serially on slides and mounted in 'Eukitt' (Mfg.: O. Kindler, Freiburg, W. Germany).

Data on trichocyte occurrence, position and arrangement and data on cellular arrangement in the germination disc were recorded, and trichocyte frequency data were calculated for each population. Checks of other individuals in each of the populations were made to confirm the results obtained from the two groups of randomly selected plants, and some photographs were obtained from several additional populations (Table 1).

Culture procedures

Hosts bearing fertile plants of *Fosliella cruciata* Bressan were collected in the field and returned to the laboratory for subsequent inoculation within 24–48 h using the procedures and culture medium described in Jones and Woelkerling (1983). Experiments using all combinations of two photon flux densities (3–6 μmol m^{-2} s^{-1} and 12–25 μmol m^{-2} s^{-1}) and three temperatures (9.5°C ± 1.5°C, 15°C ± 1°C, 21.5°C ± 1.5°C) were conducted on a cross gradient growth table (Yarish *et al* 1979) for periods of 28–84 days. Light was supplied on an 18 h light:6 h dark photoperiod using cool white fluorescent tubes. These light and temperature regimes fall within the range of conditions found at the locality from which the plants were collected.

Plants cultured at photon flux densities of 12–25 μmol m^{-2} s^{-1} were harvested after 28–35 days whereas plants cultured at 3–6 μmol m^{-2} s^{-1} grew more slowly and were harvested after 77–84 days. At the time of harvesting, most plants grown at 15°C ± 1°C or at 21.5°C ± 1.5°C had produced conceptacles, whereas nearly all plants grown at 9.5°C ± 1.5°C were sterile and were less robust in appearance. Following fixation in 1:10 commercial formalin:seawater, whole mounts were prepared as described for the field collections and data were then obtained on trichocyte occurrence, position, and arrangement, and on cellular arrangement in the germination disc. In addition, cell patterns in numerous germination discs were observed during early stages of the culture experiments.

The procedures used to collect, isolate, and grow spores of *F. cruciata* also were employed in limited studies of sporogenesis in *Pneophyllum zonale*; all spores of the latter species, however, were grown at 15–20°C in photon flux densities of 12–25 μmol m^{-2} s^{-1}.

RESULTS AND DISCUSSION

Trichocytes

Data on perithallial (Figs 1–2) and hypothallial (Figs 3–5) trichocytes from field populations are summarized in Table 2, and results from the culture experiments are presented in Table 3.

OCCURRENCE AND FREQUENCY: Among field populations, perithallial trichocytes occurred in all individuals of *Fosliella cruciata, F. cymodocea* and *Pneophyllum zonale* but never in *Pneophyllum caulerpae,* or *P. lejolisii* (Table 2). Nevertheless, it is evident from experimental data (Table 3) that the presence or absence of perithallial trichocytes within a species can be influenced both by photon flux density and by temperature. At photon flux densites of 3–6.5 μmol m^{-2} s^{-1}, perithallial trichocytes failed to develop in plants of *Fosliella cruciata* at any of the temperatures tested. At photon flux densities of 12–25 μmol m^{-2} s^{-1}, however, the frequency of perithallial trichocyte occurrence appeared to be temperature dependent, with far more individuals possessing perithallial trichocytes in populations grown at 15°C than in those grown at 10°C or 22°C.

Table 2. Data on trichocyte frequency, position and arrangement in the populations studied

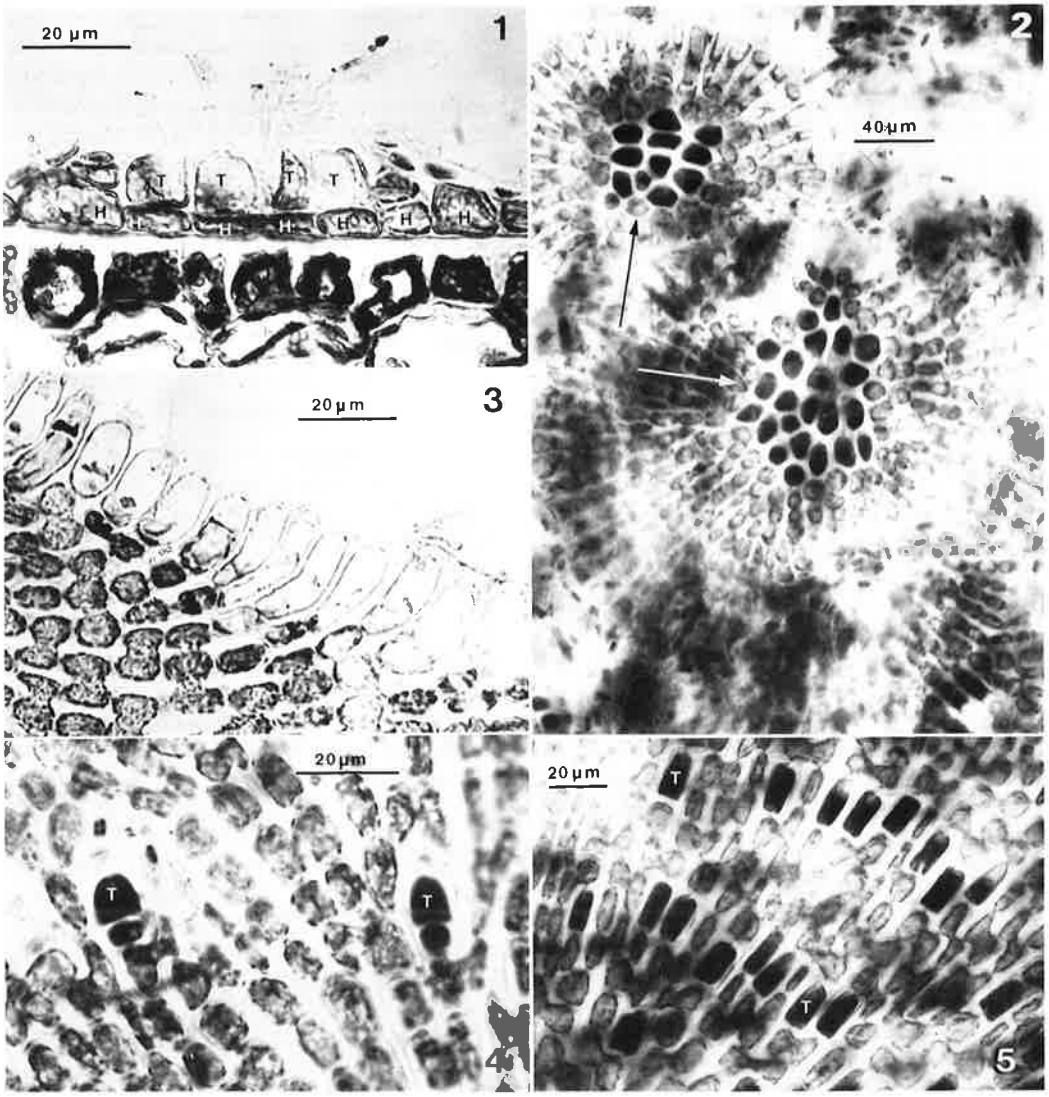
Taxon	Figs	Trichocyte position		Trichocyte frequency		Trichocyte arrangement	
		Hypothallial	Perithallial	Hypothallial (N = 100–187)	Perithallial (N = 100–187)	Hypothallial	Perithallial
F. cruciata (field)	1, 2, 4	terminal	terminal	0.71	1.00	single, pairs, lateral series of 3–4	groups of 6 or more in vegetative tissue
F. cruciata (culture)	—	terminal	terminal	0.44	0.26	as above	as above
F. cymodocea	3	terminal	terminal	1.00	1.00	single, lateral series of 3 or more	groups of 2 or more in reproductive tissue
P. caulerpae	—	intercalary	absent	0.25	0.00	single only	—
P. lejolisii	—	intercalary	absent	0.48	0.00	single only	—
P. zonale	5	intercalary	terminal	0.62	1.00	single, pairs, lateral series of 3 or more	singly or groups of 2 or more in vegetative and reproductive tissue

Table 3. Trichocyte frequency, position and arrangement in populations of *Fosliella cruciata* cultured under various light intensities and temperatures

Photon flux density (μmol m^{-2} s^{-1})	Temp. (°C)	No. of plants examined	Trichocyte position (hypothallial + perithallial)	Perithallial trichocyte arrangement	Trichocyte frequency		
					Hypothallial + perithallial	Hypothallial only	Perithallial only
12–25	10	20	terminal	groups of 6–12 trichocytes	0.65	0.65	0.05
12–25	15	35	terminal	groups of 6–12 trichocytes	1.0	0.83	0.94
12–25	20	42	terminal	groups of 6–12 trichocytes	0.71	0.45	0.57
3.0–6.5	10	23	terminal	—	0.22	0.22	0
3.0–6.5	15	33	terminal	—	0.45	0.45	0
3.0–6.5	20	34	terminal	—	0.06	0.06	0

Hypothallial trichocytes were found in all the field-collected specimens of *Fosliella cymodocea* examined but occurred with varying degrees of frequency in field populations of the other four species (Table 2). In culture, hypothallial trichocyte frequencies were higher in populations of *F. cruciata* grown in photon flux densities of 12–25 μmol m^{-2} s^{-1} than in populations grown at 3–6 μmol m^{-2} s^{-1} at all temperatures tested (Table 3). Similarly, a higher frequency of hypothallial trichocytes was found at 15°C than at 10°C or 22°C at both photon flux densities tested. These results provide experimental evidence that hypothallial (and perithallial) trichocyte occurrence can be influenced by abiotic factors.

Overall, trichocytes (whether perithallial or hypothallial) may be present in all individuals of a population (as evidenced by the field populations of *Fosliella cruciata, F. cymodocea* and *Pneophyllum zonale* and one of the experimental treatments of *Fosliella cruciata*), or trichocytes



Figs 1–5. Trichocytes.

Fig. 1. Cross section through thallus of *Fosliella cruciata* showing perithallial trichocytes (T) and cells of hypothallium (H) (LTB 12528).

Fig. 2. Surface view of thallus of *F. cruciata* with several groups (arrows) of perithallial trichocytes (LTB 10756).

Fig. 3. A series of terminal hypothallial trichocytes along thallus margin of *F. cymodocea* (LTB 12526).

Fig. 4. Trichocytes (T) terminating hypothallial filaments within thallus of *F. cruciata* (LTB 10756).

Fig. 5. Thallus of *Pneophyllum zonale* showing darkly stained intercalary hypothallial trichocytes (several indicated by T) (LTB 13400B).

may occur in some individuals of a population but be totally absent in others (as evidenced by the field populations of *Pneophyllum caulerpae,* and *P. lejolisii* and most culture populations of *Fosliella cruciata*). In no case during this study was a population found in which all individuals lacked trichocytes. In some cases, however, thorough searching was required to detect trichocytes in some field plants and some cultured plants contained only a single trichocyte each.

Chamberlain (1977a, 1977b, 1978, 1983), Ganesan (1963, 1971), Lemoine (1923), Rosenvinge (1917), and Suneson (1943) all have recorded variation in the occurrence of trichocytes

in field material of various taxa belonging to the *Pneophyllum–Fosliella* complex, and Chamberlain (1977b, 1983) has suggested that trichocyte occurrence may be light and temperature dependent. Results from the present study have confirmed and extended the findings of these workers and have provided experimental evidence documenting the effects of light and temperature on trichocyte occurrence and frequency in these algae.

TRICHOCYTE POSITION: In all field populations (Table 2) and in all experimental treatments (Table 3), the position of perithallial and of hypothallial trichocytes was constant within and among individual plants. Perithallial trichocytes, when present, always were terminal on filaments (Fig. 1). In *Fosliella cruciata* and *F. cymodocea,* hypothallial trichocytes always occurred terminally, whereas in *Pneophyllum caulerpae, P. lejolisii,* and *P. zonale,* hypothallial trichocytes always were intercalary within filaments (Figs 3–5). No abnormally large, terminal, sac-like cells such as those mentioned by Suneson (1943) and Chamberlain (1983) were observed during this study.

Within species, trichocyte position in hypothallial filaments is not necessarily correlated with trichocyte position in perithallial filaments (Table 2). In *Fosliella cruciata* and in *F. cymodocea,* for example, both hypothallial and perithallial trichocytes always are terminal. In *Pneophyllum zonale,* however, hypothallial trichocytes always are intercalary whereas perithallial trichocytes always were terminal. It is important, therefore, to specify which tissue is involved when discussing trichocyte position.

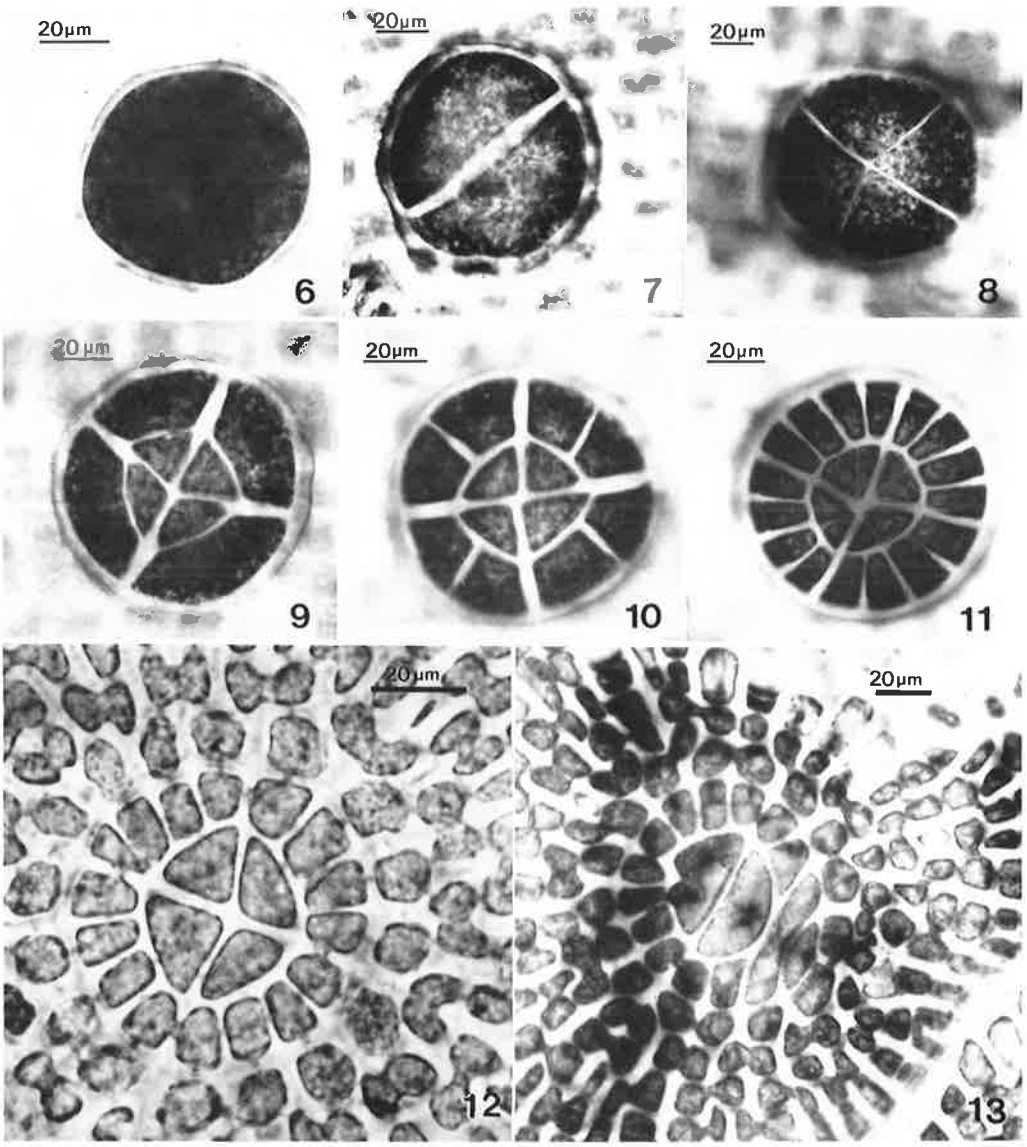
TRICHOCYTE ARRANGEMENT: Perithallial trichocytes in field plants of *Fosliella cruciata* occurred in more or less circular groups of six or more (Fig. 2) in vegetative parts of all thalli examined (Table 2), and this same arrangement was present in plants grown under a range of culture conditions (Table 3). Reproductive tissues of *F. cruciata,* in contrast, lacked perithallial trichocytes. In *F. cymodocea* and *Pneophyllum zonale,* perithallial trichocytes occurred singly or in groups of two or more. In the former species, these were confined to reproductive tissues whereas in the latter, perithallial trichocytes occurred both in vegetative and reproductive tissues. Perithallial trichocytes were not found in the other two species examined.

Hypothallial trichocytes, when present, occurred in a solitary fashion in all plants of *Pneophyllum caulerpae,* and *P. lejolisii.* In the remaining species, hypothallial trichoctyes within individual plants occurred singly, in pairs, or in lateral series of three or more in field plants; the same variation also occurred in cultured plants of *Fosliella cruciata.* In *F. cruciata* and *F. cymodocea* lateral series of three or more trichocytes occur along the thallus margin whereas in *Pneophyllum zonale,* lateral series of three or more occurred only within the thallus. Hypothallial trichocytes, however, never were found in clusters in any of the species examined.

Spore segmentation patterns

During germination and early development, spores belonging to taxa of the *Pneophyllum–Fosliella* complex undergo a series of apparently characteristic cell divisions to form a germination disc of 20–32 cells from which further thallus development occurs. Bressan (1980), Chamberlain (1982, 1983), Chihara (1974a, 1974b) and Notoya (1976a, 1976b), among others, have examined the patterns of spore segmentation in various taxa assigned to the complex, and Chamberlain (1982, 1983) has concluded that two fundamental types of segmentation pattern occur: one resulting in a four-celled central element (Figs 6–12) in the germination disc and one resulting in an eight-celled central element (Figs 14–17) in the germination disc. Furthermore, Chamberlain (1983) regarded this difference in pattern to be the most consistent and fundamental character for use in generic delineation within the complex.

In field populations of the five southern Australian species studied, the spore segmentation pattern, with one isolated exception, was constant among all individuals within each population. In *Fosliella cruciata* and *F. cymodocea,* the germination disc always included a central element of four cells (Figs 9–12, 20). During germination, a spore (Fig. 6) divides to form two equal sized cells (Fig. 7). Each of these cells then divides so as to form a septum at right angles to the first formed septa and a four-celled sporeling results (Fig. 8). The next division in each of the four cells is periclinal relative to the outer spore wall, and this results in a central group of four cells surrounded by a concentric ring of four additional cells (Fig. 9). The central four cells (i.e. the four-celled central element) then ceases dividing after producing a small epithallial cell each, and all subsequent thallus development is ini-



Figs 6–13. *Fosliella cymodocea.*

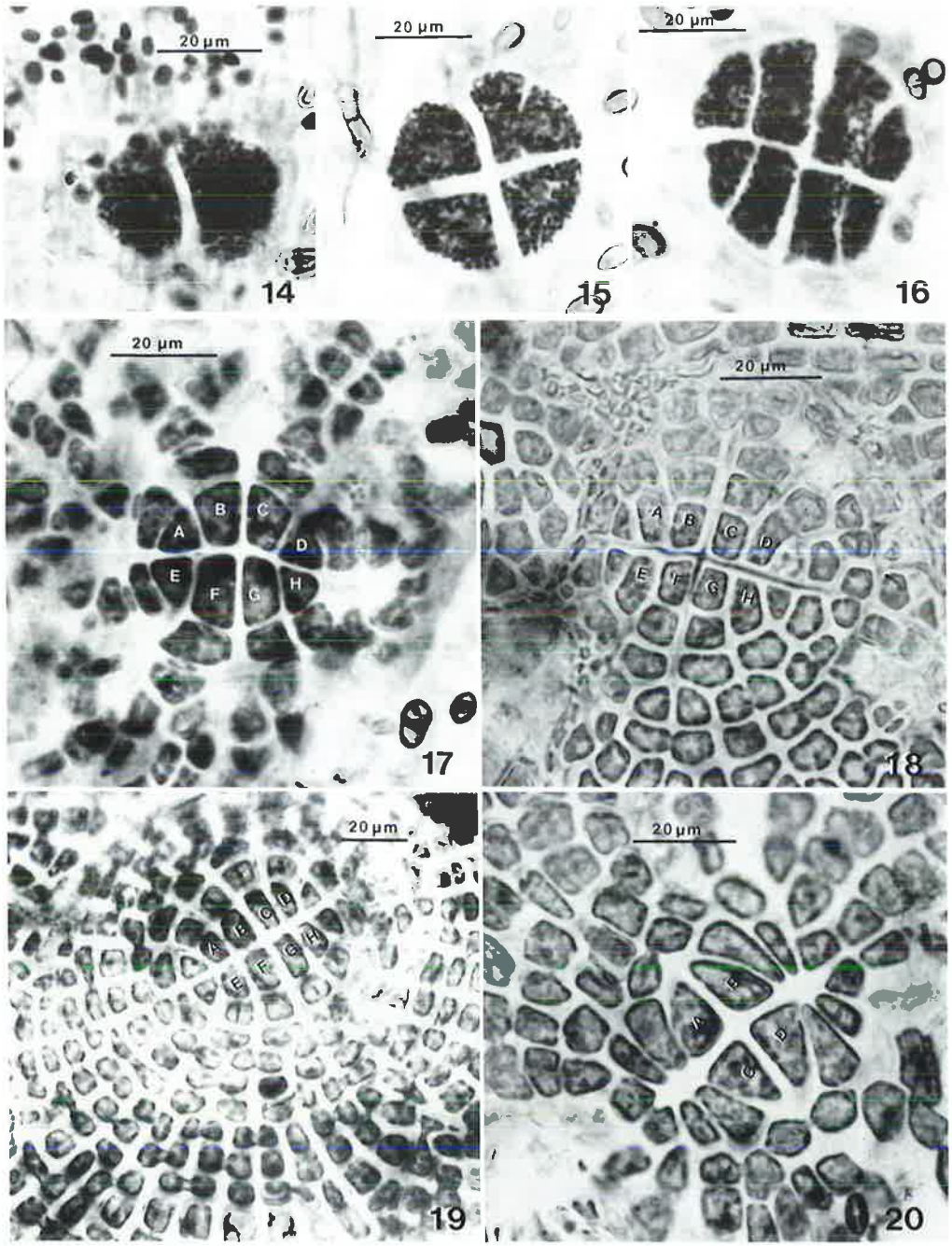
Figs 6–11. Sporogenesis showing development of a four-celled central element in the germination disc: spore (Fig. 6); two-celled stage (Fig. 7); four-celled stage (Fig. 8); eight-celled stage showing four central cells surrounded by a concentric ring of four outer cells (Fig. 9); 12-celled stage (Fig. 10); 20-celled stage (Fig. 11) (LTB 13400 A).

Fig. 12. Portion of mature plant with plainly evident 20-celled germination disc and the four-celled central element (LTB 12529).

Fig. 13. Aberrant germination disc in a field collected plant containing a two-celled central element and a surrounding disc of 14 cells, some abnormally shaped (LTB 13400 A).

tiated from the outer ring of four cells (Figs 10–12).

This contrasts with the field populations of *Pneophyllum caulerpae, P. lejolisii,* and *P. zonale* where the germination disc of all individuals examined included a central element of eight cells (Figs 17–19). During germination, the first two divisions of the spore (Figs 14, 15) are the same



Figs 14–20. Germination discs and sporogenesis.

Figs 14–16. Sporogenesis in *Pneophyllum lejolisii* showing development of an eight-celled central element: two-celled stage (Fig. 14); four-celled stage (Fig. 15); eight-celled stage showing two parallel rows of four cells each (Fig. 16).

Fig. 17. *Pneophyllum lejolisii.* Portion of mature plant showing an eight-celled central element. Cells labelled A–H.

Fig. 18. *Pneophyllum caulerpae.* Portion of mature plant showing an eight-celled central element. Cells labelled A–H.

as described above. The third division, however, does not occur periclinally but rather is parallel or slightly oblique to the first or second formed septum and results in a central group of eight cells arranged in two parallel rows of four cells each (Figs 16, 17). During subsequent development, all eight cells undergo further divisions, but the central element still remains identifiable.

Although the cellular arrangement in the central element of the germination disc appeared to be constant in nearly all individuals of each field population studied, the central element was not evident in every plant. In some cases, germination discs became overgrown by adjacent thalli or other epiphytes. In other cases, the thalli apparently underwent natural fragmentation to produce a series of new thalli devoid of germination discs. One isolated example of an aberrant germination disc was seen in a field population of *Fosliella cymodocea* (Fig. 13); in this plant, which was sterile, the central element consisted only of two cells and the surrounding ring contained 14 rather than 16 cells.

Chamberlain (1982, p. 139; 1983) reported that under "unfavourable conditions" in culture, spores of *Fosliella farinosa* germinated in a creeping manner rather than producing a distinct germination disc. In the present study, numerous spores of *F. cruciata* were germinated under varying combinations of temperature and photon flux density (Table 4). Some variability in the pattern of sporogenesis occurred in all treatments, and three developmental modes were detected: (1) formation of germination discs with regularly arranged cells; (2) formation of germination discs with randomly arranged cells; and (3) formation of thalli without defined germination discs. The first mode corresponds to that found in all field specimens of *F. cruciata* examined, while the latter two modes were not detected in the field samples. It is possible that under natural conditions the latter modes of sporogenesis, if present, produce aberrant plants which do not survive long, but further study is needed to clarify this point. In no case, however, did culture grown spores of *F. cruciata* produce a germination disc with an eight-celled central element.

Limited data for *Pneophyllum zonale* (Table 4) show analogous results: some spores produced regular germination discs with eight-celled central elements; others produced discs with random cell arrangements; and still others developed in a creeping manner to produce thalli without defined germination discs. No spores, however, produced germination discs with four-celled central elements.

TAXONOMIC IMPLICATIONS

Generic classification schemes

Currently, three different generic classification schemes are employed for algae belonging to the *Pneophyllum–Fosliella* complex. One (see Mason 1953; Masaki 1968; Johansen 1981) involves recognition of two genera: *Fosliella* for taxa possessing trichocytes and *Heteroderma* for taxa lacking trichocytes. It is evident from data obtained during the present study that this scheme is unsatisfactory. Trichocyte occurrence varied within four of the five field populations studied and varied within all experimental treatments tested. In these populations, one individual may possess trichocytes while an adjacent individual of the same species may lack them. Clearly, genera cannot be segregated on the basis of trichocyte presence/absence when such variation occurs within single populations.

The second scheme (see Cabioch 1972; Bressan 1974) involves placing all taxa into a single genus. Chamberlain (1983) has shown that the oldest available generic name for taxa assigned to the complex is *Pneophyllum* Kuetzing 1843, and were a single genus scheme to be adopted, this name would have to be employed in preference to more recently established names like *Fosliella* Howe 1920, which was used by Bressan (1974) and Cabioch (1972). The adoption of a single genus scheme is dependent, however, on providing evidence that all proposed multigeneric schemes are unsatisfactory, and thus the merits of Chamberlain's (1983) scheme must be considered first.

Chamberlain (1983) recognized two genera:

←

Fig. 19. *Pneophyllum zonale.* Portion of mature plant showing an eight-celled central element. Cells labelled A–H.

Fig. 20. *Fosliella cruciata.* Portion of mature plant showing a four-celled central element. Cells labelled A–D.

Table 4. Germination characteristics of tetraspores from populations of *Fosliella cruciata* and *Pneophyllum zonale* placed in various experimental conditions

Taxon	Experimental regime: Temperature (°C)	Experimental regime: Photon flux density (μmol m^{-2} s^{-1})	Number of spores germinated	Normal central element	Percentage germination of each mode: A*	B†	C‡
F. cruciata	15–20	3.0–6.5	105	4 cells	62	24	14
	15	3.0–6.5	138		59	12	29
	20	3.0–6.5	110		60	28	12
	15–20	12–25	82		52	13	35
	15	12–25	214		48	20	32
	20	12–25	169		40	12	48
P. zonale	15–20	12–25	200	8 cells	47	33	20

* A—germination disc with regularly arranged cells.
† B—germination disc with randomly arranged cells.
‡ C—no defined germination disc; germination via creeping filaments.

Fosliella for taxa possessing terminal hypothallial trichocytes and a four-celled central element in the spore germination disc; and *Pneophyllum* for taxa possessing intercalary hypothallial trichocytes and an eight-celled central element in the spore germination disc. Chamberlain regarded the cellular arrangement in the germination disc to be the more significant character, although the two characters appeared to be correlated.

Chamberlain's two genus scheme is supported by most data obtained during this study. Thus within field populations of all five species examined, the plants either possessed both terminal hypothallial trichocytes and four-celled central elements in the germination discs or possessed both intercalary hypothallial trichocytes and eight-celled central elements in the germination discs. No other combinations of these two characters occurred, thus supporting the hypothesis that they are correlated. Moreover, in experiments involving plants of *Fosliella cruciata* grown in a variety of photon flux density and temperature combinations, terminal but never intercalary hypothallial trichocytes developed and four-celled but never eight-celled central elements were produced. Because Chamberlain's proposal for delineating genera has been sustained by independent data from field and laboratory investigations, her generic classification scheme appears to be satisfactory and is adopted here in preference to the single genus scheme used by some authors.

During the course of her studies, Chamberlain (1982, 1983) examined 13 species in depth and, in addition, studied the type collections of at least two other taxa (*Heteroderma subtilissima* (Foslie) Foslie, type species of *Heteroderma,* and *Guerinea callithamnioides* (Crouan & Crouan) Picquenard, type species of *Guerinea*). In the present study, five species, three of which were not dealt with by Chamberlain (1982, 1983), have been examined. Thus, of the 38 species hitherto assigned to the *Pneophyllum–Fosliella* complex, 18 have been found to conform to Chamberlain's classification scheme. Populations of the remaining species now need to be studied to test Chamberlain's scheme further.

The production of aberrant germination discs in cultures of *Fosliella cruciata* and *Pneophyllum zonale* in this study and the similar findings of Chamberlain (1982, 1983) for *Fosliella farinosa* suggests that close attention should be paid to these phenomena when examining other species. Aberrations found in culture were not detected in field populations except in one plant of *F. cymodocea.* More importantly, the recorded aberrations do not directly affect the proposed generic classification scheme because in no case did species with four-celled central elements produce 'aberrant' forms with eight-celled central elements or vice versa.

Chamberlain's classification scheme is based only on vegetative characters although she (Chamberlain 1983) suggested that several characters associated with carpogonial branches and fusion cells may be of potential generic importance. These require further study. In addition, further data are needed on attributes associated with tetrasporangial conceptacle ontogeny. Townsend (1981) has placed considerable emphasis on these in delineating taxa of non-genic-

Table 5. Summary of nomenclatural changes and associated data

Fosliella cymodocea (Foslie) comb. nov.
Basionym: *Melobesia cymodocea* Foslie 1901, p. 23
Type locality: Port Phillip Bay, Victoria, Australia
Type: TRH (see Adey & Lebednik 1967, p. 32)

Pneophyllum caulerpae (Folsie) comb. nov.
Basionym: *Melobesia caulerpae* Foslie 1906, p. 16
Type locality: Castle Point, New Zealand
Type: TRH (see Adey & Lebednik 1967, p. 35)

ulate Corallinaceae (see also Turner & Woelkerling 1982), and has noted the apparently confused situation with respect to data on conceptacle ontogeny in the *Pneophyllum* (syn. *Heteroderma*)–*Fosliella* complex. An evaluation of the taxonomic potential of attributes associated with tetrasporangial conceptacle development is now needed.

Nomenclatural aspects

The adoption of the Chamberlain scheme in this study has necessitated two new nomenclatural combinations. Table 5 summarizes the details of these changes and includes associated taxonomic data.

Trichocyte arrangement

Further study is required to determine whether the arrangement and location of perithallial trichocytes is constant in particular species and thus of potential taxonomic significance. In the present study, a constant arrangement occurred in *Fosliella cruciata* and this was not affected by a range of conditions in culture. Bressan *et al* (1977) did not mention perithallial trichocytes in their discussion of *F. cruciata*. In the present study, however, perithallial trichocytes failed to develop under certain experimental conditions (Table 4), and it is possible, therefore, that the material used by Bressan *et al* (1977) grew under conditions which prevented development of perithallial trichocytes.

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Foslie and the Corallinaceae

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by

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Contents

1. INTRODUCTION

During the early stages of my studies on southern Australian Corallinaceae (Rhodophyta), it became apparent that an index to these taxa mentioned in the publications of M.H. Foslie would greatly facilitate an understanding of his changing ideas about coralline taxonomy and also would provide an efficient means of locating Foslie's data and comments about particular taxa. The project was completed over a period of several years, mostly while on field trips to remote regions of the Australian coast. The results originally were intended only for personal use, but several colleagues who became aware of the index urged that it be made available to a wider audience. The present volume has been prepared with that aim in mind and includes, in addition to the index to Foslie's publications, an analysis of Foslie's approach to the delineation of species and infraspecific taxa, and separate indexes to two additional publications (Printz 1929, Adey 1970) which are based on Foslie's herbarium material at the Royal Norwegian Scientific Society Museum in Trondheim (TRH). A catalogue of Foslie's coralline collections at TRH has been prepared by Adey and Lebednik (1967), and biographic data on Foslie have been published by Wille (1911), Printz (1929) and Høeg (1944). It is hoped that these indexes and the analysis of Foslie's approach to taxon delimitation will be of some value to others undertaking systematic research on the nongeniculate Corallinaceae.

II. AN ANALYSIS OF M.H. FOSLIE'S PUBLICATIONS ON THE CORALLINACEAE (RHODOPHYTA)

The publications and herbarium of Mikael Foslie together constitute a fundamental resource for all research on the systematics of nongeniculate Corallinaceae (Rhodphyta). From 1887 through 1909, Foslie authored 69 papers containing data on the Corallinaceae; most of these dealt exclusively with nongeniculate taxa. Based on material he collected and on specimens sent to him from many parts of the world, Foslie described 485 new coralline taxa (10 genera, 240 species, 235 infraspecific taxa - see Tables 1, 2) of which 474 species and infraspecific taxa were nongeniculate. This represents 31.3% of the 1516 basionyms of nongeniculate Corallinaceae known to me (as of December 1983). At least two other taxa (Lithophyllum incrustans f. orbicularis Foslie in Setchell and Gardner 1903, p. 358; Lithothamnion botrytoides Foslie in Rosenvinge 1898, p. 10) presented in publications of other authors also are attributed to Foslie. Foslie described far more taxa of nongeniculate Corallinaceae than any other author (Lemoine, who has described 140 specific and infraspecific taxa, is a distant second), and thus he has had a considerable impact on the taxonomy of this group of Rhodophyta.

Between 1898 and 1909 Foslie (see 1898a, 1900i, 1903b, 1909b) proposed a succession of generic/suprageneric classification schemes for non-geniculate Corallinaceae which have been commented on by a number of authors (e.g. Johansen 1981, Lemoine 1911, Littler 1972, Pilger 1908, Svedelius 1911) and will not be considered in detail here except in relation to Foslie's approach to the delineation of species and infraspecific taxa. Prior to 1898, Foslie (1890) had first used the three genus scheme (i.e. Lithophyllum, Lithothamnion, Melobesia) employed by Solms-Laubach (1881) and Hauck (1883), but then (Foslie 1895a, pp. 33-36) modified this scheme by subsuming Lithophyllum into Lithothamnion. Thus

TABLE 1. GENERIC NAMES OF CORALLINACEAE ESTABLISHED BY FOSLIE

Name	Reference
Chaetolithon	1898b: 7
Clathromorphum	1898a: 4
Dermatolithon	1898b: 11
Goniolithon	1898a: 5
Heteroderma	1909b: 56
Hydrolithon	1909b: 55
Litholepis	1905d: 5
Lithoporella	1909b: 58
Phymatolithon	1898a: 4
Porolithon	1909b: 57

Lithothamnion as understood by Foslie in 1895 encompassed virtually all nongeniculate Corallinaceae except for the very thin-crusted Melobesia-like taxa, an important point to note, since it is in the 1895 monograph that Foslie provides some direct statements about the delination of species. Because of his broad 1895 concept of Lithothamnion, Foslie's approach to species delineation in effect applied to a range of taxa which he subsequently referred to a number of other genera.

With respect to species and species concepts, Foslie (1895a, p. 29) noted firstly that

> *"the limits between the species are as a rule not easily drawn, and often still more difficult without a greater number of species from different tracts for comparison".*

Foslie (1895a, p. 37) also noted that

> *"In reference to the character of species I have, besides*

TABLE 2. NUMERIC SUMMARY OF SPECIFIC AND INFRASPECIFIC TAXA OF CORALLINACEAE ORIGINALLY DESCRIBED BY FOSLIE. DATA ARE BASED ONLY ON NEWLY DESCRIBED TAXA AND "NOMINA NOVAE"; NEW NOMENCLATURAL COMBINATIONS, CHANGES IN RANK INVOLVING RETENTION OF ORIGINAL EPITHET, AND TAXA REFERRED TO "F. TYPICA" ARE NOT INCLUDED IN THESE TALLIES.

Genus associated with original use of epithet	Number of new species	Number of new intraspecific taxa	Total number of new taxa
Archaetolithothamnion	12	1	13
Corallina	1	-	1
Dermatolithon	-	2	2
Goniolithon	28	23	51
Litholepis	5	1	5
Lithophyllum	60	60	120
Lithothamnium	117	137	254
Mastophora	5	2	7
Melobesia	11	6	17
Phymatolithon	1	3	4
TOTALS	240	235	475

the general appearance and development of the plant, particularly laid stress upon the shape and size of the conceptacles of sporangia, which in my opinion affords a good and most cases recognizable characteristic".

It is evident from these statements that Foslie delineated species of "Lithothamnion" sensu lato primarily on (1) apparent differences in external morphology and (2) apparent differences in tetrasporangial conceptacle shape and size. It is also evident that he had difficulty defining limits between species. Foslie appears never to have undertaken a critical review of the diagnostic value of various characters, and it is not clear as to how Foslie arrived at the conclusions he did about the relative value of characters. There also is no evidence in 1895 that Foslie had considered the possibility that species were being defined too narrowly or that the characters being used to define these species were of questionable value. This, however, became evident to Foslie by 1905 (see below).

Foslie (1895a, pp. 29, 30) also commented on forms indicating that

"A form may appear rather well marked in one locality, but in another transitions to other forms may be rather common, and one and the same species often varying between wide limits, approaching not only nearly allied species, but even species which in their typical development are quite different".

It is evident from this that Foslie realized that species could vary between wide limits and that within a species a range of morphological form was possible. An analysis of Foslie's publications, however, shows clearly that the numerous taxonomic forms he described nearly always are based on slight differences in external morphology and that these forms often are even less well clearly defined than are his species. Nevertheless, many such forms subsequently were accorded species status by Foslie.

Prior to 1895, Foslie had described only 10 new specific and infraspecific taxa (Table 3). Based on the criteria outlined above, however, Foslie began in 1895 to describe numerous new taxa; in the 10 year period

TABLE 3. NUMBER OF NEW SPECIES AND INFRASPECIFIC TAXA DESCRIBED BY FOSLIE DURING SPECIFIED YEARS.

Year	Number of New Taxa	Year	Number of New Taxa
1887	1	1902	10
1980	1	1903	7
1891	8	1904	29
1895	60	1905	43
1897	27	1906	68
1898	16	1907	77
1899	1	1908	13
1900	59	1909	14
1901	41		
		TOTAL	475

1895-1904, 250 new species and infraspecific taxa (almost all as forms) were established (Table 3). Beginning in 1898, these taxa were referred to various genera, but the principles governing specific and infraspecific delineation were those set down by Foslie in 1895.

In 1905, Foslie (1905) produced a second monograph on northern "lithothamnia" which encompassed the genera Lithothamnion (in a narrower sense), Phymatolithon (including Clathromorphum as a subgenus), Melobesia, and Lithophyllum (including Dermatolithon as a subgenus). In the introductory section of this account, Foslie (1905c, pp. 3,4) provided further comments on his approach to species delineation. Thus on p. 3 he indicated that

> *"... I had partly laid too great stress on the shape and size of conceptacles, as even these may vary more than then* [i.e. in 1895] *presumed. Be it said that by far the greater part of the material in hand* [in 1895] *consisted of sterile*

specimens or of specimens with conceptacles but slightly developed"

(see also 1905c, p. 132). On p. 4 Foslie noted

> *"I consider it superfluous to enter more fully upon the reasons which have induced me to reducing the species so considerably as done below. My motives will in part appear from the remarks made concerning each single species. I had so to speak to choose between two ways - either to establish a still larger number of feebly differentiated boreal-arctic species, than already done, or to reduce as below, and at the same time found some new forms. As I have indicated, I choose the latter way. It may however, seem as if I have gone too far in this reduction. But as I have been unable to draw sure lines, I think the reduction must be considered compulsory, even if some species are to be taken in a rather wide sense".*

These statements suggest that Foslie was now placing less emphasis on reproductive characters for specific and infraspecific delineation. It also is evident that Foslie concluded that many of the species he had hitherto described were only "feebly differentiated" from one another.

Elsewhere in the introductory section, Foslie (1905c, pp. 7-10) noted how various environmental factors appear to affect the external morphology of plants and on p. 9 illustrated this contention:

> *"Thus, by way of example, Lithothamnion sonderi generally occurs in the upper part of the sublittoral region in a depth of 3-10 fathoms. Here it develops excresences densely verruciform, or at any rate shows an uneven surface. On the other hand, when the species is growing in the littoral region in much exposed places at the open sea, it may become quite smooth and slightly shining".*

Foslie (p. 9) also noted

> *"In the tropics, ..., these algae are in exposed places often water-worn. If at the same time they are much encumbered by extraneous bodies, rise is given to forms much stunted and almost unrecognizable".*

And finally Foslie (p. 9) concluded

> *"It is evident from what has been stated above that the great variation of the lithothamnia is often in essential points owing to extrinsic conditions".*

In addition to the above remarks on conceptacle shape and size and on external morphology, Foslie (1905c, p. 10) also commented on coralline anatomy:

> *"Another fact contributing to the difficulty of* [de]*limitation* [of taxa] *is the great mutual uniformity of anatomical structure prevailing particularly in the species of the genera belonging to the group of the Lithothamnioneae* [Lithothamnion, Phymatolithon]. *This is less the case in the group of the Melobesieae, e.g. Lithophyllum, which is chiefly represented in the tropical and subtropical areas".*

Summarizing Foslie's comments in 1905 we see that

(1) Foslie felt that too much emphasis had been placed on conceptacle size and shape in delineating taxa;

(2) Characters associated with external morphology can vary both in temperate-boreal and in tropical species depending on environmental conditions;

(3) Taxa of the Lithothamnioneae appear to be anatomically uniform; and

(4) Far too many species had been established and a considerable reduction was necessary.

In spite of Foslie's 1905 comments, it is evident from an analysis of papers published subsequently that he continued to use apparent differences in external morphology as a major basis for erecting new taxa. During the period 1905-1909 (Table 3, p. 11), Foslie described an additional 215 specific and infraspecific taxa, and the record shows that instead of consolidating taxa, Foslie actually was establishing new ones at an increased annual rate of 43 in the 1905-1909 period, 1.72 times greater than the annual rate of 25 for the period 1895-1904!

No one has attempted a critical analysis of all of Foslie's taxa, and the current status of many of these is uncertain. Adey (1970) updated the generic placement for 232 of the 475 species and infraspecific taxa described by Foslie [see Chapter VI], but did not determine relationships between species or between forms and did not indicate how within a genus each species or how within a species each form was delineated from other Foslie taxa of the same rank. Adey and Lebednik (1967) prepared a catalogue of Foslie's coralline collections, and although a number of lectotype specimens for species were designated, mention of infraspecific taxa is lacking except in cases where Foslie later accorded such taxa species status. Moroever, Adey (1970, p. 2) deliberately excluded mention of most infraspecific taxa. Thus for many of Foslie's taxa, type specimens have yet to be identified in the Foslie herbarium.

Foslie never provided taxonomic keys or tables which summarized diagnostic characters or compared the distinguishing features of his taxa. As a result, one must contend with very general and often cryptic or nearly meaningless statements in Foslie's protologues when attempting to determine how one taxon was being differentiated from another. As one example, consider the comments for Lithothamnion boreale, one of the first nongeniculate corallines described by Foslie (1890, p. 37):

> *"It seems to be most nearly related to L. glaciale or L. calcareum, or perhaps to be an intermediate form between these two species. However, as it is separated from the former by rather essential characteristics, and as I have not seen any specimen of the latter, ..., I am obliged to regard it as a distinct species".*

Throughout Foslie's career, various taxa were delineated from one another by "essential characteristics" which never were explicitly enumerated.

Often, Foslie's statements on species relationships are labryrinthic; consider, for example, the comments for Lithothamnion syntrophicum (Foslie 1901a, p. 6);

> *"On the one side it rather resembles L. philippii in appearance*

and on the other hand closely allied to L. mesomorphum. In fact it appears to stand in the same relation to the latter as L. Philippii to L. lichenoides although the specimens at hand more approach L. mesomorphum than the mutual connection ever is to be seen between L. Philippii and L. lichenoides. However, in habit it only approaches such specimens of L. mesomorphum which are burdened with other algae or extraneous objects giving rise to a more irregular development than in typical specimens. Therefore, I consider it a separate species somewhat differing in structure too".

In other cases Foslie provides only very brief comments, as for Lithothamnion monostromaticum (Foslie 1903a, p. 3):

"The species stands nearest to Lithothamnion corticiforme".

Because most of Foslie's taxon delineations are based on general comparisons with other taxa, I became increasingly frustrated with trying to locate all relevant accounts in Foslie's papers; the Index in Chapter IV had its origins in that frustration.

In the vast majority of cases, Foslie's protologues are not accompanied by illustrations. Where figures are included, they almost always are photographs of entire plants showing general habit. Few anatomical illustrations are provided and with the exception of photos in two papers (Foslie and Howe 1906a, 1906d), these take the form of rather schematic drawings. This reinforces the fact (see Foslie 1905c, p. 10) that Foslie placed little emphasis on anatomy in delineating taxa. It also makes it more difficult to interpret Foslie's taxa in a modern context and to compare Foslie's accounts of taxa.

Foslie's ideas on the status of taxa changed frequently and rapidly. Many taxa described originally as forms later were elevated to species, or vise versa. Thus, for example, the taxon described originally as Lithothamnion coalescens (Foslie 1895a, p. 162) subsequently became Clathromorphum coalescens (Foslie 1898b, p. 8) and then C. circumscriptum f. coalescens (Foslie 1900i, p. 10), and then Phymatolithon compactum f.

coalescens (Foslie 1905, p. 88) and finally Clathromorphum compactum f. coalescens (Foslie 1908d, p. 12). Numerous other examples of this sort and be identified from use of the index data in Chapter IV. In at least several cases, the status of a taxon was changed more than once within a single paper. Thus, for example, Dermatolithon macrocarpum (Rosanoff) Foslie was reduced (Foslie 1905c, p. 117) to Lithophyllum pustulatum f. macrocarpum, but 11 pages later (Foslie 1905c, p. 128) it was again accorded species status (as Lithophyllum macrocarpum). This frequent shunting of taxa provides one indication that many of Foslie's taxa were described or shunted hastily or prematurely without careful thought as to their status or relationships.

On several occasions, Foslie (1895a, p. 29; 1897b, p. 521) emphasized the view that species delineation was very difficult in the absence of numerous specimens of the taxon concerned, and indeed declined (Foslie 1897b, p. 521, footnote) for that reason to identify some specimens sent to him by Heydrich. Yet Foslie repeatedly (e.g. 1890, p. 10; 1891, p. 37; 1895a, p. 154; 1897c, p. 15; 1898c, p. 9; 1899b, p. 3; 1900a, p. 23; 1901a, p. 14; 1904b, p. 12; 1906b, p. 14) described taxa from single, sometimes fragmentary specimens. Moreoever in many cases (e.g. 1890, p. 10; 1891, p. 37; 1897c, p. 17; 1901a, p. 14; 1906b, p. 14; 1907b, p. 29) Foslie indicated that the material available was sterile or (see Foslie 1905c, p. 3) contained only immature conceptacles. It is evident from this that Foslie's approach to taxonomy was often one of describing isolated or sterile specimens as new species or forms rather than one of assessing variability in characters of potential taxonomic importance and thereby determining the true biological limits of species and forms. It also is evident that a number of Foslie's taxa, because of their sterile or fragmentary condition, may not be assignable to genera in a modern context and ultimately may have to be treated as dubious or doubtful species or forms. Foslie (1898b, p. 3) himself admits this in

his first species list and generic sorting of non-geniculate taxa:

> *"Therefore the list does not pretend being perfect as regards the nomenclature, nor is it always to be decided with any degree of certainty whether some of the species quoted are to be referred to the one or the other genus. Nevertheless I have not in every case put a sign of interrogation to species not yet examined, setting aside such ones, only known in a steril* [sic.] *or not well developed stage, as well as several of the fossil species, whose place, at least in some cases, will perhaps for every more be more or less doubtful".*

Considering all of the evidence outlined in the above analysis, one is led to the general conclusion that Foslie's concepts of species and of infraspecific taxa are often vague and superficial, are extremely difficult to evaluate, and are surrounded by many uncertaintites, confusing accounts, and changes of mind. Prior to 1890 about 175 taxa of non-geniculate Corallinaceae had been described. Foslie added 474 new species and forms during the period 1890-1909. Rosenvinge (1917, p. 209), commenting on Foslie's works, remarked that

> *"As we know, this writer repeatedly altered his view concerning the limitation of these difficult species, and his last great work on Northern Melobesieae (Remarks 1905) bears evident witness to his indecision on this point".*

More recently, Taylor (1960, p. 376), in his book on tropical and subtropical algae of the Americas noted

> *"... it is practically impossible to glean from the literature balanced comparative accounts of species at the present",*

and Kraft (1981, p. 19) considered the Corallinaceae to be the largest and the taxonomically most difficult group of Cryptonemiales (the order to which coralline algae generally have been assigned).

In an extended analysis of specific and infraspecific delimination, van Steenis (1957, p. CCXIX) stated

> *"... I have come to the definite conclusion, based on long*

experience, that the majority of 'difficult groups' are not so intended or created in nature, but that the difficulties have been created by the monographers".

With respect to the specific and infraspecific taxonomy of nongeniculate Corallinaceae, there is little doubt that the publications of M.H. Foslie have created more difficulties than those of nearly any other author. This is especially unfortunate, for if Foslie had adopted the more critical and thorough approach of predecessors and contemporaries such as Rosanoff (1866), Solms-Laubach (1881), Kjellman (1883), and Hauck (1883) and had considered the thoughts of Hooker (1853) and Bentham (1875) on specific and infraspecific delineation, these difficulties may never have arisen.

III. A LIST OF FOSLIE PUBLICATIONS WITH DATA ON THE CORALLINACEAE

This list includes only those Foslie publications containing data on the Corallinaceae. Wille (1911) and Printz (1929) furnish information on Foslie's non-coralline papers. Annotations have been provided in cases where papers also have been issued as independently paganated reprints and in cases where possible confusion could occur over publication dates.

1887

Foslie, M. Nye havsalger. Tromsø Mus. Arsh. 10: 176-195, pl. 1-3.

1890

Foslie, M. Contribution to knowledge of the marine algae of Norway. I. East-Finmarken. Tromsø Mus. Arsh., B. 13: 1-183, 3 pl.

1891

Foslie, M. Contribution to knowledge of the marine algae of Norway. II. Species from different tracts. Tromsø Mus. Arsh., B. 14, 36-58, 3 pl.

NOTE: Also issued as an independently paganated reprint (Title page, pages 1-23, plates 1-3); reprint not indexed here. Copies seen at L, LD)

1892a

Foslie, M. Alger og Muslinger. Naturen 16: 17-21.

1892b

Foslie, M. List of the marine algae of the Isle of Wight. K. Norske Vidensk. Selsk. Skr. 1892: 267-282.

NOTE: Also issued as an independently paganated reprint (Cover/Title page, pages 1-16); reprint not indexed here. Copies seen at L, LD)

1893

Foslie, M. Den botaniske Afdelings. K. Norske Vidensk. Selsk. Skr. 1892: IX-X.

1894a

Foslie, M. Den botaniske samling. K. Norske Vidensk. Selsk. Skr. 1893: VIII-IX

1894b

Foslie, M. New or critical norwegian algae. K. Norske Vidensk. Selsk. Skr. 1893: 114-144, pl. 1-3.

NOTE: Also issued as an independently paganated reprint (Cover/Title page, pages 1-31, pl. 1-3); reprint not indexed here. Copies seen at L, LD)

1895a
Foslie, M. The Norwegian forms of Lithothamnion. K. Norske Vidensk. Selsk. Skr. 1894: 29-208, 23 pl.

NOTE: Also issued as an independently paganated reprint (Title page, pages 1-180, plates 1-23); reprint not indexed here. Copies seen at L, LD)

1895b
Foslie, M. New or critical lithothamnia. K. Norske Vidensk. Selsk. Skr. 1895(2): 1-10, 1 pl.

1897a
Foslie, M. Einige bemerkungen ueber Melobesieae. Ber. dt. bot. Ges. 15: 252-260.

1897b
Foslie, M. Weiteres ueber Melobesieae. Ber. dt. bot. Ges. 15: 521-526.

NOTE: Cover page of preprint is dated 1897; the journal issue appeared 25 Jan. 1898.

1897c
Foslie, M. On some lithothamnia. K. Norske Vidensk. Selsk. Skr. 1897(1): 1-20.

1898a
Foslie, M. Systematical survey of the lithothamnia. K. Norske Vidensk. Selsk. Skr. 1898(2): 1-7.

1898b
Foslie, M. List of species of the lithothamnia. K. Norske Vidensk. Selsk Skr. 1898(3): 1-11.

1898c
Foslie, M. Some new or critical lithothamnia. K. Norske Vidensk. Selsk. Skr. 1898(6): 1-19.

1898d
Foslie, M. Remarks on the nomenclature of the lithothamnia. K. Norske Vidensk. Selsk. Skr. 1898(9): 1-7.

1899a
Foslie, M. A visit to Roundstone in April. Ir. Nat. 8: 175-180.

1899b
Foslie, M. Notes on two lithothamnia from Funafuti. K. Norske Vidensk. Selsk. Skr. 1899(2): 1-5.

1900a
Foslie, M. New or critical calcareous algae. K. Norske Vidensk. Selsk. Skr. 1899(5): 1-34.

1900b
Foslie, M. Remarks on Melobesieae in Herbarium Crouan. K. Norske Vidensk. Selsk. Skr. 1899(7): 1-16.

1900c
Foslie, M. Die systematik der Melobesieae. (Eine berichtigung). Ber. dt. bot. Ges. 18: 239-241.

1900d
Foslie, M. Bemerkungen zu F. Hydrich's arbeit 'Die Lithothamnien von Helgoland'. Ber. dt. bot. Ges. 18: 339-340.

1900e
Foslie, M. Melobesia caspica, a new alga. Ofvers. K. svenska Vetensk. Akad. Forh. 1899(9): 131-133.

1900f
Foslie, M. Calcereous algae from Fuegia. Svenska Exped. Magellanslanderna. 3(4): 65-75.

1900g
Foslie, M. Calcereous algae from Funafuti. K. Norske Vidensk. Selsk. Skr. 1900(1): 1-12.

1900h
Foslie, M. Five new calcareous algae. K. Norske Vidensk. Selsk. Skr. 1900(3): 1-6.

1900i
Foslie, M. Revised systematical survey of the Melobesieae. K. Norske Vidensk. Selsk. Skr. 1900(5): 1-22.

1901a
Foslie, M. New melobesieae. K. Norske Vidensk. Selsk. Skr. 1900(6): 1-24.

1901b
Foslie, M. Corallinaceae. In J. Schmidt: Flora of Koh Chang. II. Bot. Tidsskr. 24: 15-22.

1901c
Foslie, M. Three new lithothamnia. K. Norske Vidensk. Selsk. Skr. 1901(1): 1-5.

1901d
Foslie, M. Bieten die Heydrich'schen melobesien-arbeiten eine sichere grundlage? K. Norske Vidensk. Selsk. Skr. 1901(2): 1-28.

1901e
Foslie, M. New forms of lithothamnia. K. Norske Vidensk. Selsk. Skr. 1901(3): 1-6.

1901f
Foslie, M. Den botaniske samling. K. Norske Vidensk. Selsk. Aarsberetn. 1900: 18.

1902a
Foslie, M. New species or forms of melobesieae. K. Norske Vidensk. Selsk. Skr. 1902(2): 1-11.

1902b
Foslie, M. Den botaniske samling. K. Norske Vidensk. Selsk. Aarsberetn. 1901: 19.

1903a
Foslie, M. Two new lithothamnia. K. Norske Vidensk. Selsk. Skr. 1903(2): 1-4.

1903b
Foslie, M. Den botaniske samling. K. Norske Vidensk. Selsk. Aarsberetn. 1902: 23-25.

1903c
Foslie, M. The lithothamnia of the Maldives and Laccadives. Pages 460-471, plates XXIV-XXV In: Gardiner, J.S. ed., The Fauna and Geography of the Maldive and Laccadive Archipelagoes. Vol. 1 (Cambridge University Press, Cambridge, England).

1904a
Foslie, M. Den boraniske samling. K. Norske Vidensk. Selsk. Aarsberetn. 1903: 22.

1904b
Foslie, M. I. Lithothamnioneae, Melobesieae, Mastophoreae. Pages 10-77, plates I-XIII In: Weber van Bosse, A. and Foslie, M.: The Corallinaceae of the Siboga expedition. Siboga Exped. 61: 1-110, pls. 1-16.

1904c
Foslie, M. Algologiske notiser. K. Norske Vidensk. Selsk. Skr. 1904 (2): 1-9.

1904d
Foslie, M. Die lithothamnien des Adriatischen meeres und Marokkos. Wiss. Meeresunters N.F. (Abt. Hegoland) 7(1): 1-40, pl. 1-3.

NOTE: Issued separately as a reprint in 1904; journal version published in 1905. Paganation is the same in both. See also a footnote (Foslie 1905a, pg. 3) for 1904 date.

1905a
Foslie, M. A new squamriacea from the Adriatic and the Mediterranean. K. Norske Vidensk. Selsk. Skr. 1905(1): 1-9.

1905b
Foslie, M. Lithothamnion vardøense, a new alga. K. Norske Vidensk. Selsk. Skr. 1905(2): 1-4.

1905c
Foslie, M. Remarks on northern lithothamnia. K. Norske Vidensk. Selsk. Skr. 1905(3): 1-138.

1905d
Foslie, M. New lithothamnia and systematical remarks. K. Norske Vidensk. Selsk. Skr. 1905(5): 1-8.

1905e
Foslie, M. Den botaniske samling. K. Norske Vidensk. Selsk. Aarsberetn. 1904: 15-18.

1906a
Foslie, M. and Howe, M.A. Two new coralline algae from Culebra, Porto Rico. Bull. Torrey bot. Club 33: 577-580, pl. 23-26.

1906b
Foslie, M. Algologiske notiser II. K. Norske Vidensk. Selsk. Skr. 1906(2): 1-28.

1906c
Foslie, M. Den botaniske samling. K. Norske Vidensk. Selsk. Aarsberetn. 1905: 17-24.

NOTE: Also issued as an independently paganated reprint (pages 1-8, no title pages); reprint not indexed. Copy seen at LD.

1906d
Foslie, M. and Howe, M.A. New American coralline algae. Bull. N.Y. Bot. Gdn. 4(13): (128)-(136), pl. 80-93.

1907a
Foslie, M. Algologiske notiser III. K. Norske Vidensk. Selsk. Skr. 1906(8): 1-34.

1907b
Foslie, M. Algologiske notiser IV. K. Norske Vidensk. Selsk. Skr. 1907(6): 1-30.

1907c
Foslie, M. Antarctic and subantarctic Corallinaceae. Wiss. Ergebn. schwed. Südpolarexped. B IV(5): 1-16, 2 pl.

1907d
Foslie, M. Marine algae. II. Corallinaceae. Natn. Antarct. Exped. (Nat. Hist.) 3: 1-2.

1907e
Foslie, M. The lithothamnia of the Percy Slaten Trust Expedition in H.M.S. Sealark. Trans. Linn. Soc. Lond., Ser. 2 (Bot.) 7: 93-108, pl. 15-16.

1907f
Foslie, M. The lithothamnia. Trans. Linn. Soc. Lond., Ser. 2 (Zool.) 12: 177-192, pl. 19-20. (Text is identical to that of 1970e and 1907e page numbers appear in brackets at the bottom of each page).

1907g
Foslie, M. Den botaniske samling. K. Norske Vidensk. Selsk. Aarsberetn. 1906: 18.

1908a
Foslie, M. Die lithothamnien der deutschen südpolar-expedition 1901-1903. Dt. südpol. Exped. (B) VIII: 205-219.

1908b
Foslie, M. Remarks on Lithothamnion murmanicum. K. Norske Vidensk. Selsk. Skr. 1908(2): 1-8, 2 pl.

1908c
Foslie, M. Bemerkungen ueber kalkalgen. Beih. bot. Zbl. (B). 23(2): 266-272.

1908d
Foslie, M. Algologiske notiser. V. K. Norske Vidensk. Selsk. Skr. 1908(7): 1-20.

1908e
Foslie, M. Pliostroma, a new subgenus of Melobesia. K. Norske Vidensk. Selsk. Skr. 1908(11): 1-7.

1908f
Foslie, M. Nye kalkalger. K. Norske Vidensk. Selsk. Skr. 1908(12): 1-9.

1908g
Foslie, M. Den botaniske samling. K. Norske Vidensk. Selsk. Aarsberetn. 1907: 17-18.

1908h
Foslie, M. Corallinaceae. pp. 209-210. In: Rechninger, K.: Botanische und zoologische ergebnisse einer wissenschaftlichen forschungsreise nach den Samoa - und Salomonsinseln. Denkschr. Akad. Wiss. Wien (B) 81: 197-318.

1909a
Foslie, M. Remarks on two fossil lithothamnia. K. Norske Vidensk. Selsk. Skr. 1909(1): 1-5.

1909b
Foslie, M. Algologiske notiser. VI. K. Norske Vidensk. Selsk. Skr. 1909(2): 1-63.

IV. AN INDEX TO TAXA OF CORALLINACEAE CITED IN FOSLIE'S PUBLICATIONS

The following list constitutes an index to all taxa of Corallinaceae mentioned in the papers listed in Chapter III. Within the index, taxa are listed alphabetically by specific or infraspecific epithet and then by the generic or generic and specific name with which the epithet is associated. Orthography follows that used by Foslie, and care must be exercised to check for possible variants which might be separated from one another in the list (e.g. "crassa" and "crassum"). For each entry, references are provided chronologically and except as noted below, all pages within each paper on which the name appears are listed. The designation "(P)" after a page number indicates the location of the protologue for that taxon; the designation "(E)" after a page number indicates the starting point for an extended account of the taxon. References to figures are included after the final page number of relevant entries. Several of Foslie's longer papers (e.g. 1895a, 1905c) have indexes; references to these index entries have not been included in the present list. Similarly, references to names in figure legends and to page numbers in independently paganated reprints have been excluded. In some papers (e.g. 1897c, 1898c, 1901d), Foslie used the abbreviation "L." for both Lithothamnion and Lithophyllum, and correct generic placement of such "L." taxa is somewhat uncertain. In this list, generic placement is based on clues provided in other Foslie papers (e.g. 1898b, 1900i) published about the same time. One paper (Foslie 1897c) is particularly troublesome since it contains descriptions of a number of new "L." taxa which subsequently (Foslie 1898b) were placed either in Lithothamnion or Lithophyllum or Goniolithon. In the present list, all of these taxa have been entered under Lithothamnion because Foslie (1895a) apparently considered Lithophyllum to be a subgenus of Lithothamnion until 1898 (Foslie 1898a, p. 5).

caribaeum sp. Lithophyllum
1907a: 22(E), 23
1907b: 28
1909b: 11(E)

carpophylli sp. Dermatolithon
1909b: 58

carpophylli sp. Goniolithon
1898b: 8

carpophylli sp. Lithophyllum
1900i: 20
1901e: 6
1909b: 51(E)

carpophylli sp. Melobesia
1897a: 253
1909b: 51

caspica sp. Litholepis
1905d: 6, 7

caspica sp. Melobesia
1900b: 7
1900e: 131(P), 133
1900i: 21
1901a: 22
1905d: 6

caulerpae sp. Heteroderma
1909b: 56

caulerpae sp. Melobesia
1906b: 16(P)

cenomanicum sp. Archaeolithothamnion
1898b: 4
1900i: 8

cephaloides sp. Lithophyllum
1903c: 467
1904b: 59
1909b: 30

cerebelloides sp. Lithophyllum
1903c: 466
1904b: 49

ceylonense sp. Goniolithon
1906c: 20(P)

chalonii sp. Goniolithon
1900i: 16

chalonii f. Goniolithon notarisii
1900a: 21
1909b: 5

chalonii sp. Lithophyllum
1900a: 21
1904d: 22
1909b: 5, 7

chamaedoris sp. Heteroderma
1909b: 57

Continued/...

1905a: 8
1905c: 7, 36, 37, 38, 44, 47, 58, 69, 70, 125
1906b: 12(E), 14
1906d: (128), (130), (132)
1907a: 6, 7
1907b: 21
1907e: 99, 100, 101
1907f: 183, 184, 185
1908a: 214(E)
1908c: 268
1908d: 9
1908f: 3, 4
1908g: 17
1909b: 5

fruticulosum f. Lithothamnion fasciculatum
1895a: 46, 48
1898c: 8
1900i: 13
1901b: 17
1903c: 464
1904b: 19
1904d: 7

fuegiana f. Lithothamnion kerguelenum
1905e: 17(P)
1906b: 9
1907c: 5
1908a: 207

fuegianum sp. Lithophyllum
1901d: 24(E)
1907c: 10
1909b: 20

fuegianum sp. Lithothamnion
1906b: 9(E)
1907c: 3, 5(E), 6; pl. 1, figs 4-6

fumigatum sp. Lithothamnion
1901a: 7(P), 8
1904b: 13
1905e: 16
1907b: 18
1907c: 3, 7

funafutiense sp. Lithothamnion
1901a: 8, 19, 20
1901b: 17(E)
1904b: 18, 19
1904d: 15
1907a: 4
1907b: 18
1907e: 98
1907f: 182

funafutiensis f. Lithothamnion philippii
1899b: 3(P)
1900g: 3, 4, 5(E), 6
1900i: 14
1901b: 17

funduense sp. Lithophyllum
1909b: 38, 40

funduensis f. Lithophyllum oncodes
1909b: 38(E)

gabrieli sp. Lithothamnion
1905d: 3(P)
1907a: 4

galapagense sp. Epilithon
1909b: 55

galapagense f. Gonlolithon frutescens
1907a: 18(P)

Continued/...

truncata f. Lithophyllum africanum
1900h: 3(P), 4
1900i: 18
1909b: 42

tualensis f. Lithothamnion australe
1904b: 24(P), 25, 26, 27, 28, 29; text Fig. 11, pl. 2, Figs 10-17
1907c: 9
1907e: 101
1907f: 185

tuberculata f. Lithothamnion fornicatum
1900i: 12(P)
1905c: 39(E), 40, 41, 46

tuberculata f. Lithothamnion polymorphum
1895a: 108, 114(P), 115, 122, 129; pl. 17, Figs 17-19
1900i: 19

tuberculata f. Phymatolithon polymorphum
1900i: 9
1905c: 76(E), 77
1908d: 10

tuberculatum sp. Lithophyllum
1906b: 9, 21(P), 22
1907a: 27, 33

tuberosa f. Lithophyllum affine
1898b: 9
1900i: 17

tuberosa f. Lithothamnion affine
1897c: 13(P)

tuberosum sp. Lithophyllum
1898b: 9

tuberosum sp. Lithothamnion
1900i: 14

tumidulum sp. Dermatolithon
1909b: 58

tumidulum sp. Lithophyllum
1901e: 5(P), 6
1901f: 18
1905d: 8
1907b: 29
1909b: 50(E)

tumidum sp. Lithophyllum
1901f: 18

turonicum sp. Archaeolithothamnion
1898b: 4
1900i: 8

tusterense sp. Lithothamnion
1905c: 65(P)
1908b: 4, 5

typica f. Clathromorphum circumscriptum
1900i: 10

typica f. Lithophyllum hapalidioides
1905c: 128, 130

typica f. Lithophyllum kaiserii
1903c: 467
1907e: 104
1907f: 188

typica f. Lithophyllum kotschyanum
1909b: 34, 35, 36

typica f. Lithophyllum macrocarpum
1909b: 47

typica f. Lithophyllum moluccense
1901d: 24
1904b: 67, 68, 69, 70

typica f. Lithophyllum okamurae
1909b: 30

typica f. Lithophyllum oncodes
1909b: 38, 40

typica f. Lithophyllum papillosum
1904d: 27

typica f. Lithophyllum polyclonum
1905e: 18
1909b: 52

typica f. Lithophyllum pustulatum
1909b: 46

typica f. Lithophyllum racemus
1898b: 9
1900i: 17
1904d: 23
1907e: 101
1907f: 185

typica f. Lithophyllum yendoi
1906b: 19

typica f. Lithothamnion apiculatum
1895a: 82, 84, 85, 86, 87, 89
1898b: 5
1900i: 12
1905c: 38

typica f. Lithothamnion colliculosum
1905c: 34, 36

typica f. Lithothamnion conchatum
1906b: 6

typica f. Lithothamnion crassum
1895a: 59, 60
1895b: 3, 10
1897a: 258
1897b: 525

typica f. Lithothamnion dehiscens
1895a: 72, 74, 75
1898b: 5
1905c: 39

V. AN INDEX TO TAXA CITED BY PRINTZ (1929, PAGES 28-48).

The following index includes all taxa of Corallinaceae mentioned by Printz (1929, pp. 29-48) in his work on Foslie's collections. Printz (1929) also presented a biographic sketch of Foslie, compiled a nearly complete list of Foslie publications, and summarized Foslie's notes on a series of 75 included plates. This work commonly is cited in bibliographies as "Foslie 1929" or as "Foslie 1929 (ed. H. Printz)", but such citations are misleading since Foslie did not write any of the text. Printz (1929, p. 5) clearly indicates that he (Printz) wrote the entire text including the keys, and also authored the figure legends based on notes left by Foslie. Of the 75 plates in the volume, 30 were prepared prior to Foslie's death, and the remaining 45 were prepared by Printz from specimens in the Foslie collections.

The list presented by Printz (1929, pp. 29-48) includes taxa depicted on the 75 plates and is largely but not entirely alphabetized within each genus. For some entries, various synonyms, presumed misidentifications and names of taxa described by authors other than Foslie also were listed by Printz. Taxa referred by Foslie (1909b, pp. 54-59) to Dermatolithon, Hydrolithon, Lithoporella, and Porolithon are listed under various other genera by Printz (1929), and taxa listed by Foslie (1909b) under Epilithon and Heteroderma have been excluded from consideration by Printz (1929).

The list which follows is organized into a single alphabetical sequence by specific or infraspecific epithet. In some cases, a particular name occurs in several places on the same page of the Printz list, so complete perusal of the cited page is necessary to ensure that all entries are found.

ROBUSTA	f. Lithothamnion fornicatum	1929: 40
RUGOSUM	sp. Lithothamnion	1929: 44, 45, 47
RUPESTRE	sp. Lithophyllum	1929: 37
RUPINCOLA	f. Lithothamnion lichenoides	1929: 43
RUPTILE	sp. Lithothamnion	1929: 45
RUPTILIS	f. Lithothamnion syntrophicum	1929: 45
SAMOENSE	sp. Lithophyllum	1929: 38
SANDVICENSE	sp. Lithophyllum	1929: 38
SANDVICENSIS	f. Lithophyllum coarctatum	1929: 32
SANDVICENSIS	f. Lithophyllum dentatum	1929: 38
SAXATILIS	f. Lithothamnion nodulosum	1929: 44
SCABRIDUM	sp. Goniolithon	1929: 31
SCHMIDTII	sp. Archaeolithothamnion	1929: 28
SCHMITZII	sp. Lithophyllum	1929: 45
SCHMITZII	sp. Lithothamnion	1929: 32, 45
SCUTELLOIDES	sp. Lithothamnion	1929: 45
SEJUNCTUM	sp. Lithothamnion	1929: 45
SETCHELLII	sp. Goniolithon	1929: 31
SETCHELLII	sp. Lithothamnion	1929: 31
SHIOENSE	sp. Lithophyllum	1929: 38
SIAMENSE	sp. Lithothamnion	1929: 45
SIBOGAE	sp. Archaeolithothamnion	1929: 28
SIMILE	sp. Lithophyllum	1929: 38
SIMILIS	f. Lithothamnion norwegicum	1929: 44
SIMULANS	sp. Lithothamnion	1929: 45
SIMULANS	f. Lithothamnion siamense	1929: 45
SOLUBILE	sp. Goniolithon	1929: 31
SOLUBILIS	f. Goniolithon propinquum	1929: 31
SOLUTA	f. Lithothamnion fruticulosum	1929: 46
SOLUTUM	sp. Lithothamnion	1929: 44, 46
SONDERI	sp. Lithothamnion	1929: 44, 45
SORIFERUM	sp. Lithothamnion	1929: 46
SPECIOSA	f. Lithothamnion synanablastum	1929: 46
SPECIOSUM	sp. Lithothamnion	1929: 46
SPECTABILE	sp. Goniolithon	1929: 31
SPHAERICA	f. Lithothamnion fornicatum	1929: 40
SPHAERICA	f. Lithothamnion tophiforme	1929: 46
SPISSUM	sp. Lithothamnion	1929: 46
SQUAMULIFORME	sp. Lithothamnion	1929: 46
SQUAMULOSA	f. Lithothamnion lenormandi	1929: 43
SQUAMULOSUM	sp. Lithothamnion	1929: 43
SQUARROSA	f. Lithothamnion soriferum	1929: 46
SQUARRULOSA	f. Lithothamnion calcareum	1929: 39
SQUARRULOSUM	sp. Lithothamnion	1929: 42
STICTAEFORMIS	f. Lithophyllum expansum	1929: 34
STICTAEFORMIS	sp. Melobesia	1929: 34
STRICTUM	sp. Goniolithon	1929: 31
SUBANTARCTICA	f. Lithophyllum decipiens	1929: 38
SUBANTARCTICUM	sp. Lithophyllum	1929: 38
SUBDURA	f. Lithothamnion philippii	1929: 44

SUBFASTIGIATA	f. Lithothamnion glaciale	1929: 41
SUBFLABELLATA	f. Lithothamnion erubescens	1929: 40
SUBHEMISPHAERICA	f. Lithophyllum gardineri	1929: 34
SUBLAEVIGATA	f. Lithothamnion sonderi	1929: 45
SUBLAEVIS	f. Lithothamnion lenormandi	1929: 43
SUBLAEVIS	f. Phymatolithon polymorphum	1929: 47
SUBPLICATA	f. Lithophyllum marlothii	1929: 35
SUBRAMOSA	f. Lithophyllum oncodes	1929: 36
SUBREDUNCA	f. Lithophyllum kotschyanum	1929: 35
SUBREDUNCUM	sp. Lithophyllum	1929: 35
SUBSIMPLEX	f. Goniolithon displatum	1929: 29
SUBSIMPLEX	f. Lithothamnion calcareum	1929: 39
SUBSIMPLEX	f. Lithothamnion glaciale	1929: 41
SUBSPHAERICA	f. Lithothamnion fornicatum	1929: 40
SUBTENELLUM	sp. Lithophyllum	1929: 38
SUBTILIS	f. Goniolithon frutescens	1929: 30
SUBTILIS	sp. Lithophyllum craspedium	1929: 33
SUBTILIS	f. Lithophyllum fasciculatum	1929: 35
SUBTILIS	f. Lithophyllum kotschyanum	1929: 35
SUBTILIS	f. Lithothamnion indicum	1929: 42
SUPERPOSITUM	sp. Lithothamnion	1929: 46
SYNANABLASTUM	sp. Lithothamnion	1929: 46
SYNTROPHICUM	sp. Lithothamnion	1929: 45, 46
TAHITICA	f. Lithothamnion japonicum	1929: 46
TAHITICUM	sp. Lithothamnion	1929: 46
TALTALENSE	sp. Lithothamnion	1929: 46
TAMIENSE	sp. Lithothamnion	1929: 36
TENUE	sp. Lithophyllum	1929: 46
TENU	sp. Lithothamnion	1929: 46
TENUISSIMUM	sp. Lithothamnion	1929: 46
TESTACEA	f. Phymatolithon compactum	1929: 29
TESTACEUM	sp. Clathromorphum	1929: 29
THELOSTEGIUM	sp. Lithothamnion	1929: 46
TIMORENSE	sp. Archaeolithothamnion	1929: 28
TOPHIFORME	sp. Lithothamnion	1929: 46
TOROSA	f. Lithothamnion glaciale	1929: 47
TOROSA	f. Phymatolithon investiens	1929: 47
TORQUESCENS	sp. Lithophyllum	1929: 36
TORQUESCENS	f. Lithophyllum moluccense	1929: 36
TORTUOSUM	sp. Goniolithon	1929: 38
TORTUOSUM	sp. Lithophyllum	1929: 38
TRINCOMALIENSIS	f. Lithophyllum okamurai	1929: 36
TRUNCATA	f. Lithophyllum africanum	1929: 32
TUALENSIS	f. Lithothamnion australe	1929: 39
TUBERCULATA	f. Lithothamnion fornicatum	1929: 40
TUBERCULATA	f. Phymatolithon polymorphum	1929: 47
TUBERCULATUM	sp. Lithophyllum	1929: 38
TUMIDULUM	sp. Lithophyllum	1929: 33, 38
TUSTERENSE	sp. Lithothamnion	1929: 46
TYPICA	f. Clathromorphum compactum	1929: 29

TYPICA	f. Clathromorphum loculosum	1929: 29
TYPICA	f. Goniolithon accretum	1929: 29
TYPICA	f. Goniolithon dispalatum	1929: 29
TYPICA	f. Goniolithon frutescens	1929: 30
TYPICA	f. Goniolithon laccadivicum	1929: 30
TYPICA	f. Goniolithon mamillare	1929: 30
TYPICA	f. Goniolithon myriocarpum	1929: 30
TYPICA	f. Goniolithon propinquum	1929: 31
TYPICA	f. Goniolithon strictum	1929: 31
TYPICA	f. Lithophyllum aequabile	1929: 31
TYPICA	f. Lithophyllum byssoides	1929: 32
TYPICA	f. Lithophyllum coarctatum	1929: 32
TYPICA	f. Lithophyllum consociatum	1929: 32
TYPICA	f. Lithophyllum craspedium	1929: 33
TYPICA	f. Lithophyllum daedaleum	1929: 34
TYPICA	f. Lithophyllum decussatum	1929: 33
TYPICA	f. Lithophyllum discoideum	1929: 33
TYPICA	f. Lithophyllum expansum	1929: 34
TYPICA	f. Lithophyllum gardineri	1929: 34
TYPICA	f. Lithophyllum hapalidioides	1929: 35
TYPICA	f. Lithophyllum kotschyanum	1929: 35
TYPICA	f. Lithophyllum moluccense	1929: 36
TYPICA	f. Lithophyllum okamurai	1929: 36
TYPICA	f. Lithophyllum oncodes	1929: 36
TYPICA	f. Lithophyllum pachydermum	1929: 37
TYPICA	f. Lithophyllum polyclonum	1929: 37
TYPICA	f. Lithothamnion colliculosum	1929: 39
TYPICA	f. Lithothamnion engelhartii	1929: 40
TYPICA	f. Lithothamnion forniculatum	1929: 41
TYPICA	f. Lithothamnion fruticulosum	1929: 46
TYPICA	f. Lithothamnion funafutiense	1929: 41
TYPICA	f. Lithothamnion glaciale	1929: 41
TYPICA	f. Lithothamnion granii	1929: 41
TYPICA	f. Lithothamnion incertum	1929: 42
TYPICA	f. Lithothamnion indicum	1929: 42
TYPICA	f. Lithothamnion intermedium	1929: 42
TYPICA	f. Lithothamnion lenormandi	1929: 43
TYPICA	f. Lithothamnion mesomorphum	1929: 43
TYPICA	f. Lithothamnion neglectum	1929: 43
TYPICA	f. Lithothamnion nodulosum	1929: 44
TYPICA	f. Lithothamnion occidentale	1929: 44
TYPICA	f. Lithothamnion pacificum	1929: 44
TYPICA	f. Lithothamnion philippii	1929: 44
TYPICA	f. Lithothamnion phymatodeum	1929: 45
TYPICA	f. Lithothamnion prolixum	1929: 45
TYPICA	f. Lithothamnion simulans	1929: 45
TYPICA	f. Lithothamnion solutum	1929: 46
TYPICA	f. Lithothamnion soriferum	1929: 46
TYPICA	f. Lithothamnion tophiforme	1929: 46
TYPICA	f. Lithothamnion ungeri	1929: 46

VI. AN INDEX TO NOMENCLATURAL CHANGES MADE BY ADEY (1970)

As a result of studies of type specimens in the Foslie herbarium, Adey (1970) made extensive nomenclatural changes and undertook to place the Foslie taxa studied into various genera as circumscribed in the same paper. Adey (1970, p. 2) confined his studies to specific types and to types of forms later raised to species by Foslie. Of the 234 taxa considered by Adey, 193 were described originally as species by Foslie, 39 were described originally as forms by Foslie, and two were described by authors other than Foslie. Adey's study remains the only attempt to update Foslie's taxa en masse, but covers less than half the total number of taxa Foslie described (see Table 2, p. 9).

The list which follows is an alphabetical index (by specific or infraspecific epithet) to the taxa dealt with by Adey (1970) and is provided here to augment and to facilitate use of the data provided in Chapters IV and V. For each entry, the Foslie basionym and publication data are presented on the left and the generic disposition by Adey (1970) is given on the right. Adey (1970) provided no index of this sort but did deal with names alphabetically within each of the 15 genera he covered.

ABSIMILE
Lithophyllum, Foslie 1907b: 27 = Pseudolithophyllum, Adey 1970: 12

ABSONUM
Lithothamnion, Foslie 1907b: 6 = Leptophytum, Adey 1970: 29

ACANTHINUM
Lithophyllum, Foslie 1907a: 26 = Neogoniolithon, Adey 1970: 8

ACCENDENS
Lithophyllum, Foslie 1907a: 25 = Pseudolithophyllum, Adey 1970: 12

ACCLINE
Lithothamnion, Foslie 1907b: 20 = Lithothamnium, Adey 1970: 19

ACCOLA
Litholepis, Foslie 1907a: 22 = Lithoporella, Adey 1970: 14

ACCRETUM
Goniolithon, Foslie & Howe 1906d: (131) = Neogoniolithon, Adey 1970: 8

ACERVATUM
Lithothamnion, Foslie 1907b: 4 = Phymatolithon, Adey 1970: 28

ACROPETUM
Goniolithon, Foslie and Howe 1906a: 577 = Neogoniolithon, Adey 1970: 8

AEMULANS
Lithothamnion fruticulosum f. aemulans Foslie & Howe 1906d: (130) = Mesophyllum aemulans, Adey 1970: 22

AEQUABILE
Lithophyllum discoideum f. aequabilis Foslie 1905e: 12 = Pseudolithophyllum aequabile, Adey 1970: 17

AEQUINOCTIALE
Lithophyllum, Foslie 1909b: 46 = Porolithon, Adey 1970: 10

AEQUUM
Lithophyllum, Foslie 1907a: 23 = Pseudolithophyllum, Adey 1970: 12

AFFINE
Goniolithon, Foslie 1907b: 22 = Neogoniolithon, Adey 1970: 8

AFFINIS
Litholepis, Foslie 1906b: 17 = Heteroderma, Adey 1970: 16

AFRICANUM
Archaeolithothamnion, Foslie 1906c: 19 = Archaeolithothamnium, Adey 1970: 17

AFRICANUM
Lithophyllum, Foslie 1900h: 3 = Porolithon, Adey 1970: 10

ANDRUSSOWII
Lithophyllum, Foslie 1898c: 16 = Lithophyllum, Adey 1970: 4

ANINAE
Lithophyllum, Foslie 1907b: 28 = Lithophyllum, Adey 1970: 4

ANNULATUM
Lithothamnion, Foslie 1906c: 18 = Mesophyllum, Adey 1970: 22

ANTILLARUM
Lithophyllum, Foslie & Howe 1906a: 579 = Porolithon, Adey 1970: 10

ASCRIPTICIUM
Lithophyllum pustulatum f. ascripticium Foslie 1907a: 34 = Tenarea ascripticia, Adey 1970: 6

ASPERULUM
Lithothamnion repandum f. asperula Foslie 1906b: 5 = Leptophytum asperulum, Adey 1970: 29

ASSITUM
Goniolithon, Foslie 1907b: 23 = Neogoniolithon, Adey 1970: 8

ATLANTICA
Mastophora, Foslie 1906b: 27 = Lithoporella, Adey 1970: 14

AUCKLANDICUM
Lithothamnion fumigatum f. aucklandicum Foslie 1905e: 16 = Mesophyllum aucklandicum, Adey 1970: 22

AUSTRALASICUM
Archeolithothamnion, Foslie 1907a: 12 = Archaeolithothamnium, Adey 1970: 18

AUSTRALE
Lithothamnion coralloides f. australis Foslie 1895a: 90 = Lithothamnium australe, Adey 1970: 19

BANDANUM
Lithothamnion, Foslie 1904b: 12 = Lithothamnium, Adey 1970: 19

BERMUDENSE
Lithophyllum, Foslie & Howe 1906d: (132) = Tenarea, Adey 1970: 6

BERMUDENSIS
Melobesia, Foslie 1901a: 22 = Lithoporella, Adey 1970: 15

BISPORUM
Lithothamnion, Foslie 1906c: 18 = Leptophytum, Adey 1970: 30

BORGESENII
Goniolithon, Foslie 1901a: 19 = Hydrolithon, Adey 1970: 11

BORNETII
Lithothamnion, Foslie 1898c: 9 = Leptophytum, Adey 1970: 30

BRACHYCLADUM
Lithothamnion, Foslie 1900a: 3 = Mesophyllum, Adey 1970: 22

BRASILIENSE
Lithothamnion, Foslie 1900a: 4 = Lithothamnium, Adey 1970: 19

BREVIAXE
Lithothamnion, Foslie 1895a: 44 = Lithothamnium, Adey 1970: 19

BREVICLAVIUM
Goniolithon, Foslie 1907a: 20 = Hydrolithon, Adey 1970: 11

CALIFORNICUM
Lithothamnion, Foslie 1900h: 3 = Lithothamnium, Adey 1970: 19

CANARIENSE
Lithothamnion, Foslie 1906c: 17 = Mesophyllum, Adey 1970: 22

CANESCENS
Melobesia, Foslie 1900h: 6 = Tenarea, Adey 1970: 7

CARIBAEUM
Lithophyllum decipiens f. caribaeum Foslie 1906b: 18 = Neogoniolithon caribaeum, Adey 1970: 8

CASPICA
Melobesia, Foslie 1900e: 131 = Tenarea, Adey 1970: 7

CAULERPAE
Melobesia, Foslie 1906b: 16 = Heteroderma, Adey 1970: 16

CEYLONENSE
Goniolithon, Foslie 1906c: 20 = Neogoniolithon, Adey 1970: 8

CHAMAEDORIS
Lithophyllum, Foslie & Howe 1906d: (134) = Lithophyllum, Adey 1970: 5

CHATAMENSE
Lithothamnion, Foslie 1906c: 18 = Mesophyllum, Adey 1970: 23

CHILENSE
Archeolithothamnion, Foslie 1904c: 6 = Archeolithothamnium, Adey 1970: 18

COARCTATUM
Lithophyllum, Foslie 1907a: 31 = Porolithon, Adey 1970: 10

COLLICULOSUM
Lithothamnion, Foslie 1891: 43 = *Lithothamnium*, Adey 1970: 19

CONCHATUM
Lithothamnion, Foslie 1902a: 6 = *Mesophyllum*, Adey 1970: 23

CONGESTUM
Goniolithon, Foslie 1898c: 13 = *Lithophyllum*, Adey 1970: 5

CONJUNCTA
Mastophora, Foslie 1907b: 30 = *Lithoporella*, Adey 1970: 15

CONSOCIATUM
Lithophyllum, Foslie 1905e: 15 = *Pseudolithophyllum*, Adey 1970: 12

CONSPECTA
Lithophyllum, Foslie 1907b: 29 = *Tenarea*, Adey 1970: 7

COULMANICUM
Lithothamnion, Foslie 1905e: 16 = *Leptophytum*, Adey 1970: 30

CRASPEDIUM
Lithophyllum, Foslie 1900a: 26 = *Porolithon*, Adey 1970: 10

CRENULATUM
Lithothamnion magellanicum f. *crenulatum* Foslie 1905e: 17 = *Mesophyllum crenulatum*, Adey 1970: 23

CRISPESCENS
Lithothamnion simulans f. *crispescens* Foslie 1904b: 16 = *Mesophyllum crispescens*, Adey 1970: 23

CROUANI
Lithophyllum, Foslie 1898c: 17 = *Lithophyllum*, Adey 1970: 5

CYMODOCEAE
Melobesia, Foslie 1901a: 23 = *Heteroderma*, Adey 1970: 16

CYSTOCARPIDEUM
Lithothamnion, Foslie 1906b: 7 = *Mesophyllum*, Adey 1970: 23

DAEDALEUM
Lithophyllum, Foslie & Howe 1906d: (133) = *Lithophyllum*, Adey 1970: 5

DECIPIENS
Lithothamnion, Foslie 1897c: 20 = *Hydrolithon*, Adey 1970: 11

DETRUSUM
Lithophyllum, Foslie 1906b: 21 = *Pseudolithophyllum*, Adey 1970: 12

DIMOTUM
Archeolithothamnion, Foslie & Howe 1906d: (128) = *Archeolithothamnium*, Adey 1970: 18

DISCOIDEUM
Lithophyllum, Foslie 1900f: 73 = *Pseudolithophyllum*, Adey 1970: 12

DISCREPANS
Lithothamnion, Foslie 1907b: 8 = *Mesophyllum*, Adey 1970: 23

DISPALATUM
Goniolithon, Foslie 1908f: 6 = *Neogoniolithon*, Adey 1970: 8

DISPAR
Lithophyllum tumidulum f. *dispar* Foslie 1907b: 29 = *Tenarea dispar*, Adey 1970: 7

DURUM
Archeolithothamnion, Foslie 1907a: 11 = *Archeolithothamnium*, Adey 1970: 18

ECTOCARPON
Lithothamnion, Foslie 1907b: 11 = Mesophyllum, Adey 1970: 23

ELATOCARPUM
Goniolithon, Foslie 1900a: 23 = Lithothamnion, Adey 1970: 19

ENGELHARTI
Lithothamnion, Foslie 1900a: 18 = Mesophyllum, Adey 1970: 23

EROSUM
Lithophyllum, Foslie 1906b: 20 = Neogoniolithon, Adey 1970: 8

ERUBESCENS
Lithothamnion, Foslie 1900a: 9 = Mesophyllum, Adey 1970: 23

EXASPERATUM
Lithothamnion, Foslie 1907a: 9 = Mesophyllum, Adey 1970: 24

EXPLANATA
Lithophyllum, Foslie 1906b: 25 = Heteroderma, Adey 1970: 16

FALKLANDICUM
Lithophyllum marlothii f. falklandicum Foslie 1905e: 17 = Pseudolithophyllum falklandicum, Adey 1970: 12

FARLOWII
Lithophyllum, Foslie 1901a: 12 = Pseudolithophyllum neofarlowii, Adey 1970: 13

FEROX
Lithothamnion, Foslie 1907b: 7 = Mesophyllum, Adey 1970: 24

FETUM
Lithophyllum, Foslie 1907a: 24 = Pseudolithophyllum, Adey 1970: 13

FINITIMUM
Goniolithon setchellii f. finitima Foslie 1907a: 15 = Neogoniolithon finitimum, Adey 1970: 8

FLORIDANUM
Lithothamnion, Foslie 1906b: 11 = Mesophyllum, Adey 1970: 24

FORNICATUM
Lithothamnion, Foslie 1891: 38 = Lithothamnium, Adey 1970: 20

FRAGILISSIMUM
Lithothamnion, Foslie 1904b: 13 = Mesophyllum, Adey 1970: 24

FRETENSE
Lithothamnion, Foslie 1907a: 8 = Lithothamnium, Adey 1970: 20

FRUTESCENS
Goniolithon, Foslie 1900g: 9 = Neogoniolithon, Adey 1970: 9

FUEGIANUM
Lithothamnion kerguelenum f. fuegiana Foslie 1905e: 17 = Mesophyllum fuegianum, Adey 1970: 24

FUMIGATUM
Lithothamnion, Foslie 1901a: 7 = Mesophyllum, Adey 1970: 24

FUNAFUTIENSE
Lithothamnion philippi f. funafutiensis Foslie 1899b: 3 = Lithothamnium funafutiense, Adey 1970: 20

GABRIELI
Lithothamnion, Foslie 1905d: 3 = Mesophyllum, Adey 1970: 24

GALAPAGENSIS
Lithothamnion, Foslie 1907a: 9 = Melobesia, Adey 1970: 30

GARDINERI
Lithophyllum, Foslie 1907a: 30 = Porolithon, Adey 1970: 10

GIBBOSUM
Lithothamnion, Foslie 1907a: 7 = Lithothamnium, Adey 1970: 20

GIBBSII
Melobesia, Foslie 1907b: 26 = Heteroderma, Adey 1970: 16

GRACILE
Lithophyllum, Foslie 1907b: 28 = Lithophyllum, Adey 1970: 5

GRANII
Lithothamnion flabellatum f. granii Foslie 1895a: 98 = Lithothamnium granii, Adey 1970: 20

GRANULIFERUM
Lithothamnion, Foslie 1905e: 16 = Leptophytum, Adey 1970: 30

GRUMOSUM
Lithothamnion, Foslie 1897c: 16 = Lithophyllum, Adey 1970: 5

HAPTERICOLUM
Lithothamnion, Foslie 1906b: 8 = Mesophyllum, Adey 1970: 24

HARIOTII
Goniolithon, Foslie 1907a: 13 = Neogoniolithon, Adey 1970: 9

HETEROCLADUM
Lithothamnion, Foslie 1905e: 16 = Lithothamnium, Adey 1970: 20

HETEROMORPHUM
Lithothamnion brasiliense f. heteromorpha, Foslie 1900a: 4 = Lithothamnium heteromorphum, Adey 1970: 20

HYPERELLUM
Lithophyllum, Foslie 1900a: 27 = Pseudolithophyllum, Adey 1970: 13

IMBRICATUM
See Adey 1970, p.24. This does not involve a taxon described by Foslie.

IMITANS
Lithophyllum, Foslie 1909b: 13 = Lithophyllum, Adey 1970: 5

IMPAR
Lithophyllum, Foslie 1909b: 13 = Pseudolithophyllum, Adey 1970: 13

IMPROCERUM
Goniolithon, Foslie 1907b: 24 = Hydrolithon, Adey 1970: 11

INCERTUM
Lithothamnion, Foslie 1904c: 5 = Mesophyllum, Adey 1970: 24

INCISA
Lithothamnion patena f. incisa Foslie 1906b: 6 = Mesophyllum incisum, Adey 1970: 24

INCONSPICUUM
Lithothamnion, Foslie 1907b: 19 = Mesophyllum, Adey 1970: 24

INCRASSATUM
Lithophyllum incrustans f. incrassatum 1900a: 29 = Lithophyllum incrassatum, Adey 1970: 5

INDICA
Litholepis, Foslie 1907a: 21 = Lithoporella, Adey 1970: 15

INOPS
Lithophyllum, Foslie 1907b: 27 = Phymatolithon, Adey 1970: 28

INSIGNE
Lithothamnion, Foslie 1906b: 9 = Mesophyllum, Adey 1970: 24, 25

INTERMEDIUM
Lithophyllum, Foslie 1906b: 23 = Lithophyllum, Adey 1970: 5
non Lithothamnium (see Adey 1970, p.20)

INVESTIENS
Lithothamnion, Foslie 1895a: 157 = Phymatolithon, Adey 1970: 28

IRREGULARE
Lithothamnion, Foslie 1907a: 6 = Pseudolithophyllum, Adey 1970: 13

JAPONICUM
Lithothamnion, Foslie 1900a: 6 = Lithothamnium, Adey 1970: 20

JUGATUM
Lithophyllum, Foslie 1906b: 26 = Pseudolithophyllum, Adey 1970: 13

LACCADIVICUM
Goniolithon brassica-florida f. laccadivica, Foslie 1903c: 469 = Neogoniolithon laccadivicum, Adey 1970: 9

LAEVIGATUM
Lithothamnion, Foslie 1895a: 167 = Phymatolithon, Adey 1970: 29

LAMELLATUM
Lithothamnion, Foslie 1903a: 4 = Mesophyllum, Adey 1970: 25

LAPIDEA
Mastophora, Foslie 1906b: 27 = Lithoporella, Adey 1970: 15

LEMNISCATUM
Lithothamnion, Foslie 1907b: 11 = Mesophyllum, Adey 1970: 25

LEPTURA
Melobesia, Foslie 1906b: 16 = Heteroderma, Adey 1970: 16

LIMITATA
Melobesia lejolisii f. limitata, Foslie 1905c: 102 = Heteroderma limitata, Adey 1970: 16

MACROBLASTUM
Lithothamnion, Foslie 1897c: 16 = Mesophyllum, Adey 1970: 25

MADAGASCARIENSIS
Lithothamnion erubescens f. madagascariensis, Foslie 1901e: 3 = Mesophyllum madagascariensis, Adey 1970: 25

MALDIVICUM
Lithothamnion, Foslie 1903b: 23 = Lithothamnium, Adey 1970: 20

MARGINATA
Melobesia, Foslie 1902a: 10 = Melobesia, Adey 1970: 30

MAURITIANUM
Lithophyllum, Foslie 1907a: 32 = Lithophyllum, Adey 1970: 5

MEDITERRANEA
Litholepis, Foslie 1906b: 17 = Lithoporella, Adey 1970: 15

MEGALOCYSTUM
Goniolithon, Foslie 1904b: 48 = Neogoniolithon, Adey 1970: 9

MELOBESIOIDES
Mastophora, Foslie 1903b: 24 = Lithoporella, Adey 1970: 15

MESOMORPHUM
Lithothamnion, Foslie 1901a: 5 = Mesophyllum, Adey 1970: 25

MINUTULA
Melobesia, Foslie 1904c: 8 = Heteroderma, Adey 1970: 16

MIRABLE
Archeolithothamnion, Foslie 1898c: 3 = Lithothamnium, Adey 1970: 20

MISAKIENSE
Goniolithon, Foslie 1905d: 4 = Neogoniolithon, Adey 1970: 9

MOLUCCENSE
Lithothamnion, Foslie 1897c: 12 = Lithophyllum, Adey 1970: 5

MONOSTROMATICUM
Lithothamnion, Foslie 1903a: 3 = Heteroderma, Adey 1970: 16

MONTEREYICUM
Lithothamnion, Foslie 1906b: 14 = Lithothamnium, Adey 1970: 21

MUNITUM
Lithophyllum, Foslie & Howe 1906d: (132) = Neogoniolithon, Adey 1970: 9

MURICATUM
Phymatolithon, Foslie 1906c: 19 = Phymatolithon, Adey 1970: 29

MYRIOCARPUM
Lithothamnion, Foslie 1897c: 19 = Neogoniolithon, Adey 1970: 9

NATALENSE
Lithophyllum, Foslie 1907a: 24 = Pseudolithophyllum, Adey 1970: 13

NEGLECTUM
Lithothamnion mulleri f. neglecta, Foslie 1900f: 69 = Mesophyllum neglectum, Adey 1970: 25

NEOFARLOWII
See FARLOWII

NITIDUM
Lithothamnion, Foslie 1901e: 4 = Mesophyllum, Adey 1970: 25

NODULOSUM
Lithothamnion, Foslie 1895a: 144 = Lithothamnium, Adey 1970: 21

NOTATUM
Lithothamnion, Foslie 1906b: 4 = Phymatolithon, Adey 1970: 29

OBTECTULUM
Lithothamnion kerguelenum f. obtectula Foslie 1898c: 10 = Clathromorphum obtectulum, Adey 1970: 27

OCCIDENTALE
Lithothamnion fruticulosum f. occidentalis Foslie 1906b: 12 = Lithothamnium occidentale, Adey 1970: 21

OCELLATUM
Lithothamnion, Foslie 1895a: 140 = Phymatolithon, Adey 1970: 29

OKAMURAI
Lithophyllum, Foslie 1900h: 4 = Lithophyllum, Adey 1970: 5

OLIGOCARPUM
Lithophyllum, Foslie 1906c: 22 = Porolithon, Adey 1970: 10

ORBICULATUM
Lithothamnion, Foslie 1895a: 171 = Lithophyllum, Adey 1970: 5

OROTAVICUM
Goniolithon, Foslie 1906c: 20 = Neogoniolithon, Adey 1970: 9

PACHYDERMUM
Lithophyllum onkodes f. pachydermum, Foslie 1904c: 5 = Porolithon pachydermum, Adey 1970: 11

PACIFICA
Goniolithon notarisii f. pacifica Foslie 1907a: 12 = Neogoniolithon pacificum, Adey 1970: 9

PACIFICUM
Lithothamnion sonderi f. pacifica, Foslie 1902a: 4 = Lithothamnion pacificum, Adey 1970: 21

PALLESCENS
Lithothamnion, Foslie 1895b: 4 = Lithophyllum, Adey 1970: 5

PARCUM
Lithothamnion, Foslie 1907b: 14 = Clathromorphum, Adey 1970: 27, 28

PHILIPPI
Lithothamnion, Foslie 1897c: 7 = Mesophyllum, Adey 1970: 25

PHYMATODEUM
Lithothamnion, Foslie 1902a: 3 = Lithothamnion, Adey 1970: 21

PLATYPHYLLUM
Goniolithon, Foslie 1898c: 13 = Lithophyllum, Adey 1970: 5

POLYCEPHALUM
Lithophyllum, Foslie 1905e: 16 = Tenarea, Adey 1970: 7

POLYCLONA
Lithophyllum, Foslie 1905e: 18 = Tenarea, Adey 1970: 7

PRAETEXTATUM
Lithophyllum, Foslie 1907a: 31 = Porolithon, Adey 1970: 11

PROBOSCIDEUM
Lithothamnion, Foslie 1897c: 14 = Lithophyllum, Adey 1970: 5

PROLIFER
Lithothamnion, Foslie 1904b: 18 = Mesophyllum, Adey 1970: 25

PROLIXUM
Lithothamnion, Foslie 1908d: 9 = Mesophyllum, Adey 1970: 25

PROPONTIDIS
Lithothamnion, Foslie 1898c: 4 = Lithothamnion, Adey 1970: 21

PROTOTYPUM
Lithothamnion, Foslie 1897c: 18 = Tenarea, Adey 1970: 7

PTYCHOIDES
Lithophyllum okamurai f. ptychoides, Foslie 1907a: 29 = Pseudolithophyllum ptychoides, Adey 1970: 13

PUNCTATUM
Lithophyllum, Foslie 1906c: 22 = Lithophyllum, Adey 1970: 5

PURPURASCENS
Lithothamnion funafutiense f. purpurascens, Foslie 1901b: 18 = Mesophyllum purpurascens, Adey 1970: 26

RASILE
Lithophyllum, Foslie 1907a: 34 = Tenarea, Adey 1970: 7

RECLINATUM
Lithothamnion conchatum f. reclinata, Foslie 1906b: 6 = Clathromorphum reclinatum, Adey 1970: 28

REINBOLDII
Lithophyllum, Foslie 1901c: 5 = Hydrolithon, Adey 1970: 11

REPANDUM
Lithothamnion, Foslie 1904c: 4 = Leptophytum, Adey 1970: 30

RETUSUM
Lithothamnion, Foslie 1897c: 15 = Lithophyllum, Adey 1970: 5

RHIZOPHORAE
Goniolithon, Foslie & Howe 1906d: (130) = Neogoniolithon, Adey 1970: 9

ROSANOFFII
Lithothamnion, Foslie 1908d: 5 = Melobesia, Adey 1970: 30

RUGOSUM
Lithothamnion, Foslie 1900f: 66 = Lithothamnion, Adey 1970: 21

RUPESTRE
Lithophyllum, Foslie 1907a: 26 = Mesophyllum, 1970: 26

RUPTILE
Lithothamnion syntrophicum f. ruptilis, Foslie 1905e: 18 = Lithothamnion ruptile, Adey 1970: 21

SAMOENSE
Lithophyllum, Foslie 1906b: 20 = Pseudolithophyllum, Adey 1970: 13

SANDVICENSE
Lithophyllum dentatum f. sandviciensis Foslie 1901a: 11 = Porolithon scandvicense, Adey 1970: 11

SARGASSI
Melobesia marginata f. sargassi Foslie 1904a: 22 = Heteroderma sargassi, Adey 1970: 17

SAUVAGEAUI
Litholepis, Foslie 1905d: 6 = Lithoporella, Adey 1970: 15

SCABRIDUM
Goniolithon, Foslie 1907a: 13 = Neogoniolithon, Adey 1970: 9

SCHMIDTII
Archeolithothamnion, Foslie 1901b: 16 = Archeolithothamnium, Adey 1970: 18

SEJUNCTUM
Lithothamnion, Foslie 1906b: 3 = Lithothamnium, Adey 1970: 21

SETCHELLII
Lithothamnion, Foslie 1897c: 18 = Neogoniolithon, Adey 1970: 9

SHIOENSE
Lithophyllum, Foslie 1906c: 23 = Pseudolithophyllum, Adey 1970: 13

SIAMENSE
Lithothamnion, Foslie 1901b: 19 = Mesophyllum, Adey 1970: 26

SIBOGAE
Archeolithothamnion, Foslie 1901c: 3 = Archeolithothamnium, Adey 1970: 18

SIMILE
Lithophyllum, Foslie 1909b: 30 = Lithophyllum, Adey 1970: 6

SIMULANS
Lithothamnion siamense f. simulans, Foslie 1901b: 19 = Mesophyllum simulans, Adey 1970: 26

SOLUBILE
Goniolithon, Foslie 1907b: 21 = Neogoniolithon, Adey 1970: 9

SPECIOSUM
Lithothamnion synanablastum f. speciosa, Foslie 1900a: 11 = Mesophyllum speciosum, Adey 1970: 26

SPECTABILE
Goniolithon, Foslie 1901a: 16 = Neogoniolithon, Adey 1970: 9, 10

SPISSUM
Lithothamnion, Foslie 1907b: 19 = Lithothamnium, Adey 1970: 21

SQUAMULIFORME
Lithothamnion, Foslie 1905e: 17 = Mesophyllum, Adey 1970: 26

STRICTUM
Goniolithon, Foslie 1901a: 14 = Neogoniolithon, Adey 1970: 10

SUBANTARCTICUM
Lithophyllum decipiens f. subantarcticum Foslie 1906b: 18 = Pseudolithophyllum subantarctum, Adey 1970: 14

SUBTENELLUM
Goniolithon, Foslie 1898c: 11 = Lithophyllum, Adey 1970: 6

SUBTILISSIMA
Melobesia, Foslie 1904b: 55 = Heteroderma, Adey 1970: 17

SUPERPOSITUM
Lithothamnion, Foslie 1900a: 8 = Mesophyllum, Adey 1970: 26

SYNTROPHICUM
Lithothamnion, Foslie 1901a: 6 = Mesophyllum, Adey 1970: 26

TAHITICUM
Lithothamnion japonicum f. tahitica, Foslie 1907a: 8 = Lithothamnium tahiticum, Adey 1970: 21

TALTALENSE
Lithothamnion, Foslie 1906b: 4 = Leptophytum, Adey 1970: 30

TASMANICUM
Lithophyllum zostericolum f. tasmanicum, Foslie 1907a: 33 = Pseudolithophyllum tasmanicum, Adey 1970: 14

TENUISSIMUM
Lithothamnion, Foslie 1900a: 20 = Phymatolithon, Adey 1970: 29

THELOSTEGIUM
Lithothamnion, Foslie 1907a: 4 = Mesophyllum, Adey 1970: 26

TIMORENSE
Archeolithothamnion, Foslie 1904b: 42 = Archeolithothamnium, Adey 1970: 18

TUBERCULATUM
Lithophyllum, Foslie 1906b: 21 = Pseudolithophyllum, Adey 1970: 14

TUMIDULUM
Lithophyllum, Foslie 1901e: 5 = Tenarea, Adey 1970: 7

VALENS
Lithothamnion, Foslie 1909b: 3 = Lithothamnium, Adey 1970: 21

VALIDUM
Lithophyllum okamurai f. valida, Foslie 1906c: 23 = Lithophyllum validum, Adey 1970: 6

VALIDUM
Lithothamnion rugulosum f. validum Foslie 1901a: 4 = Lithothamnium validum, Adey 1970: 21

VARIABILE
Lithothamnion, Foslie 1906b: 10 = Mesophyllum, Adey 1970: 26

VERRUCOSUM
Goniolithon, Foslie 1900a: 24 = Neogoniolithon, Adey 1970: 10

VERSABILE
Goniolithon, Foslie 1907a: 15 = Neogoniolithon, Adey 1970: 10

VERSICOLOR
Lithothamnion, Foslie 1907a: 3 = Mesophyllum, Adey 1970: 26

VESCUM
Lithothamnion, Foslie 1907b: 3 = Mesophyllum, Adey 1970: 26, 27

WHIDBEYENSE
Lithophyllum, Foslie 1906c: 21 = Mesophyllum, Adey 1970: 27

YENDOI
Goniolithon, Foslie 1900a: 25 = Pseudolithophyllum, Adey 1970: 14

YESSOENSE
Lithophyllum, Foslie 1909b: 17 = Lithophyllum, Adey 1970: 6

ZONATOSPORUM
Archeolithothamnion, Foslie 1906b: 14 = Archeolithothamnium, Adey 1970: 18

ZOSTERICOLA
Lithophyllum, Foslie 1900h: 5 = Heteroderma, Adey 1970: 17

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39

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STUDIES ON AUSTRALIAN MANGROVE ALGAE. III. VICTORIAN COMMUNITIES: STRUCTURE AND RECOLONIZATION IN WESTERN PORT BAY

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Abstract: The algal communities associated with *Avicennia* pneumatophores in Western Port Bay, Victoria, Australia (145°E:38°S) are composed primarily of the red algae *Bostrychia*, *Caloglossa* and *Catenella*. Trends from seaward to landward indicate a decrease in frequency of occurrence, relative cover, and mean absolute biomass for all algal genera but differing trends occur for each genus in terms of relative biomass, and this is reflected in associated pattern analyses. In terms of vertical community structure, all algae occur most frequently in the 5–10 cm segment above mudline, whereas above 20 cm, values for all measured parameters decline. Vertical structure in the seaward and landward regions is compared, but pattern analyses indicate that no biologically distinctive pattern is present. Deliberately denuded pneumatophores quickly become recolonized; greater algal development occurs above 10 cm above the mudline than below 10 cm, and the new community is differently structured.

Key words: mangrove algae; mangrove recolonization; algal community structure; *Auicennia*; *Bostrychia*; *Caloglossa*; *Catenella*

INTRODUCTION

Recent reviews (Chapman, 1976; Saenger *et al.*, 1977; King, 1981; Clough, 1982) dealing with Australian mangrove ecosystems provide no quantitative data on algal community structure or on algal recolonization. However, Beanland & Woelkerling (1983) have reported that the frequency distribution of mangrove-associated algae in South Australia may be influenced by the cover given by the canopy. Although Post (see Post, 1963 for a review) has provided a series of general descriptive accounts of mangrove algal communities, investigations of algal community structure elsewhere apparently have been restricted to comparisons of the intertidal and sublittoral algal floras on stilt roots of *Rhizophora mangle* in tropical Puerto Rico. Almodovar & Biebl (1962) concluded that vertical zonation of algae on *R. mangle* stilt roots reflected a tolerance to varying salt concentrations, whilst Biebl (1962) observed that algal species growing on the intertidal portions of stilt roots generally were more resistant to osmotic

shock, drying, and temperature extremes than were algal species growing on sublittoral portions of stilt roots. Almodovar & Pagan (1971) later found that removal of shade caused disappearance of algae from the intertidal portions of stilt roots and lowered the species diversity of the sublittoral flora. Burkholder & Almodovar (1974) also provided biomass information and certain physiological data on algal epiphytes of *Rhizophora* but did not relate these data to algal zonation.

Although mangrove algae are subject to grazing by marine animals (Schodde *et al.*, 1982) and are thought to provide an important energy source in mangrove ecosystem food webs (Kuenzler, 1974), investigations into the nature of algal recolonization of denuded mangrove roots appear to be lacking entirely. Various authors (e.g. Stephenson *et al.*, 1931; Macnae & Kalk; 1962, Milward, 1982) have noted that tropical and temperate mangrove algae can be colonized extensively by various animals, but data on the effects of such colonization have not been provided. Thus, little information appears to be available either on the nature or the rate of algal recolonization of mangrove roots subjected to disruptive forces.

This paper outlines results of investigations into algal community structure and algal recolonization within the mainly intertidal mangrove ecosystem of Western Port Bay, Victoria, Australia, and follows an earlier report (Davey & Woelkerling, 1980) on algal community composition and distribution within Victorian mangroves generally. One aim of this study has been to determine what trends, if any, of horizontal and vertical distribution of algae occur on the pneumatophores of *Avicennia marina* (Forster) Vierhapper in terms of frequency and cover, relative biomass and absolute biomass. As well, algal recolonization of deliberately denuded pneumatophores in terms of changes in frequency of occurrence, absolute biomass, and relative biomass was investigated over an 18-wk period. Possible influences of salinity and relative light intensity on algal distribution are also considered.

Materials and Methods

Community structure studies were undertaken at seven localities (Table I) in Western Port Bay during 1977 (see Davey & Woelkerling, 1980, Fig. 1 for map) which were devoid of direct estuarine influence and which possessed mangrove stands up to 200 m wide at the points of sampling. Using random, paired coordinates, two or four entire pneumatophores proximate to five equidistant base points along a straight line transect traversing the entire mangrove fringe (Fig. 1) were collected at each study site. In all, 16 pneumatophores were chosen in which four comprised the seaward quarter (A), eight the central half (B and C), and four the landward quarter (D) of each transect. All pneumatophores were preserved in 1 : 10 : : formalin sea water, and returned to the laboratory for subsequent analyses.

Initial inspections of pneumatophores indicated that virtually all of the algal material present belonged to the red algal genera *Bostrychia*, *Caloglossa* and *Catenella* and that

other algal taxa occurred only in isolated instances, usually as single plants. Consequently, collection of detailed information was confined to the three above-mentioned genera. *Caloglossa leprieurii* (Montagne) J. Agardh and *Catenella nipae* Zanardini were the sole species in their respective genera, but *Bostrychia* species included *B. intricata* (Bory) Montagne, *B. moritziana* (Sonder in Kuetzing) J. Agardh, and *B. radicans* (Montagne) Montagne, which grew intermixed so thoroughly that species separation for data collection and analysis proved impractical. Consequently, all data are reported at the generic level.

TABLE I

Study sites for algal community structure and recolonization investigations: CS, community structure; R, recolonization.

Locality	Mangrove fringe width (m)[a]	Maximum tree height (m)[a]	Type of study
Crib Point	50	3	CS; R
Hastings	110	3	CS
Newhaven	50	2	CS
Rhyll	55	2.5	CS; R
Swan Corner	40	3	CS
Tooradin	150	3.5	CS; R
Yaringa	200	3	CS

[a] At sampling site.

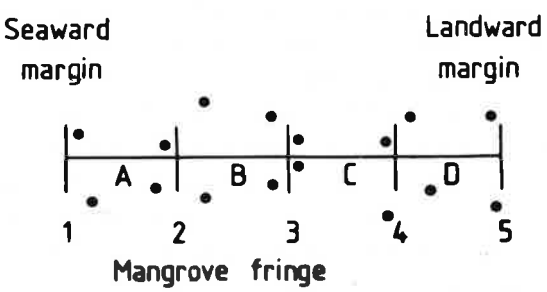

Fig. 1. Diagram of a transect through a mangrove fringe: the five equidistant base points (Nos. 1–5) divide the transect into four equal sectors (A–D); within each sector four randomly selected pneumatophores (dots) were chosen for analyses.

For each entire pneumatophore, relative cover estimates for *Bostrychia*, *Caloglossa* and *Catenella* were obtained using a series of defined categories (Table II). All pneumatophores were cut into 5-cm segments from the mudline upwards for subsequent analyses of algal zonation. The mudline constituted the baseline in this study because the intertidal zone traversing the mangrove fringe was essentially level. Then following collection of presence–absence data from each segment for frequency determinations, the material of *Bostrychia*, *Caloglossa*, and/or *Catenella* was scraped into separate watch

glasses and dried at 70 °C to constant weight. Salinity and light intensity levels were also measured at each transect base point.

TABLE II

Categories employed in estimating the degree of algal cover on *Avicennia* pneumatophores.

Category	Degree of cover
0	No cover; taxon absent
1	A single plant present
2	<5%
3	5– 19%
4	20– 39%
5	40– 59%
6	60– 79%
7	80–100%

Pattern analyses involved both ordination and classification procedures employing matrices generated with the use of Gower's coefficient (Sneath & Sokal, 1973, p. 135). The Bray–Curtis (1957) ordination outlined by Cox (1972) and the Gower (1966) principal coordinates analysis used by Whiffin (1977) also were employed. Matrices of entire data sets were compacted prior to the analyses by replacing each identical set of values with a single matrix entry. Thus, certain points on the resulting diagrams represent more than one pneumatophore or pneumatophore segment.

For algal recolonization studies, single 0.5 m^2 quadrats containing 37–40 pneumatophores were established in March near the seaward margins of mangrove fringes at Crib Point, Tooradin, and Rhyll.

All pneumatophores were denuded by handpicking the attached algae whilst smaller plants were removed using fine forceps. However, it is possible that unseen residual fragments may have persisted on some pneumatophores. The algae removed were preserved and returned to the laboratory for biomass determinations of the constituent genera. After 6 and 12 wk, between 9 and 19 randomly selected pneumatophores were collected from each quadrat, preserved, and returned to the laboratory for analyses. After 18 wk, all remaining pneumatophores were harvested for analyses. During an average semi-diurnal tidal cycle in Western Port Bay, pneumatophores near the seaward margin are completely emersed for ≈ 4 h, whereas portions of pneumatophores above 10 cm from the mudline can be emergent for > 5 h. Hence, each pneumatophore was cut into two segments, the lower comprising the basal 10 cm and the upper comprising the remaining portions which measured between 8–13 cm in length. Within each segment presence–absence data for frequency determinations and biomass information were obtained for *Bostrychia*, *Caloglossa* and *Catenella*.

Results and Discussion

COMMUNITY STRUCTURE

General aspects

Because of the random distribution of algae on pneumatophores within Victorian mangrove ecosystems (Davey, 1977), the results presented in this study have been analysed by pooling the relevant data from each locality. Of 112 pneumatophores involved in this part of the study, 105 harboured algae (frequency 0.94). Of these 105 pneumatophores, *Bostrychia* occurred most commonly (0.88) followed by *Caloglossa* (0.68) and *Catenella* (0.50). Total mean algal biomass per cm of pneumatophore was 7.18 mg. Of this, *Catenella* plants accounted for 3.47 mg (relative biomass = 0.48), *Bostrychia* plants contributed 1.90 mg (relative biomass = 0.27), and *Caloglassa* plants involved 1.81 mg (relative biomass = 0.25).

In order to emphasize apparent trends, the mangrove fringe was divided arbitrarily into four sectors in the horizontal direction and pneumatophores were divided arbitrarily into six segments in the vertical direction. However, changes in the parameters measured occur gradually (rather than abruptly) in both the horizontal and vertical directions, and these changes probably reflect gradients along a vegetation continuum. Some variation also occurred among the seven study sites (e.g. plants of *Caloglossa* were recorded from the landward sectors of only five of the seven localities), and it must be stressed that the data reflect an overall situation rather than a detailed analysis of a single transect.

Table III

Summary of biological data relating to horizontal community structure: data recorded for four quarters of the fringe with "A" being most seaward and "D" being most landward.

	A	B	C	D
Frequency of occurrence				
Bostrychia	0.86	0.93	0.89	0.82
Caloglossa	0.79	0.68	0.68	0.57
Catenella	0.61	0.79	0.43	0.18
Algal material	1.00	0.96	1.00	0.79
Mean biomass (mg/cm of pneumatophore)				
Bostrychia	3.38	1.10	2.28	0.84
Caloglossa	5.35	1.41	0.16	0.33
Catenella	9.07	3.89	0.57	0.34
Total	17.80	6.40	3.01	1.51
Mean relative biomass[a]				
Bostrychia	0.19	0.17	0.76	0.56
Caloglossa	0.30	0.22	0.05	0.22
Catenella	0.51	0.61	0.19	0.22

[a] Mean biomass/total biomass per quarter.

Horizontal aspects

Within the communities studied, decreases in algal frequency from seaward to landward as well as relative cover and mean algal biomass are evident (Table III). For example, total mean biomass in the landward quarter (D) is only 8% of that found in the seaward quarter, and the mean biomass of particular algae has decreased by factors of 4–70 from seaward to landward sectors. In addition, marked changes take place in relative biomass from one sector to another.

Different trends appear to occur for each of the three algal genera involved. In terms of frequency of occurrence, values for *Bostrychia* remain relatively constant and are invariably higher than values for *Caloglossa* and *Catenella* which respectively show moderate and marked declines between the seaward and the landward sectors. Although total mean biomass declined markedly from seaward to landward regions for all three genera, the rate of decline in mean biomass for *Bostrychia* is 2.8 times less than that for *Catenella*. As a result, the mean relative biomass of *Bostrychia* increased substantially in the two most landward sectors (C and D), while that of *Catenella* declined markedly (Table III). Mean relative biomass of *Caloglossa*, in contrast, fluctuated within comparatively narrow limits. Thus, even though the mean biomass of *Bostrychia* tends to decline from seaward to landward margins, the comparatively slow rate of decline (relative to *Caloglossa* and *Catenella*) results in relatively more substratum surface becoming available for *Bostrychia* colonization, which indeed occurs, probably as a result of its particular growth habit. *Bostrychia* plants possess a filamentous, decumbent growth which may allow for more rapid and complete colonization of available substratum space.

The general trends suggested by the data in Table III cannot be accounted for by observed differences in surface-mud salinity, relative light intensity (data not included), and/or distance from the seaward margin of the mangrove fringe. Simple and multiple regression analyses of biological data on environmental data produced no meaningful correlations, and other environmental factors (e.g. length of emersion, osmotic resistance, temperature changes) need to be examined in future studies in an attempt to account for the observed trends. Biebl (1962) determined that *Bostrychia tenella, Caloglossa leprieurii* and *Catenella opuntia* were the most resistant intertidal algae to the effects of desiccation than were any others on *Rhizophora* stilt roots. These results suggest that any interspecific competition occurring among the three taxa on *Avicennia* pneumatophores in Western Port Bay will not affect their ultimate survival, as the tolerance to salinity and light intensity shown by *Bostrychia*, *Caloglossa* and *Catenella* appears not to differ markedly enough for distinct patterns to emerge (Davey, 1977).

Results of the Bray–Curtis ordination and the principal components analyses were virtually identical and indicate that no distinctive horizontal pattern of absolute biomass involving the three algal genera is present within the communities studied (Fig. 2). A more definitive pattern, however, occurs for relative biomass where pneumatophores predominantly colonized (i.e. relative biomass level for one of the algae exceeds 0.67)

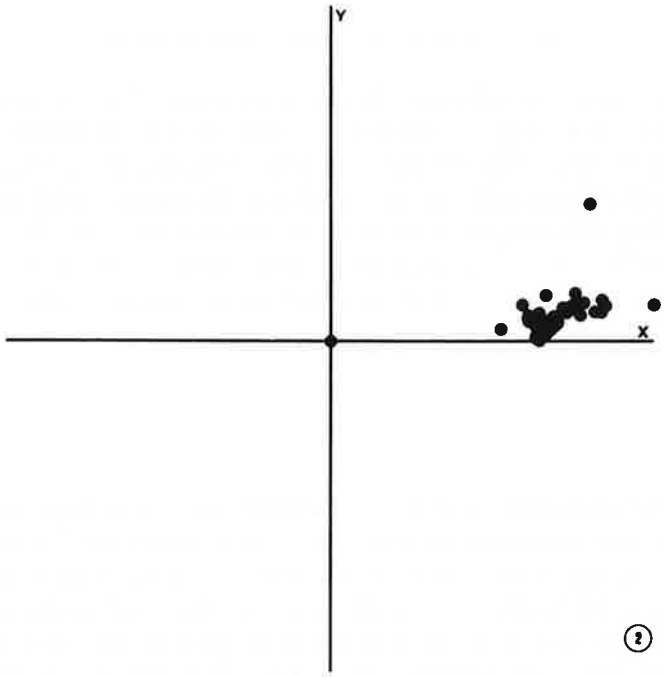

Fig. 2. Bray–Curtis ordination from data relating to horizontal absolute biomass.

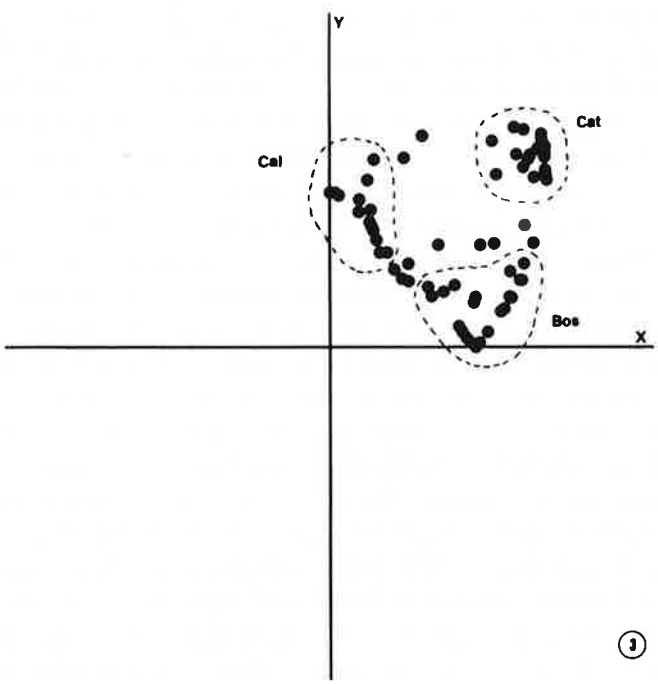

Fig. 3. Bray–Curtis ordination from data relating to horizontal relative biomass: dashed lines enclose points for which relative biomass exceeds 0.67 for *Bostrychia* (Bos), *Caloglossa* (Cal) and *Catenella* (Cat).

by *Bostrychia*, *Caloglossa* and *Catenella* each are positioned at separate "corners" of the trianguloid plot (Fig. 3). Moreover, most of the *Bostrychia*-predominated pneumatophores come from the landward half of the mangrove fringe, most of the *Caloglossa*-predominated pneumatophores grow in the most seaward sector, and most of the *Catenella*-predominated pneumatophores are situated in the "B" sector between the seaward quarter and the landward half of the mangrove fringe. Sharply delimited zones of *Bostrychia*, *Caloglossa*, and *Catenella*, however, are not evident; rather gradual transitions occur from one sector to another as evidenced by the intermediate points in Fig. 3.

Vertical aspects

Several trends emerged from analysis of data relating to vertical community structure. First, greatest frequencies of occurrence for all three genera and for algal material as a whole were recorded in the 5–10 cm segment above mudline (Table IV). Above 15 cm, abrupt declines in frequencies occurred and more than half of the pneumatophore segments were devoid of algal material. Secondly, greatest mean biomass levels were found either in the 5–10 cm segment (*Catenella*; total biomass) or in the 10–15 cm (*Bostrychia*; *Caloglossa*) segment (Table IV). Mean biomass levels in the 0–5 cm segments were only 23–41% of those in the 5–10 cm segments. Above 15 cm, steady declines in biomass were noted and above 25 cm, algal material was sparse and sporadic. Relatively high turbidity and particulate matter levels in the 0–5 cm region and more pronounced emersion effects above 15 cm in part may account for the apparent overall trends, but further studies are required to test these hypotheses.

The overall mean relative biomass values of *Bostrychia* and *Caloglossa* tend to increase in segments up to 20 cm and then decline, while overall values for *Catenella* tend to decrease from lowermost to uppermost segments (Table IV). The two notable exceptions to these trends (0.66 for *Caloglossa* in the >25 cm segment and 0.43 for *Catenella* in the 20–25 cm segment) resulted from exceptionally high biomass levels on two separate pneumatophore segments growing at the seaward margin of the mangrove fringe. The data taken as a whole suggest that plants of *Catenella* are more adversely affected by prolonged emersion than are plants of *Caloglossa* or *Bostrychia*.

In segments below 15 cm, total mean biomass in the seaward quarter is 10.3–12.4 times greater than total mean biomass for the corresponding segments in the landward quarter, and in segments above 15 cm, at least 17.3 times as much biomass occurs in the seaward quarter (Table V). Biomass levels in segments from the central half are always intermediate. Similar trends in biomass distribution occur in virtually all segments for *Caloglossa* and *Catenella* and in all segments above 5 cm for *Bostrychia*.

Trends in the vertical distribution of absolute biomass within seaward, central and landward sectors vary somewhat from genus to genus. For *Catenella*, maximum mean biomass levels in all sectors occur in the 5–10 cm segment. For *Bostrychia*, maximum mean biomass shifts from the 15–20 cm segment in the seaward sector to the 10–15 cm

segment in the central and landward sectors, and for *Caloglossa*, the maximum shifts from the 15–20 cm segment (seaward) to the 5–10 cm segment (central and landward). In all cases, biomass levels decline steadily in segments above those where maximum biomass occurs.

TABLE IV

Summary of biological data relating to overall vertical community structure: values recorded for six segments; position of segments (e.g. 5–10) indicates height in cm above mudline.

	0–5	5–10	10–15	15–20	20–25	>25
Frequency of occurrence						
Bostrychia	0.65	0.72	0.64	0.34	0.19	0.05
Caloglossa	0.38	0.51	0.43	0.28	0.15	0.07
Catenella	0.31	0.41	0.27	0.15	0.06	0.01
Algal material	0.76	0.86	0.71	0.44	0.24	0.09
Mean biomass (mg/cm)						
Bostrychia	0.55	1.35	2.43	2.07	1.08	0.12
Caloglossa	0.44	1.88	2.07	1.63	0.77	0.46
Catenella	2.68	6.84	2.73	0.85	0.65	0.12
Total	3.67	10.07	7.23	4.55	2.50	0.70
Mean relative biomass						
Bostrychia	0.15	0.13	0.34	0.45	0.26	0.17
Caloglossa	0.12	0.19	0.29	0.36	0.31	0.66
Catenella	0.73	0.68	0.37	0.19	0.43	0.17

TABLE V

Summary of mean biomass data (mg/cm) relating to vertical community structure in the seaward quarter, central half, and landward quarter of the mangrove fringe.

	0–5	5–10	10–15	15–20	20–25	>25 cm
Seaward quarter						
Bostrychia	0.30	1.74	4.55	5.55	3.08	0.09
Caloglossa	1.32	4.31	5.63	5.80	2.60	1.71
Catenella	8.58	19.68	4.19	1.43	2.13	0.0
Total	10.20	25.73	14.37	12.78	7.81	1.80
Central half						
Bostrychia	0.60	1.47	2.18	1.12	0.61	0.19
Caloglossa	0.15	1.39	1.15	0.24	0.12	0.06
Catenella	1.00	3.37	3.23	0.96	0.23	0.13
Total	1.75	6.23	6.56	2.32	0.96	0.38
Landward quarter						
Bostrychia	0.71	0.73	0.79	0.48	<0.01	<0.01
Caloglossa	0.12	0.43	0.34	0.23	0.22	0.0
Catenella	0.15	0.92	0.26	0.03	0.0	0.0
Total	0.98	2.08	1.39	0.74	0.22	<0.01

Data relating to frequency of occurrence and relative biomass distribution (vertical) in seaward, central and landward sectors have not been presented but show trends identical to those expressed in the overall data (Table IV). Meaningful cover data could not be obtained due to the small size of the segments.

Because of the marked difference in biomass levels occurring in the two sectors, pattern analyses relating to the vertical distribution of absolute and relative biomass were undertaken for both the seaward and landward quarters. In no case, however, did a distinctive pattern of vertical distribution emerge. Rather, the results indicate that any given 5 cm pneumatophore segment, regardless of its position above the mudline, can be predominated by any one of the three algal genera, although most pneumatophore segments above 20 cm are devoid of algae particularly in the central and landward sectors. Species of *Bostrychia*, *Caloglossa* and *Catenella* can be exposed for prolonged periods of time at low tide, yet they are able to survive considerable osmotic shock (Biebl, 1962) caused by evaporation increasing salt concentration (Almodovar & Biebl, 1962). The tidal inundations are often less frequent at the landward margins as parts of the mangrove fringe sometimes lie at or outside the limit of normal high tide, and as a result, pneumatophores are exposed for extended periods of time.

RECOLONIZATION

Data on frequency of recolonization (Table VI) indicate that algal material quickly became reestablished on nearly all of the denuded pneumatophores involved in the study. For all three algal genera, recolonization took place with greater frequency above 10 cm than below 10 cm. Throughout the 18-wk period, *Catenella* never recolonized more than half of the pneumatophores sampled, while *Caloglossa* always occurred on a majority of pneumatophores. Frequency values fluctuated in most cases over the 18-wk sampling period and no consistent pattern of frequency values versus time emerged. Reasons for these fluctuations remain uncertain but could include partial removal of particular taxa by grazing, competition for substratum, or sloughing off of the outer bark of the pneumatophores.

Total algal biomass increased throughout the monitoring period both below and above the 10 cm levels (Table VII), and although the greater proportion of overall biomass always remained above the 10-cm mark, the proportion of algal biomass developing below 10 cm became greater in each successive interval (13.1% after 6 wk; 22.5% after 12 wk; 29.6% after 18 wk). Moreover, the amount of total biomass below 10 cm approximately doubled in each successive interval whereas above 10 cm, it increased only by factors of 1.1–1.3.

Greater emersion times and hence consequent isolation from water movement of pneumatophore segments above 10 cm may be conducive to initial colonization and spore attachment, resulting in subsequently higher frequencies of occurrence (Table VI). These same factors also could result in more marked environmental fluctuations and lead to reductions in growth rates and biomass production. Thus algae which do become

established below 10 cm (where emersion times are shorter) are situated in a comparatively more stable environment, possibly facilitating higher growth rates and biomass production. However, the characteristic associations of *Bostrychia*, *Caloglossa* and *Catenella* on mangrove pneumatophores are adapted to survive considerable periods of desiccation by the water-holding capacity of their masses of intergrown branches (Dawson, 1966, p. 268).

TABLE VI

Frequency of algal recolonization of denuded pneumatophores at various time intervals.

Taxon	Overall	Below 10 cm	Above 10 cm
6 wk (32 pneumatophores sampled)			
Bostrychia	0.69	0.22	0.47
Caloglossa	0.59	0.25	0.50
Catenella	0.38	0.19	0.31
Algal material	0.97	0.66	0.97
12 wk (37 pneumatophores sampled)			
Bostrychia	0.65	0.24	0.54
Caloglossa	0.86	0.38	0.56
Catenella	0.46	0.30	0.35
Algal material	0.97	0.86	0.97
18 wk (48 pneumatophores sampled)			
Bostrychia	0.44	0.19	0.29
Caloglossa	0.67	0.38	0.56
Catenella	0.42	0.17	0.33
Algal material	0.96	0.71	0.96

The three algal genera showed somewhat different trends in absolute biomass change over the 18-wk period. For *Caloglossa*, absolute biomass increased continuously both below and above the 10-cm mark. For *Catenella* absolute biomass in both pneumatophore sectors declined after reaching peaks at 12 wk. *Bostrychia* biomass below 10 cm increased continuously, but the *Bostrychia* biomass above 10 cm and the overall mean *Bostrychia* biomass declined after the first 6 wk. Although trends in absolute biomass levels varied, the proportion of biomass present above 10 cm declined in successive intervals for all three genera and accounted for only 68–74% of the total biomass after 18 wk.

In terms of relative biomass (Table VII), *Caloglossa* became increasingly important with time both below and above 10 cm and after 18 wk accounted for 70% of the overall biomass. *Bostrychia* plants, which contributed the greatest relative biomass values after 6 wk, formed a continuously decreasing proportion of the total biomass thereafter. *Catenella* relative biomass levels never exceeded 0.34 and with one exception (12 wk, below 10 cm) always accounted for the smallest portion of the total biomass present.

Although the taxa recolonizing the pneumatophores were identical to those which

TABLE VII

Mean biomass data relating to algal recolonization of denuded pneumatophores at various time intervals.

	6 wk			12 wk			18 wk		
	< 10 cm	> 10 cm	Overall	< 10 cm	> 10 cm	Overall	< 10 cm	> 10 cm	Overall
Mean biomass (mg/cm)									
Bostrychia	0.18	1.68	1.57	0.22	1.20	0.71	0.33	0.95	0.48
Caloglossa	0.18	0.85	0.58	0.35	1.30	0.85	1.16	2.52	1.86
Catenella	0.05	0.18	0.15	0.30	0.50	0.39	0.17	0.48	0.31
Total	0.41	2.71	2.30	0.87	3.00	1.95	1.66	3.95	2.65
Mean relative biomass (material of a given taxon/total algal material)									
Bostrychia	0.44	0.62	0.68	0.25	0.40	0.36	0.20	0.24	0.18
Caloglossa	0.44	0.31	0.25	0.41	0.43	0.44	0.70	0.64	0.70
Catenella	0.12	0.07	0.07	0.34	0.17	0.20	0.10	0.12	0.12
Total	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

were removed at the start of the study, relative biomass values for the recolonizing community after 18-wk development differed markedly from those for the original community. *Catenella* prevailed in the original community with a relative overall biomass of 0.59, but became the most minor element in the recolonizing community with a declining relative overall biomass value of 0.12 after 18 wk. *Caloglossa*, in contrast, became far more important in the recolonizing community; the relative overall biomass rose from 0.25 in the original community to 0.70 after 18 wk of recolonization. Only minor changes occurred in *Bostrychia* overall relative biomass (0.16 in original community; 0.18 in recolonizing community). Thus mangrove algal community disruption can result in replacement by a differently structured community. The wider ecological consequences of such changes are unknown. These results, however, are preliminary and hence meaningful only for the period under investigation. In order to compare critically algal frequency and distribution prior to and subsequent to denuding the pneumatophores, the fertility of each taxon, seasonal effects of the tides as well as physico-chemical parameters of the sea water must first be ascertained.

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Effects of a hypersalinity gradient on epiphytic Corallinaceae (Rhodophyta) in Shark Bay, Western Australia

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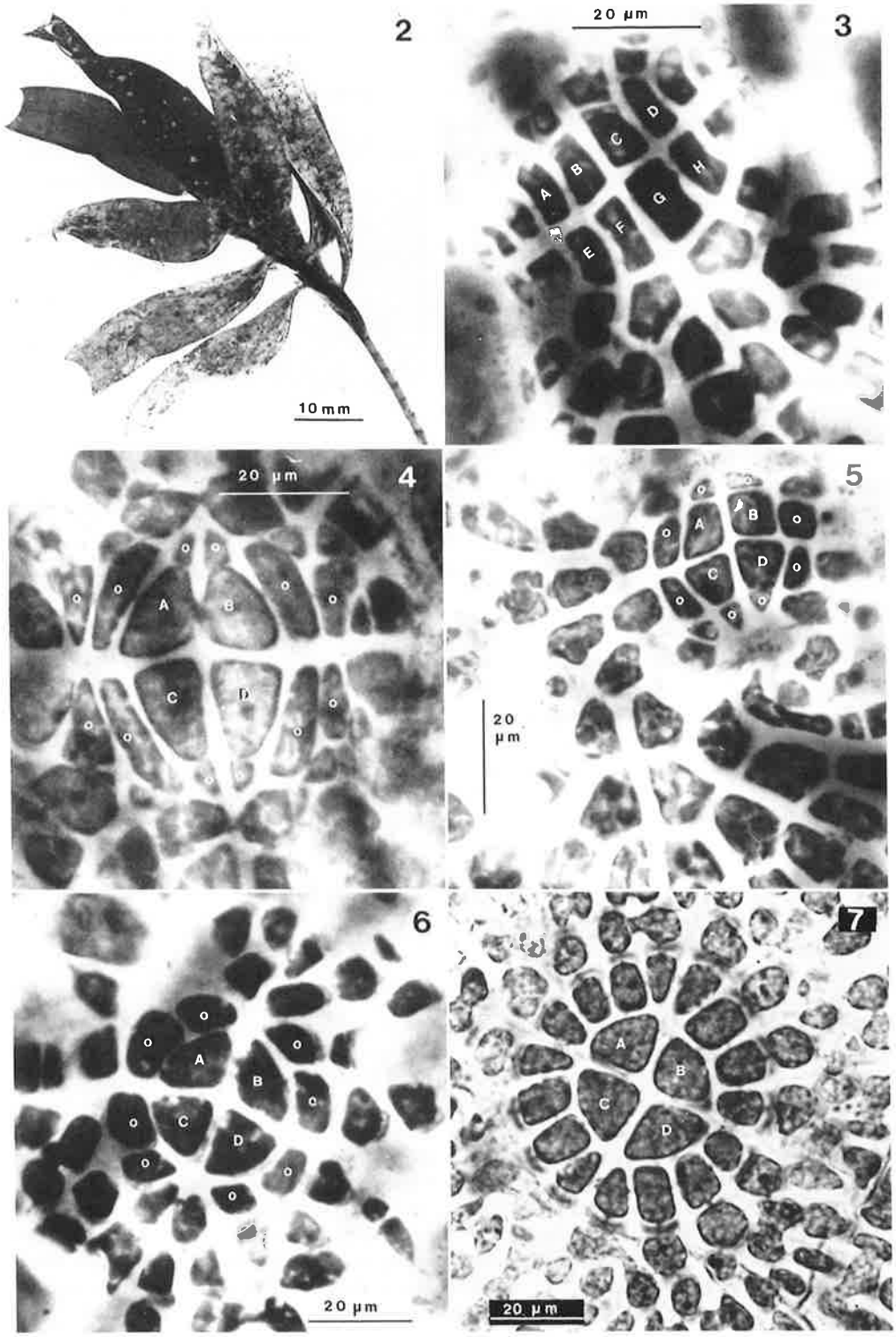
The extent to which a natural hypersalinity gradient (37–55‰) in Shark Bay, Western Australia, affects those Corallinaceae (Rhodophyta) epiphytic on the leaves of the seagrass *Amphibolis antarctica* has been examined. Four species of *Fosliella* and one each of *Pneophyllum* and *Melobesia* were identified. The species composition of the epiphyte community did not change along the gradient, and both the basic germination disc patterns and position of trichocytes within each taxon remained constant. With the exception of stations at 47.2 and 49.3‰ salinity, the overall density of epiphytic coralline algae on *Amphibolis* leaves decreased markedly as salinity levels rose. At all stations, most individuals on the oldest *Amphibolis* leaves lacked germination discs. For *Pneophyllum* the proportion of plants without germination discs was at least 88% at salinities up to 49.3‰, but dropped at the highest salinities. For *Fosliella* the proportion ranged from 74 to 95% with no relationship to salinity level. Fertility decreased with increasing salinity. The ratio of gametangial to sporangial plants rose from 1:1 at 37.3‰ to 4:1 at 55‰. Development of the epiphytic coralline community within leaf clusters occurred in a consistent sequence at all stations. On the young leaves, spores settled and divided to produce germination discs and intact thalli. On older leaves, the plants became fragmented but remained sterile. Subsequently, conceptacles were produced, almost exclusively on portions lacking germination discs. With increasing salinity, percent cover of both leaves and stems decreased. Increasing salinity slows the rate of growth and development of both the host and the coralline community. This observation is consistent with mechanisms known to operate in other algae and in angiosperms.

INTRODUCTION

Recent accounts (Davies 1970; Ducker *et al* 1977; Harlin 1980; Bramwell & Woelkerling 1984), show that species of the *Pneophyllum* (syn. *Heteroderma*)–*Fosliella* complex (Corallinaceae, Rhodophyta) occur abundantly on leaves of the endemic Australian seagrass *Amphibolis antarctica* (Labillardière) Sonder & Ascherson ex Ascherson (Cymodoceaceae). In Shark Bay, Western Australia (Fig. 1), this perennial angiosperm, which has lignified stems and produces clusters of short, strap-shaped leaves (Fig. 2; see also Robertson 1984), accounts for 90% of the total seagrass cover and grows in salinities up to 64‰ (Walker 1985). Its occurrence is the major factor contributing to shoal formation within the 13 000 km² embayment, which, in turn, plays an important role in the development of the hypersaline basins (Davies 1970). Shark Bay possesses a salinity gradient (35–70‰), increasing towards the innermost reaches, with vertical haloclines that are relatively stable (Logan & Cebulski 1970). This salinity regime arises from an extremely high evaporation rate relative to precipitation and fresh water inflow (Table 1), combined with steady offshore wind and isolated water basins. These factors result in an ideal environment to examine the impact of hypersalinity on coralline algae under natural conditions. Preliminary investigations on samples collected in Shark Bay in 1982 verified that species of the *Pneophyllum*–*Fosliella* complex occurred as leaf epiphytes throughout the salinity range in which the host grows. We therefore decided to examine this system further to determine whether and how a natural hypersalinity gradient affects the occurrence, morphology, density and fertility of these cor-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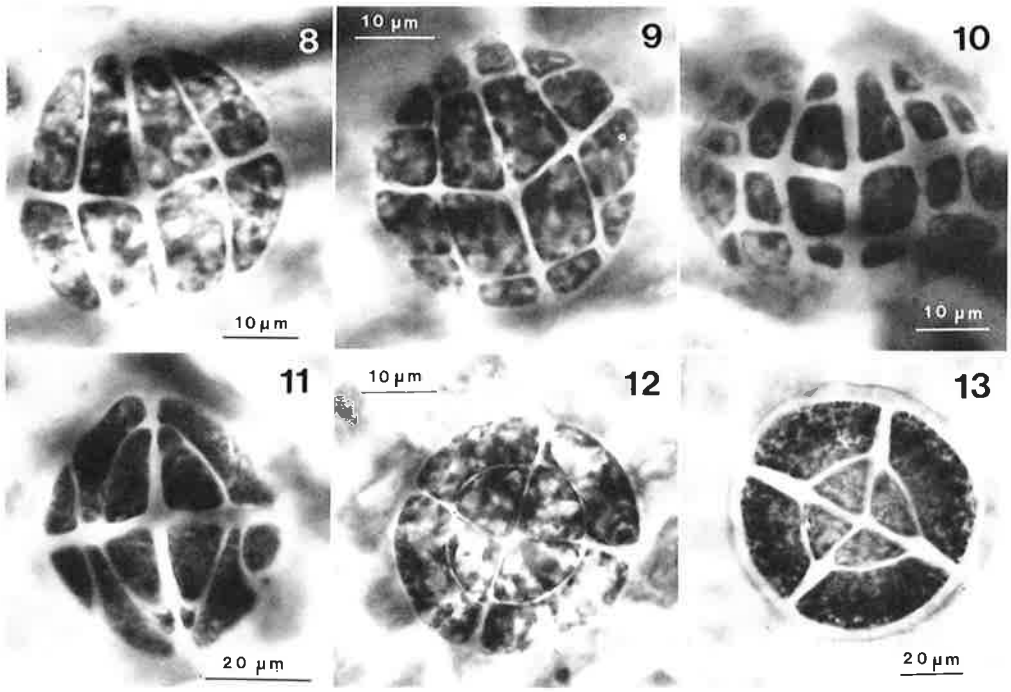


Figs 8–13. Young germination discs.
Figs 8–10. *Pneophyllum caulerpae*: eight-celled (Fig. 8), 16-celled (Fig. 9), and nearly complete (Fig. 10) stages. LTB 14686.
Fig. 11. Young disc of *Fosliella cruciata.* LTB 14714.
Fig. 12. Young disc of *Fosliella* A. LTB 14687.
Fig. 13. Young disc of *Fosliella cymodoceae.* LTB 14724.

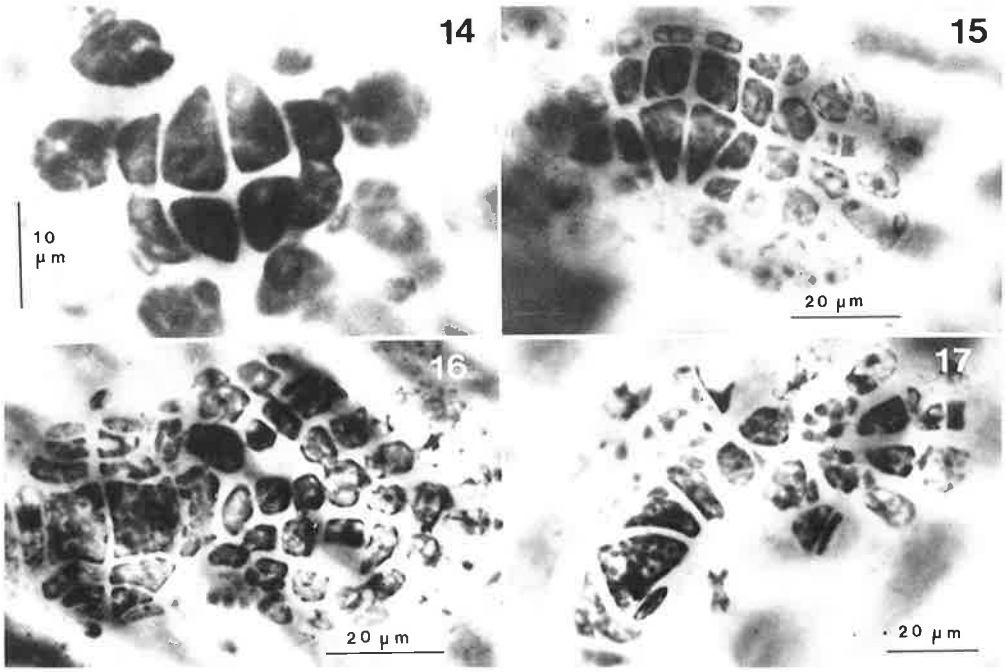
OBSERVATIONS

Species occurrence and morphology

OCCURRENCE: Of the six species of nongeniculate Corallinaceae recorded from *Amphibolis* leaves (Table 2), *Fosliella cruciata* and *Pneophyllum caulerpae* appeared at all stations and showed no clear responses to salinity levels in terms of frequency or density. Plants of *Fosliella* A and *Fosliella* B grew at all stations where salinities were less than 50‰, while at higher salinities only a few individuals of *Fosliella* B occurred. Plants of *Fosliella cymodoceae* were present only at salinities of 47.2 and 55‰ in our 1984 samples, but were found at lower salinities in the 1982 collections and occur at oceanic salinities (35‰) in southern Australia (Bramwell & Woelkerling 1984; Jones & Woelkerling 1984). Thus, with the possible exception of *Fosliella* A,

←

Figs 2–7.
Fig. 2. A single cluster of *Amphibolis antarctica* leaves from Dirk Hartog Island with epiphytic coralline algae. Youngest leaves not visible.
Fig. 3. Germination disc of *Pneophyllum caulerpae* showing eight-celled (A–H) central element. LTB 14717.
Fig. 4. Germination disc of *Fosliella cruciata* showing four-celled central element (A–D) and surrounding cells (O). LTB 14714.
Fig. 5. Germination disc of *Fosliella* B showing four-celled central element (A–D) and surrounding cells (O). LTB 14716.
Fig. 6. Germination disc of *Fosliella* A showing four-celled central element (A–D) and surrounding cells (O). LTB 14715.
Fig. 7. Germination disc of *Fosliella cymodoceae* showing four-celled central element (A–D) and a ring of 16 surrounding cells. LTB 14724.



Figs 14–17. Aberrant discs.
Fig. 14. Aberrant disc of *Fosliella* A in which four cells are missing from outer ring. Compare with Fig. 6. LTB 14715.
Fig. 15. Aberrant disc of *Fosliella* B in which two of the four central cells have remained undivided. Compare with Fig. 5. LTB 14688.
Fig. 16. Aberrant disc of *Pneophyllum caulerpae* in which central cells have fused to form two large cells. Compare with Fig. 3. LTB 14693.
Fig. 17. Aberrant disc, probably of *Fosliella cruciata* in which a complete distortion of cells has occurred. Compare with Fig. 4. LTB 14714.

we found no evidence to suggest that hypersalinity prevents the occurrence of any species of *Fosliella* or *Pneophyllum* in Shark Bay. *Melobesia membranacea* appeared only at one station (38.3‰) where it also had been found in our preliminary survey of 1982 material. While it may be possible that this species is restricted to near oceanic salinities, our small sample size precludes generalization, and culture studies are needed to clarify this matter. Based on relative frequency and relative density (calculated from the data in Table 2a), *Pneophyllum caulerpae* dominates the coralline communities at all salinities except 37.3 and 42.5‰, where *Fosliella* B is more important. This does not take account, however, of plants not identifiable to species; these constitute the majority of individuals at all stations (Table 2b).

SPORE GERMINATION: Spore germination patterns are not affected by changes in salinity. For *Pneophyllum caulerpae* (Fig. 3) and for each of the four species of *Fosliella* (Figs 4–7), the basic segmentation pattern remained constant throughout the Shark Bay salinity gradient. Plants of *Fosliella cymodoceae,* found only at 47.2 and 55‰ in our 1984 samples, had germination discs identical to those found by Jones & Woelkerling (1984) at oceanic salinities in southern Australia.

On younger leaves of *Amphibolis,* where spores of *Pneophyllum* and *Fosliella* settle and germinate to produce young plants, some aberrations in the normal spore segmentation patterns were observed (Figs 14–17). These aberrations were detected at various salinities, including 37.3‰, and do not appear related to the hypersalinity gradient. At all stations, they accounted for less than 1% of the germination discs observed. Aberrants of *Fosliella cymodoceae* were not detected in the Shark Bay samples, and Jones & Woelkerling (1984) recorded only a single example in their southern Australian collections.

While some aberrants were identifiable to

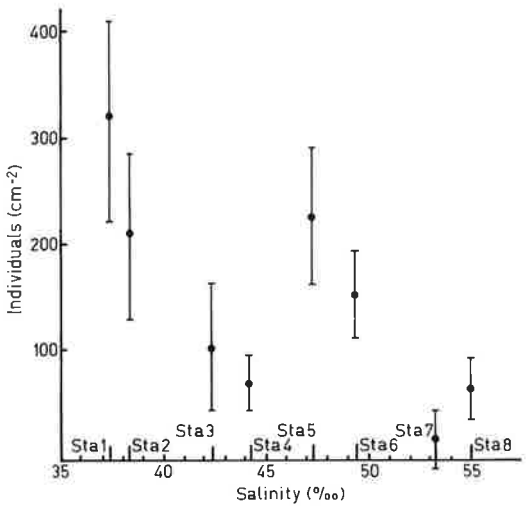


Fig. 18. Population density of epiphytic coralline algae on *Amphibolis* leaves in relation to salinity levels in Shark Bay. Bars indicate standard deviation about the mean.

species (Figs 14–16) with reasonable certainty, others (Fig. 17) were not. Discs intermediate between species were not found, however, and in no case did a species with a four-celled central element produce an eight-celled aberrant or vice versa. The fate of thalli produced from aberrant discs is unknown. No aberrant discs were detected on older host leaves (thus suggesting that these discs do not survive long), and it is not known whether vegetative tissues produced by aberrant discs can survive as fragments.

TRICHOCYTES: There appear to be no correlations between hypothallial trichocyte occurrence and salinity level within species of *Fosliella* and *Pneophyllum* found in Shark Bay. At all salinities below 50‰, most individuals produced trichocytes (Table 2b) and at no time was trichocyte production completely suppressed. At 53.2 and 55‰ all individuals examined had hypothallial trichocytes.

The position of hypothallial trichocytes remained constant within each taxon throughout the hypersalinity gradient. In all four species of *Fosliella,* hypothallial trichocytes always occurred terminally on filaments, whereas in *Pneophyllum caulerpae,* hypothallial trichocytes were always intercalary within filaments. No abnormally large, terminal sac-like cells (Suneson 1943, p. 25; Chamberlain 1983, p. 323) were observed in Shark Bay plants referable to *Pneophyllum.* In fragments (i.e. individuals without germination

Table 2. Frequency and density of coralline algae on outermost leaves of *Amphibolis antarctica* from specified salinities at Shark Bay, WA. Values were derived from 10 leafy shoots at each salinity

	Frequency								Mean density cm^{-2} host							
Salinity (‰)	37.3	38.3	42.5	44.1	47.2	49.3	53.2	55.0	37.3	38.3	42.5	44.1	47.2	49.3	53.2	55.0
(a) Individuals with germination discs																
Fosliella cruciata	0.4	0.9	0.1	0.3	0.6	0.5	0.2	0.2	1	4	<1	1	3	2	<1	<1
F. cymodoceae	0	0	0	0	0.2	0	0	0.1	0	0	0	0	<1	0	0	3
Fosliella sp. A	0.4	0.1	0.5	0.5	0.6	0.2	0	0	1	<1	2	2	2	<1	0	0
Fosliella sp. B	0.9	0.8	0.6	0.3	0.7	0.7	0	0.1	8	2	6	1	3	2	0	<1
Pneophyllum caulerpae	0.8	1.0	0.2	0.7	0.9	0.9	0.9	1.0	4	20	1	5	18	9	3	14
Melobesia membranacea	0	0.2	0	0	0	0	0	0	0	<1	0	0	0	0	0	0
(b) Individuals without germination discs (fragments)																
Fosliella spp.	1.0	1.0	1.0	1.0	1.0	1.0	0.2	0.4	230	27	60	24	51	30	<1	4
Pneophyllum sp.	1.0	1.0	1.0	1.0	1.0	1.0	0.8	1.0	78	150	38	40	133	70	15	41
Genus uncertain (without trichocytes)	1.0	1.0	0.1	0.6	1.0	0.9	0	0	10	6	<1	1	16	9	0	0

Table 3. Density and fertility of *Fosliella* spp. (Fos) and *Pneophyllum* sp. (Pne) on outermost leaves of *Amphibolis antarctica* from specified salinities at Shark Bay, WA. Means and standard deviations were calculated on samples from 10 collection points for each salinity

	Salinity (‰)															
	37.3		38.3		42.5		44.1		47.2		49.3		53.2		55.0	
	Fos	Pne	Fos	Pne	Fos	Pne	Fos	Pne	Fos	Pne	Fos	Pne	Fos	Pne	Fos	Pne
(a) Total no. individuals cm^{-2}	240(81)	82(33)	34(20)	170(87)	69(46)	39(28)	28(16)	45(14)	60(30)	151(59)	35(13)	79(29)	1(2)	18(26)	8(22)	55(29)
(b) Percentage total individuals																
(1) With identifiable germination discs	5(3)	4(3)	21(16)	11(7)	11(10)	2(4)	9(10)	12(19)	23(27)	12(19)	17(17)	7(6)	17(36)	43(32)	26(36)	33(21)
(2) Lacking germination discs (fragments)	95(4)	96(3)	79(16)	89(7)	89(10)	98(4)	91(9)	88(19)	77(27)	88(19)	83(17)	93(6)	83(36)	57(32)	74(36)	67(21)
(c) Percentage total individuals																
(1) Which are sterile	65(12)	56(19)	83(14)	59(25)	80(17)	63(27)	93(9)	80(20)	93(8)	77(15)	91(10)	57(20)	100(0)	97(5)	95(10)	89(17)
(2) With male conceptacles	17(13)	7(6)	8(9)	9(7)	7(5)	12(8)	4(6)	11(11)	4(4)	7(3)	5(5)	19(10)	0	2(4)	1(2)	4(8)
(3) With female conceptacles	8(3)	9(7)	1(2)	13(12)	3(4)	6(7)	2(5)	4(5)	<1	6(7)	4(5)	10(8)	0	0	0	4(7)
(4) With sporangial conceptacles	10(6)	23(12)	7(8)	7(8)	5(8)	12(11)	3(6)	4(7)	<1	6(6)	1(3)	13(14)	0	<1	0	2(3)
(d) Gametophyte: sporophyte ratio (Fos and Pne)	1:1		2:1		1.5:1		3:1		2:1		2:1		>2:1		4:1	

Table 4. Developmental sequence of coralline algae within leaf clusters of *Amphibolis antarctica* at specified salinities in Shark Bay, WA. Numbers are position of leaf in cluster (1 = youngest, 2, 3, . . . , oldest)

	Salinity (‰)							
	37.3	38.3	42.5	44.1	47.2	49.3	53.2	55.0
(a) Event								
(1) No apparent spore settlement	1	1–2	1–2	1–3	1–3	1–2	1–3	1–4
(2) Spore settlement, germination and development of intact thalli	2–6	3–5	3–6	4–6	3–7	3–7	4–6	5–7
(3) Marked thallus fragmentation (no. fragments > no. discs present)	7	6	7	7	7	8	7	8
(4) Onset of conceptacle production	9	7	9	9	9	8	—	11
(b) No. leaves cluster^{-1}	15	10	9	12	12	11	7	13
(c) Position of outermost leaf monitored for Tables 3 and 4, mean	9.1	9.8	8.8	7.9	9.8	8.1	6.1	9.5
(SD)	(1.3)	(1.5)	(1.5)	(1.9)	(1.9)	(1.1)	(1.6)	(2.0)

discs which consequently were not identified to species), hypothallial trichocytes were either all terminal or all intercalary within individuals at all stations.

Density and fertility

With the exceptions of stations at 47.2 and 49.3‰ the overall density of epiphytic, nongeniculate coralline algae on *Amphibolis* leaves decreased markedly as salinity levels rose (Fig. 18). The two exceptional stations were situated at or near the Faure Sill (Fig. 1), where halocline instability can result in changes of as much as 10‰ in salinity over a spring tide (Logan & Cebulski 1970). Such fluctuations were not apparent at the time of sampling, but they do lead to temporary salinity reductions and inflows of oceanic water, and this may be one reason for the higher density of coralline epiphytes at these stations.

No clear trends in the relative density of *Fosliella* vs *Pneophyllum* were evident across the hypersalinity gradient (Table 3a); at 37.3 and 42.5‰, *Fosliella* densities were higher while at the remaining stations *Pneophyllum* densities were higher. Similarly, changes in density of *Fosliella* plants and of *Pneophyllum* plants show no clear-cut relationship to changes in salinity.

At all stations, a majority of individuals present on the outermost leaves of *Amphibolis* lacked germination discs (Table 3b). For *Pneophyllum* the proportion of fragments in the population was at least 88% at salinities up to 49.3‰ but dropped markedly to 57–67% at higher salinities.

Fertility decreased with increasing salinity (Table 3c); at 37.3‰, 35–44% of individuals bore conceptacles whereas at 55‰ only 5–11% were fertile. At all stations, the percentage of *Fosliella* plants that were fertile always was lower than the percentage of fertile *Pneophyllum* plants, and no female plants of *Fosliella* were seen above 49.3‰. At 37.3‰, the proportions of gametangial and sporangial plants were equal (Table 3d) but the ratio of gametangial to sporangial plants varied between 1.5:1 and 4:1 at greater salinities. In general, male plants were more common than female or sporangial plants, but this probably is due to a higher level of fragmentation of male plants rather than a greater production of male plants from spores. Similarly, higher rates of fragmentation could account for changes in the ratio of gametangial to sporangial individuals.

Community development

The development of the coralline epiphyte community within *Amphibolis* leaf clusters occurred in a consistent sequence at all stations (Table 4). In *Amphibolis*, new leaves are produced within the center of each cluster and become increasingly more peripheral with age; thus the outermost leaf is always the oldest (Fig. 2). Coralline community development is initiated on the younger (but not the youngest) leaves of an *Amphibolis* cluster from spores which settle and divide to produce germination discs and intact vegetative thalli. As host leaves become older (and thus become more peripherally situated in the leaf cluster), marked fragmentation of individual thalli occurs resulting in numerous sterile individuals lacking germination discs. Conceptacle production is confined almost exclusively to in-

Table 5. Percent cover of coralline algae on outermost leaves and on stems of *Amphibolis antarctica* at specified salinities in Shark Bay, WA. Means and standard deviations were derived from 10 collection points at each salinity

	Salinity (‰)						
	37.3	38.3	42.5	44.1	47.2	49.3	53.2	55.0
(a) Leaves, percent cover	85(8)	70(20)	31(28)	11(4)	43(19)	31(15)	1(1)	8(7)
(b) Stems								
Height (mm)	401(111)	285(40)	398(91)	471(68)	377(52)	259(45)	321(62)	484(192)
Percent cover								
Geniculate species	2(1)	25(16)	35(26)	16(16)	24(18)	1(1)	0	0
Nongeniculate species	92(3)	69(11)	74(12)	79(7)	72(7)	43(11)	24(15)	28(26)

dividuals lacking germination discs. Of nearly 15000 individuals observed during this study, only four possessed both conceptacles and a germination disc.

Higher salinity slows down the rate of development both of host leaves and the coralline community. In Shark Bay, leaf turnover time (i.e. the length of time between leaf production and leaf abscission) increases with increasing salinity (Walker 1985). This means that in clusters with a given number of leaves, the epiphytic coralline communities on the outermost leaf are older at higher salinities than at lower salinities. Moreover, as salinities increased, so did the number of central leaves lacking any coralline epiphyte development (Table 5). While intact thallus development, fragmentation, and conceptacle production tended to occur at roughly the same leaf position at all stations (Table 5), the leaves occupying those positions at higher salinities are older than the comparable leaves at lower salinities. At 53.2‰, conceptacle production was infrequent (Table 3), possibly because the number of leaves retained per cluster was low (Table 4).

With increasing salinity, the percentage cover of coralline epiphytes on the oldest (outermost) leaf of a cluster decreased markedly (Table 5). Similar trends were apparent among the Corallinaceae found on *Amphibolis* stems (Table 5).

TAXONOMIC IMPLICATIONS

Generic classification

Results from the present study provide further evidence to support Chamberlain's (1983) generic classification scheme in which *Fosliella* is characterized by the production of a four-celled central element in the germination disc and terminal hypothallial trichocytes and *Pneophyllum* is characterized by the production of an eight-celled central element in the germination disc and intercalary hypothallial trichocytes. Jones & Woelkerling (1984) found that these character combinations remained constant within natural populations at oceanic salinities (*ca* 35‰) and concluded that they do not vary under a variety of photon-flux density and temperature regimes. The Shark Bay data show that these character combinations also remain constant throughout a natural hypersalinity gradient. Moreover, the Shark Bay system involved two species (*Fosliella* A and *Fosliella* B) not previously tested for char-

acter constancy, and this brings to 20 (see Jones & Woelkerling 1984, p. 192) the number of species so far examined in this respect.

Fosliella, as circumscribed by Chamberlain (1983), appears to be distinctive and readily separated from other genera referable to the subfamily Mastophoroideae (Johansen 1981, p. 11). As noted by Chamberlain (1983, p. 354), however, the situation with *Pneophyllum* is much less clear-cut, and further studies are needed to determine whether and how *Pneophyllum* can be delineated from *Pseudolithophyllum sensu* Adey (1970a). Australian plants referred to *Pneophyllum* during the present study as well as those of Jones & Woelkerling (1984) and those of Bramwell & Woelkerling (1984) all possess vegetative thalli with little or no perithallial tissue and which therefore have readily observable germination discs and hypothallial trichocytes. Some species referred to *Pneophyllum* by Chamberlain (1983), in contrast, produced several to 12 or more layers of perithallial cells throughout most or all of the vegetative thallus, thereby obscuring germination discs and hypothallial trichocytes. Based on present knowledge, such thalli could be placed as readily in *Pseudolithophyllum sensu* Adey (1970a) as they could in *Pneophyllum.*

Species concepts within *Fosliella*

The number of species referable to *Fosliella sensu* Chamberlain (1983) on a world scale remains uncertain. Chamberlain (1983, pp. 341–342) included three species and suggested that more probably occurred, but she did not consider species concepts in detail since only one species has been found in Great Britain. Based on material from Shark Bay as well as on data provided by Jones & Woelkerling (1984), however, it appears that species within *Fosliella* can be delineated, at least in part, on the basis of differences in cell arrangement within the germination disc. Four distinct patterns (Figs 4–7) were found in the Shark Bay collections, and each of these remained constant and distinctive throughout the hypersalinity gradient. For *Fosliella cruciata* and *F. cymodoceae,* Jones & Woelkerling (1984) recorded similar constancy in relation to various photon-flux density and temperature regimes. In neither study were discs of intermediate morphology found, thus supporting the hypothesis that differences in cell arrangement within the germination disc are stable characters which can be used to delineate species. Additional studies are needed to test this hypothesis further and to determine whether patterns of cell arrangement within the germination disc are correlated with other characters, especially those associated with conceptacle roof morphology. Chamberlain (1983) found that species of *Pneophyllum* could be separated, in part, on differences in conceptacle roof morphology. At present, however, too few data are available on conceptacle characters for taxa assignable to *Fosliella,* to allow firm conclusions to be drawn.

All species of *Fosliella* are characterized by the occurrence of four central cells within the germination disc which are *not* involved in thallus development once the germination disc has been formed. Within the genus, however, there are at least two distinct modes by which these four central cells are formed. In *Fosliella farinosa* (see Chamberlain 1984) and in *Fosliella* B (Figs 5, 8–10), sporogenesis is via the parallel mode (Chamberlain 1984, fig. 20). In this mode two rows of four cells are formed after the third round of cell divisions (Fig. 8). The central four cells normally cut off one additional cell each (Fig. 9), and no further development occurs from these cells. All subsequent thallus development (Figs 10, 15) occurs *only* from the outermost four cells of the original octad (Fig. 8). (In *Pneophyllum* all eight cells become involved in further thallus development.) The other three species of *Fosliella* found in our Shark Bay samples show a concentric mode of sporogenesis (Chamberlain 1984, fig. 20). After the third round of cell divisions in this mode, the central group of four cells is *surrounded* by a concentric ring of four outer cells (Figs 11–13). The mode of spore ontogeny (parallel vs concentric) is readily determined even in mature plants (Figs 4–7) since in the parallel mode, the four central cells appear four-sided in surface view whereas in the concentric mode, the four central cells appear three-sided in surface view. The full taxonomic significance of this difference has yet to be assessed, but further study may show that parallel versus concentric spore ontogeny could provide a basis for the recognition of two subgenera within *Fosliella.*

ECOLOGICAL IMPLICATIONS

Factors limiting growth in coralline algae

In Shark Bay, the species composition of the coralline community on *Amphibolis* leaves did not

change, but a marked reduction of cover, density, and fertility occurred at high salt concentrations, thus implying that thallus growth and development are adversely affected. Virtually nothing is known about how coralline algae respond metabolically to hypersalinity, but growth in other algae is known to decrease under salt stress (Munns *et al* 1983). This decrease might result from (i) decrease in photosynthetic rate (Ogata & Matsui 1965; Gordon *et al* 1980; Gilmour *et al* 1982); (ii) metabolic interference by ion concentration (Greenway & Munns 1980; Munns *et al* 1983; Gimmler *et al* 1984); (iii) competition for carbon skeleton with an osmoticum (Hellebust 1976; Krauss 1978; Reed 1980; Munns *et al* 1983); or (iv) limitation of an essential element. Ginzburg & Ginzburg (1981) found that strains of *Dunaliella* tolerate higher salt concentrations "when light intensity was high and carbon abundant". In Shark Bay neither light nor carbon is likely to be limiting. Smith & Atkinson (1983) have shown that partial pressure of CO_2 is well in excess of air equilibrium. Lower (less negative) isotope discrimination ratios for *Corallina chilensis* Decaisne (−11.6, Smith & Epstein 1970) and *Corallina* sp. (−10.0, Parker 1964) are consistent (in the absence of diffusion limitation) with the possibility that coralline algae use bicarbonate as a supplementary source of carbon. Reactive phosphorus in Shark Bay decreased to below detectable at 43‰. If phosphorous concentration alone were responsible for the result, change would be seen between oceanic and 43‰, but the further decreases at higher salinities would not be explained.

There is only scant information on the effects of salinity on coralline algae. Plants of *Corallina officinalis* Linnaeus exposed to 53‰ salinity for up to 2 hr showed enhanced cellular concentrations of K^+ (Kirst & Bisson 1979). Where ion exclusion operates as a mechanism for protection against high internal ion concentration (Bisson & Kirst 1979; Munns *et al* 1983), it presumably would be based on active transport and thus be energy demanding and growth limiting. Growth of the nongeniculate species *Clathromorphum circumscriptum* (Stromfelt) Foslie decreased 25 to 70% when salinity was experimentally reduced from 33.5 to 24‰ (Adey 1970b). In the St Lawrence estuary in eastern Canada, small size classes of this species were reproductive at 28‰ but sterile at 24‰ (Gendron & Cardinal 1980, 1983). From these studies and from those in Shark Bay it appears that optimal salinity for many coralline algae is that of normal seawater.

Effect of epiphytic coralline algae on host plants

One potential effect of the epiphytic coralline algae could be to increase the boundary layer of the host plant surface. This layer could, in a manner consistent with Fick's law (Raven *et al* 1982), increase the barrier to diffusion and, *inter alia,* lower carbon dioxide fixation. Conover (1968) has demonstrated the importance of natural diffusion gradients to metabolism in *Zostera marina* Linnaeus. There is evidence from other seagrass–epiphyte systems that increasing the epiphyte load decreases seagrass photosynthesis (Sand-Jensen 1977; Bulthuis & Woelkerling 1983; Silberstein & McComb unpublished). Reduction of light (shading) has been postulated as the explanation for reduced photosynthesis. Either or both mechanisms might account for the fact that Walker (1985) found maximum biomass and production of *Amphibolis* at 42‰ rather than at lower salinities. Collections for our study were from *Amphibolis* beds identical to or approximating those examined by Walker. We found marked decrease from the extremely high densities of epiphytes in oceanic waters. Epiphytic algae cannot be serving to protect *Amphibolis* from excessive light, because the old leaves on which most of the epiphytes appear are not photosynthetically active (Walker 1985). Moreover, these epiphytes do not weight down their host as happens for other seagrasses (Harlin 1975, 1980) because the stems are stiff and erect, and the leaves are small and replaced rapidly. In 1982 a new leaf appeared every week in 42‰ (Walker 1985).

Contribution to carbonate budget

Up to 20% of the particulate matter in cores from sediment in Shark Bay (Hagan & Logan 1974, p. 139) has been described as coralline algae. Species of *Fosliella* and *Pneophyllum,* however, could not be distinguished visually from the rest of the core matrix, although some geniculate corallines could be identified (Logan, personal communication). Old *Amphibolis* leaves are negatively buoyant and therefore sink *in situ* (Walker & McComb unpublished). The average leaf life span is 65 days at 42‰, and new leaves are produced every 4 to 17 days depending upon the

season and salinity (Walker 1985). Thus the substrate available to support coralline algae is more extensive than is immediately obvious. When an *Amphibolis* leaf has decomposed, the carbonate is deposited in the beds. Seagrasses have been in the bay for *ca* 4500 years (Davies 1970). Thus the total contribution of $CaCO_3$ would be cumulative, but we are not suggesting a specific amount.

Interactions with other epibiota

No information is available on grazing on coralline algae in Shark Bay, although grazing has been reported elsewhere (Johansen 1981). Competition for space did not appear critical. At highest salinities where most space was available, other species of algae were rare. On most of the plants at all stations coralline algae accounted for 80% of the surface cover. Most of the epiphytic animals were bryozoa and hydrozoa. The presence of coralline algae results in a roughened leaf surface which may facilitate the attachment of other epiphytes (Humm 1964; Ducker & Knox 1984). The fact that we found encrusting algae beneath both the fleshy algae and animals that we removed supports this speculation.

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A Taxonomic Reassessment of *Spongites* (Corallinaceae, Rhodophyta) Based on Studies of Kützing's Original Collections

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Results from critical studies of the original collections upon which *Spongites* Kützing, 1841 is based have led to the designation of *S. fruticulosa* as lectotype species and to the resurrection and recognition of *Spongites* as a distinct genus of Corallinaceae (Rhodophyta). *Spongites* is characterized by the absence of geniculae, uniporate tetrasporangial conceptacles, a multistratose non-palisade and non-coaxial medulla ("hypothallium") and cortex ("perithallium"), fusions between cells of adjacent filaments, and trichocytes which are solitary or arranged in a vertical series. Since at least 1883, the Kützing epithet "*fruticulosa*" has been misapplied widely to a taxon with multiporate tetrasporangial conceptacles, whereas the type collection of *S. fruticulosa* possesses uniporate tetrasporangial conceptacles. Of the six original species, three (*S. fruticulosa*, *S. racemosa*, *S. stalactitica*) are retained in *Spongites*; *S. dentata* is referred to *Lithophyllum* and *S. nodosa* to *Lithothamnion* as distinct species; and *S. confluens* is regarded to be conspecific with *Lithophyllum incrustans* Philippi. Detailed morphogological–anatomical accounts of specimens in the type collections are presented along with relevant historical data on the genus and on the various species studied. The relationships of *Spongites* to *Neogoniolithon* and to other genera of Corallinaceae also are discussed.

Kützing (1841, p. 30) established the genus *Spongites* (Corallinaceae, Rhodophyta) for certain "nullipores" (an obsolete name for various non-geniculate Corallinaceae which seemingly lacked pores—see Johansen, 1981, p. 212) which were specifically distinct from one another but which hitherto had been united under the binomial *Cellepora spongites* (Pallas) Linnaeus (1767, p. 1286) [Basionym: *Eschara spongites* Pallas (1766, p. 45); both Pallas and Linnaeus regarded this taxon to be an animal]. Kützing assigned six species (all newly described) to the genus based on collections from various localities in the Mediterranean Sea, and he circumscribed *Spongites* to encompass taxa with calcareous thalli that were knobby or globular, stalactite-like and occasionally also jagged or dentate. He also noted that the plants were marine, grew attached to a substrate, were nearly always red or reddish (rarely greenish), and retained this colouration upon drying if specimens were obtained in a fresh, living state.

Kützing (1841, p. 29) used the term "nullipores" in a general sense (see Lamarck, 1816, p. 203; 1836, p. 311; Decaisne 1842a, p. 127; Johansen, 1981, p. 212) to denote a group of organisms; he did not equate the term "nullipores" with the genus *Nullipora* Lamarck (1801, p. 374), and Kützing (1841, p. 29) emphasized that he was dealing *only* with certain nullipores which hitherto had been misidentified as *Cellepora spongites*. At the time of its inception, Kützing (1841, p. 29) also regarded *Spongites* to be generically distinct from *Lithothamnium* Philippi (1837) and from *Lithophyllum* Philippi (1837). This is evidenced by three facts: Kützing (1841) did not cite Philippi's (or any other) genera as synonyms of *Spongites*; Kützing (1841) did not recognize any of Philippi's taxa as species within the genus *Spongites*; and the

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name *Cellepora spongites*, with which Kützing (1841) associated his "misidentified" material, is not mentioned in Philippi's account.

Two years later, however, Kützing (1843a, p. 386) reduced both *Lithothamnium* and *Lithophyllum* to subgeneric groups within *Spongites*. Most subsequent authors have not accepted this 1843 arrangement; indeed *Lithothamnion* (*sensu* Heyrich, 1897a; see below) and *Lithophyllum* have become widely recognized and now constitute the two largest genera of non-geniculate Corallinaceae while Kützing's genus *Spongites* has fallen into obscurity. Recent studies of Philippi's original collections of *Lithothamnium* (Woelkerling, 1983a) and *Lithophyllum* (Woelkerling, 1983b) have led to reassessment of present day concepts of these two genera and to the proposed conservation of *Lithothamnion* Heyrich (1897a) against *Lithothamnium* Philippi (1837). The relationships between *Spongites* and Philippi's taxa, however, have not been reassessed, and the question of whether *Spongites* should be recognized as a distinct genus of Corallinaceae has remained unanswered (see also Lebednik, 1977, p. 381). Moreover, *Spongites* apparently has not been lectotypified (Silva in Farr, Leussink & Stafleu, 1979), and none of the type collections of the six species originally included in *Spongites* have been examined in relation to modern-day taxonomic concepts, even though at least several presently are recognized as distinct species by many authors.

During a visit to the Rijksherbarium in Leiden in May 1980, the original collections of the six species assigned to *Spongites* were located, thus providing an opportunity to deal with a number of unresolved problems. In this paper, results of critical examinations of these six collections are presented and the taxonomic implications of the findings are considered in detail. Specific aims have been to clarify the relationships between the type specimens and the modern-day concepts of the six Kützing taxa, to lectotypify the genus *Spongites*, and then to consider the status of *Spongites* in relation to other non-geniculate genera of Corallinaceae, especially *Neogoniolithon* Setchell and Mason. Brief historical accounts of *Spongites* and of the six original species also are included.

MATERIALS AND METHODS

Data were obtained from the type specimens which currently are housed at L (Rijksherbarium, Leiden, Netherlands). Microtechnique procedures follow Woelkerling (1980a) and a representative set of permanent slides from all collections examined has been retained at LTB (Department of Botany, La Trobe University, Bundoora, Victoria, Australia). Cellular measurements quoted include the decalcified cell walls, as in most cases the protoplasts of the dried specimens were distorted. Wherever cell measurements are given in the text, "L" denotes cell length, "D" denotes cell diameter, "H" denotes cell height, "H/D" denotes the ratio of cell height to cell diameter, and "L/D" denotes the ratio of cell length to cell diameter. Scanning electron microscopy procedures are outlined in Woelkerling (1978) and herbarium abbreviations are taken from Holmgren, Keuken & Schofield (1981). Identification of handwritings was effected by comparison with samples on herbarium specimens in L and MEL (National Herbarium of Victoria, Royal Botanic Gardens, Melbourne, Victoria, Australia), with correspondence lodged at L and MEL, and with data in Koster (1948).

HISTORICAL BACKGROUND

The year after Kützing (1841) established *Spongites*, Decaisne (1842a, p. 126; 1842b, p. 114; see also 1843, p. 104) subsumed it (apparently along with all other non-geniculate taxa of Corallinaceae) into *Melobesia* Lamouroux (1812), and *Spongites* became one of three subgenera ("Sectio II") recognized by Decaisne. Endlicher (1843, p. 49) followed Decaisne, but Kützing (1843a, pp. 385, 386) maintained *Spongites* as a distinct genus, referred it and other non-geniculate taxa to the family Spongitaceae (as Spongiteae), and broadened the generic limits of *Spongites* by including *Lithothamnium* Philippi (1837) and *Lithophyllum* Philippi (1837) as subgeneric groups. Because Kützing (1843a) equated Philippi's taxa with *Spongites*, he should have adopted

in 1843 one of Philippi's generic names (dating from 1837) rather than using his own (dating from 1841). In subsequent publications, Kützing (1843b, 1845, 1849, 1869) continued to recognize *Spongites* as circumscribed in 1843.

Although *Spongites* was treated as a distinct genus in some additional publications (e.g. Zanardini, 1843, 1844; Crouan & Crouan, 1852, No. 248; Ardissone, 1864; Martens, 1866; Zeller, 1877; Henriques, 1880), a series of alternative proposals appeared during the period 1846–1866. Lindley (1846, p. 25) and Harvey (1847) followed Decaisne (1842a, b, 1843) in including *Spongites* within *Melobesia*. Areschoug (1852, pp. 510, 520) in contrast, placed *Spongites* partly in *Melobesia* and partly in *Lithothamnium* Philippi, a system afterwards employed by Ardissone (1883, pp. 442, 452). Harvey (1860, p. 6) regarded *Spongites* to be congeneric with *Lithothamnium*; this arrangement also was used by Farlow (1881, p. 179), Schmitz (1889, p. 455), Schmitz & Hauptfleisch (1897, p. 542), and Hauptfleisch (1897, p. 560). Finally, Rosanoff (1866, pp. 79, 96) referred *Spongites* partly to *Lithophyllum* Philippi and partly to *Lithothamnium* Philippi. This scheme was adopted subsequently by De Toni (1905, pp. 1729, 1778), Mazza (1916–1922, pp. 1092, 1093; 1917a, p. 96; 1917b, p. 205), and Kylin (1956, pp. 205, 207). None of these proposals, however, were based on studies of Kützing's original collections or of the generitype specimens of *Melobesia, Lithothamnium*, and *Lithophyllum*. Moreover, since *Spongites* has not been lectotypified, the nomenclatural disposition of the genus never has been determined unequivocally, and thus there is no firm evidence to support any of these proposals.

Spongites apparently has not been recognized as a distinct genus since 1880, and Foslie (1898*a*, p. 3) seems to have been convinced that it should not be resurrected. Since then, only several authors (e.g. Lemoine, 1911, p. 6; Printz, 1929, pp. 16–17; Lebednik, 1977, pp. 380, 381) have mentioned *Spongites*, generally in a historical context. Farr *et al.* (1979, p. 1655) state (without providing documentation or listing species) that five of the six species originally included in *Spongites* are referrable to *Lithophyllum* and one to *Lithothamnion*; this opinion conforms to that of De Toni (1905, pp. 1743, 1779, 1783, 1786) but has not been verified by a study of the relevant type collections.

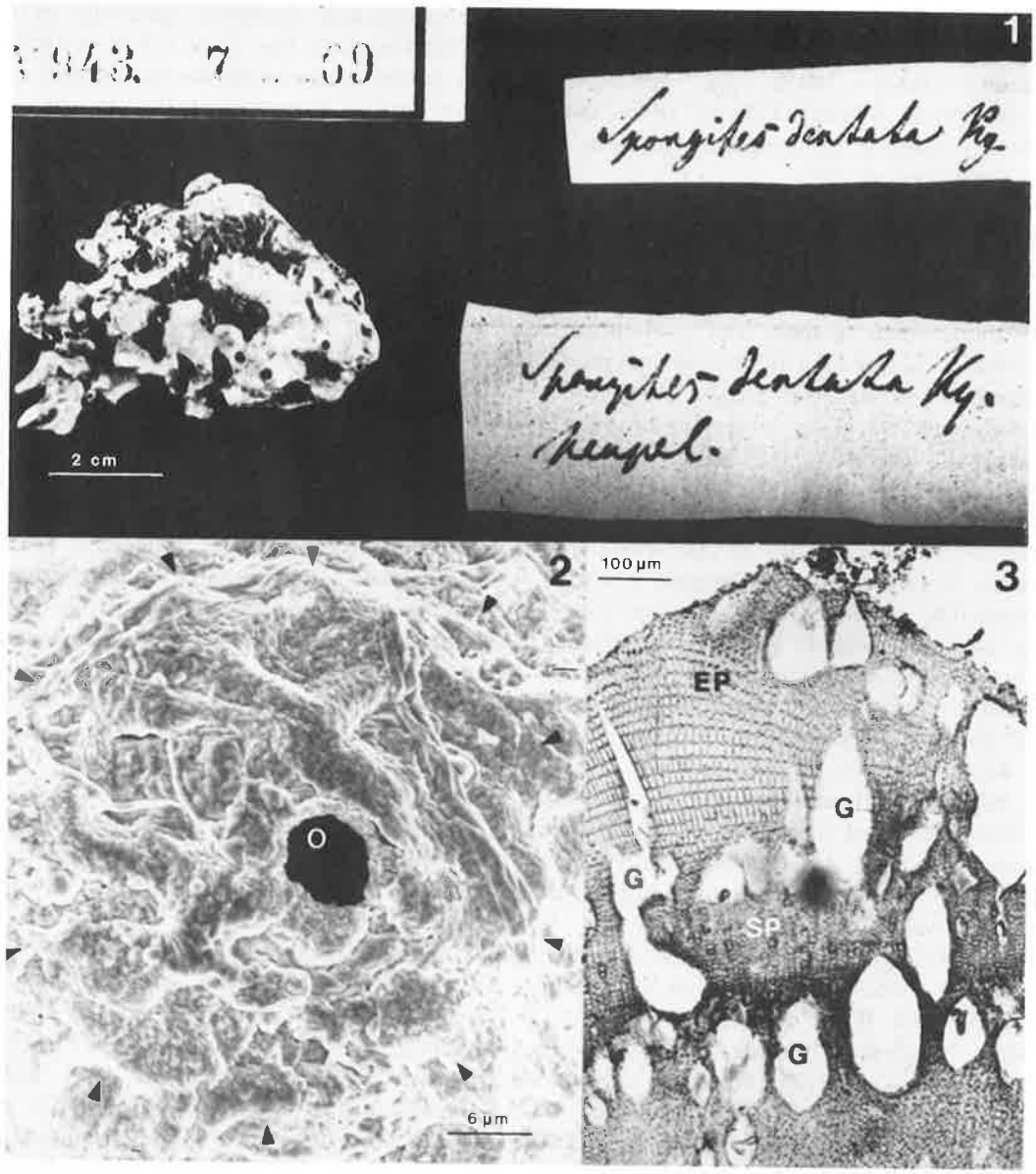
THE KÜTZING COLLECTIONS

"*Spongites dentata* Kützing"

Nomenclatural history. Kützing (1841, p. 33) established *S. dentata* for plants that consisted of greenish-red irregularly jagged calcareous masses with somewhat compressed and occasionally anastomosed branches and with conceptacles protruding as small, hollow mounds. He also remarked that this species differs from others anatomically in having more vertically elongate parenchyma cells and that, ventrally, these cells end in very thin filaments.

Since 1841, *S. dentata* Kützing has been recognized as a distinct species within the genera *Lithophyllum* (e.g. Foslie, 1898b, 1900a, 1909; Preda, 1908; Funk, 1927; Feldmann, 1939; Hamel & Lemoine, 1953; Cabioch, 1968; Bressan, 1974), *Lithothamnium* (e.g. Hauck, 1883; Foslie, 1895; Heydrich, 1897a, b), *Melobesia* (e.g. Decaisne, 1842a, b; Endlicher, 1843), and *Spongites* (e.g. Kützing, 1843a, b, 1849). It also has been listed as a species inquirenda (e.g. Areschoug, 1852) and has been treated as a distinct variety of *Lithophyllum incrustans* Philippi (Heydrich, 1901), or of *Crodelia incrustans* (Philippi) Heydrich (Heydrich, 1911).

Holotype collection. The original collection of *S. dentata* Kützing (Fig. 1) consists of a single irregularly shaped calcareous mass up to 32 mm long, 25 mm wide, and 20 mm thick, which is coarsely tuberculate and possesses excrescences of various shapes and sizes. The material probably represents a



FIGS 1–3. Holotype of *Lithophyllum dentatum* (Kützing) Foslie (*Spongites dentata* Kützing). Fig. 1. Holotype collection (L 943..7..69) with accompanying labels in Kützing's script. Fig. 2. Scanning electron micrograph of uniporate conceptacle more or less flush with thallus surface. Note ostiole (O). Arrow heads indicate margin of conceptacle roof. Fig. 3. L.S. through part of thallus showing eroded surface, elongate perithallial cells (EP), short perithallial cells (SP), and tissue gaps (G).

fragment from a larger specimen. Surface texture is more or less smooth. Few conceptacles are evident; conceptacle roofs are uniporate and scarcely protrude above the thallus surface (Fig. 2).

Anatomically, the holotype material of *S. dentata* is very similar to lectotype material of *Lithophyllum incrustans* Philippi (see Woelkerling, 1983b). Because most of the surface layer of the *S. dentata* holotype is damaged or destroyed and because there is no distinct thallus margin in the holotype specimen, information on meristems is lacking and one can only speculate that two

meristems probably are involved in vegetative thallus production as is the case for *Lithophyllum incrustans*.

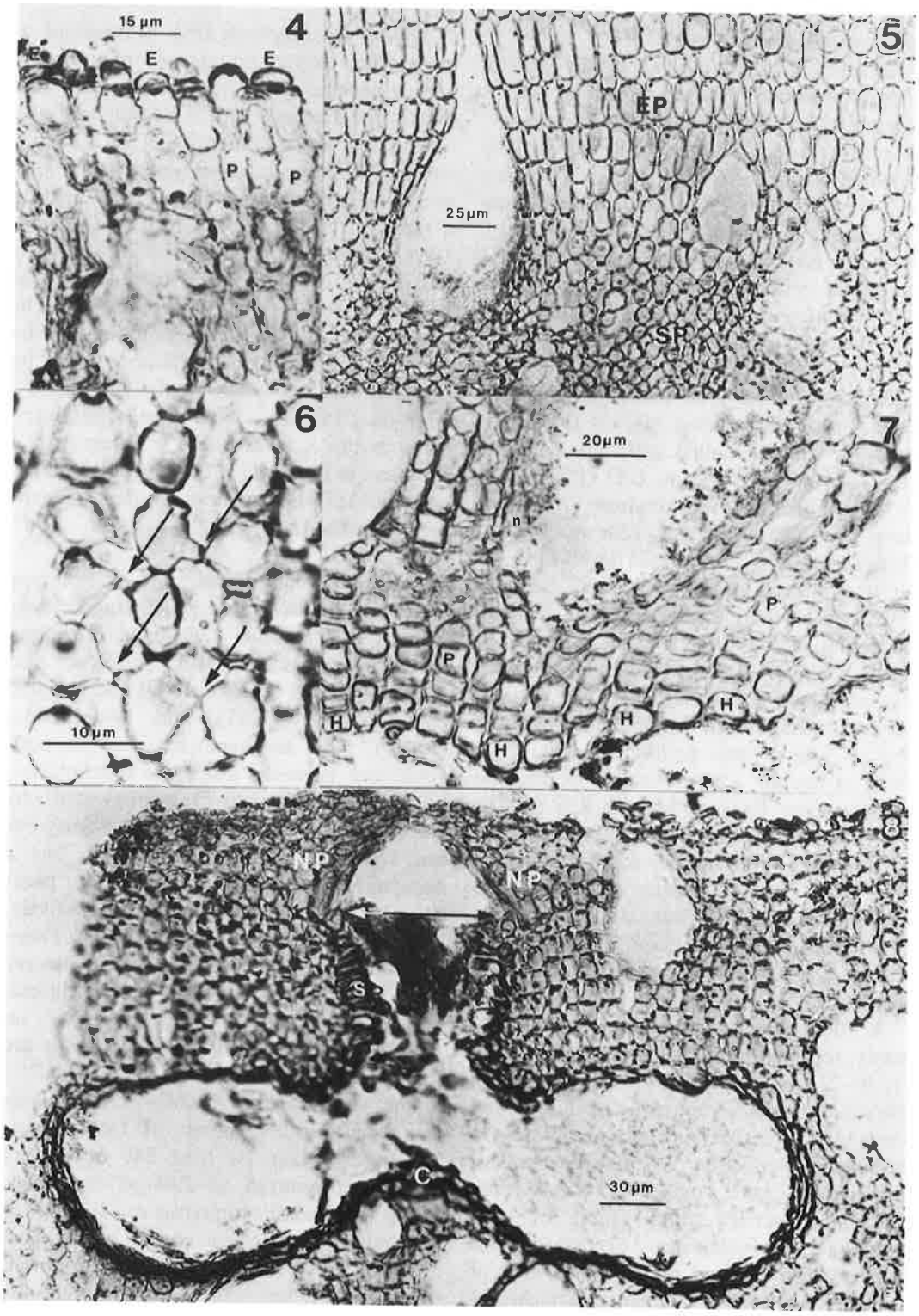
Structurally, the thallus looks the same in longitudinal and transverse sections, and is composed of numerous, readily identifiable, laterally conjoined, more or less vertically oriented filaments (Figs 3–5) which collectively appear organized into three tissues (epithallium, perithallium, hypothallium). Based on observations of several small intact areas, the epithallium (Fig. 4) is unistratose and composed of rounded to narrowly elliptical cells 3–6 μm high and 7–11 μm in diameter (H/D 0·4–0·8). The subjacent perithallium (Figs 3, 5) contains numerous layers of cells. In some regions (Figs 3, 5) most or all perithallial cells are elongate [L 12–41 μm, D 8–11 μm, L/D (1·2–) 1·8–4 (–5·1)], while in other regions (Figs 3, 4) most or all perithallial cells are squat [L 6–16 μm, D 6–11 μm, L/D 0·6–1·4 (–2·3)]. Vertical transitions between these two cell types are rather abrupt (Fig. 5), usually occurring in the space of two to four cell layers. Cells of adjacent filaments are joined by secondary pit connections (Fig. 6), and these connections are far more common in regions where squat perithallial cells occur than in regions where elongate perithallial cells develop. Reasons for this and for the presence of two distinct cell types in the perithallium are unknown. Tissue gaps (Fig. 3) of various shapes and sizes also occur in the perithallium, and some gaps extend to the thallus surface. The origin and function (if any) of these tissue gaps also are unknown.

A unistratose hypothallium (Fig. 7) subtends the perithallium. Hypothallial cells [L 10–22 μm, D 6–11 μm, L/D 1–2 (–3·2)] are square to somewhat elongate in sectional view but never become palisade-like as in *Metamastophora* (see Woelkerling, 1980a), *Lithoporella* (see Turner & Woelkerling, 1982a), or certain other genera of non-geniculate Corallinaceae. Secondary pits (but not cell fusions) may connect cells of adjacent hypothallial filaments. Attachment to the substrate probably is via cellular adhesion; neither rhizoids nor haustoria were found.

The only conceptacle (Fig. 8) observed in section was empty and was becoming buried within perithallial tissue. The chamber was 330 μm in diameter, up to 84 μm high and contained the remnants of a central columella. The ostiole was about 65 μm long and 35–50 μm in diameter, and was lined by a series of enlarged, swollen cells (Masaki, 1968, referred to these as papillary cells or papillae) comparable to those of *Metamastophora* (Woelkerling, 1980a). The conceptacle roof originally contained seven to 10 layers of cells interconnected by primary and secondary pits. Subsequently, additional tissues have been produced (presumably from the subepithallial meristem in the roof) with the result that the conceptacle was becoming buried and the ostiole covered over (Fig. 8).

Taxonomic implications. The holotype specimen of *S. dentata* Kützing clearly belongs to the genus *Lithophyllum* Philippi as circumscribed by Masaki (1968; see also Adey, Masaki & Akioka, 1974) and adopted by Johansen (1981) and Woelkerling (1983b). The lectotype material is non-geniculate, possesses uniporate conceptacles, has perithallial cells interconnected by secondary pits (cell fusions unknown) but not arranged in conspicuous tiers, has a non-palisade hypothallium, and is not parasitic (haustoria do not occur). Collectively, these characteristics distinguish *Lithophyllum* from other genera of Corallinaceae (see Woelkerling, 1983b). Nomenclatural details and related taxonomic data on *Lithophyllum dentatum* (Kützing) Foslie are summarized in Table I.

The relationships of *Lithophyllum dentatum* to other species of *Lithophyllum* remain uncertain. At least 546 other taxa have been referred to *Lithophyllum* since 1837, and until comparative studies of relevant type collections can be undertaken, it seems best not to make unsupported taxonomic judgements which potentially could create further nomenclatural and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taxonomic confusion. Comparisons of type material of *Lithophyllum dentatum* and *Lithophyllum incrustans* Philippi (see Woelkerling, 1983b) show that the two specimens are concordant anatomically. Morphologically, however, the two differ—*Lithophyllum dentatum* is coarsely tuberculate with excrescences of various shapes and sizes while *Lithophyllum incrustans* lacks excrescences totally. Attributes associated with excrescence occurrence, shape, and size have been used commonly (e.g. Hamel & Lemoine, 1953; Dawson, 1960; Taylor, 1960; Masaki, 1968; Johansen, 1976) as diagnostic characteris in *Lithophyllum*, but except for Steneck & Adey (1976), there appear to be no data on the extent of variability which can occur in these characters and thus their taxonomic value is rather uncertain. Until necessary studies are carried out, it seems best to maintain *Lithophyllum incrustans* and *Lithophyllum dentatum* as distinct species.

TABLE I. Selected nomenclatural and taxonomic data on *Spongites confluens* (= *Lithophyllum incrustans*), *S. dentata*, and *S. nodosum*

Lithophyllum dentata (Kützing) Foslie, 1898b, p. 10
Basionym: *S. dentata* Kützing, 1841, p. 33
Other synonyms:
Lithothamnium dentatum (Kützing) Hauck, 1883, p. 273 (non Capeder, 1900, p. 178)
Melobesia dentata (Kützing) Decaisne, 1842a, p. 126
Crodelia incrustans f. *dentata* (Kützing) Heydrich, 1911, p. 16
Lithophyllum incrustans f. *dentata* (Kützing) Heydrich, 1901, p. 190
Type locality: Gulf of Neapel, Italy
Lectotype specimen: L 943 . . 7 . . 69 (see Fig. 1)

Lithophyllum incrustans Philippi
Synonyms:
S. confluens Kützing, 1841, p. 32. [Type locality: Spalato (Adriatic Sea) Italy. Lectotype specimen: L 943 . . 7 . . 78 (see Fig. 9), growing with lectotype specimen of *S. racemosa* Kützing]
Lithothamnion polymorphum f. *confluens* (Kützing) Vinassa, 1892, p. 59
Note: Additional nomenclatural and taxonomic data on *Lithophyllum incrustans* are provided by Woelkerling (1983b)

Lithothamnion nodosum (Kützing) comb. nov.
Basionym: *S. nodosa* Kützing, 1841, p. 32
Other synonym: *Melobesia nodosa* (Kützing) Decaisne, 1842a, p. 126
Type locality: Mediterranean Sea
Lectotype specimen: L 943 . . 7 . . 79 (see Fig. 14)

"*Spongites confluens* Kützing"

Nomenclatural history. Kützing (1841, p. 32) established *S. confluens* for plants with the following characteristics: (1) thallus forming a stony grey–violet crust with a smooth uneven upper surface and with excrescences irregular and merging into one another so as to produce a wave-like appearance; (2) "Fruchthöhlen" (conceptacles?) smaller than in other species and not prominent on the upper thallus surface; (3) thallus cells in section arranged in distinct, regular horizontal and vertical rows; and (4) contiguous cells interconnected by tubules (i.e. primary and secondary pits). Kützing noted that *S. confluens* was growing together with *S. racemosa* (q.v.) on a conglomerate, and he remarked that *Lithophyllum incrustans* Philippi (1837, p. 388) may be conspecific with *S. confluens* but that his (Kützing's) specimens did not look like the Ellis illustration (1755, pl. 27, fig. 2dD) mentioned by Philippi. Kützing (1869, pl. 97) subsequently illustrated the type specimen.

Since 1841, *S. confluens* has been recognized as a distinct species (e.g. Kützing, 1843a, b, 1845, 1849, 1869), has been treated as a species inquirenda (e.g. Areschoug, 1852, p. 519), has been regarded as a distinct form (Vinassa, 1892, p. 59; Foslie, 1900b, p. 19) of *Lithothamnium polymorphum* (L.) Areschoug and has been placed into synonomy with *Lithophyllum incrustans*

FIGS 4–8. Holotype of *Lithophyllum dentatum*. Fig. 4. L.S. showing isolated epithallial cells (E) and subtending perithallial cells (P). Fig. 5. Transition between a region of elongate perithallial cells (EP) and short perithallial cells (SP). Fig. 6. Secondary pit connections (arrows) between cells of adjacent perithallial filaments. Fig. 7. L.S. showing part of unistratose hypothallium (H) and lower part of perithallium (P). Fig. 8. T.S. of uniporate conceptacle. Note swollen cells (S) lining the ostiole, remnants of a columella-like structure (C), original position of ostiole at surface (arrow) and production of new perithallial tissue (NP) above roof which will result in the conceptacle becoming buried.

Philippi (e.g. Solms-Laubach, 1881, p. 16; De Toni, 1905, p. 1786; Foslie, 1908, p. 272; Lemoine, 1911, p. 121), or with *Lithothamnium incrustans* f. *harveyi* Foslie (e.g. Foslie, 1895, p. 122), or with *Lithothamnium polymorphum* (L.) Areschoug (e.g. Ardissone, 1883, p. 452; Hauck, 1883, p. 272; Piccone, 1889, p. 51), or with *Lithophyllum racemus* (Lamouroux) Foslie (e.g. Mazza, 1916–1922, p. 1135; 1917b, p. 205). Except for Kützing's, none of these taxonomic judgements were based on studies of the original collections of *S. confluens*.

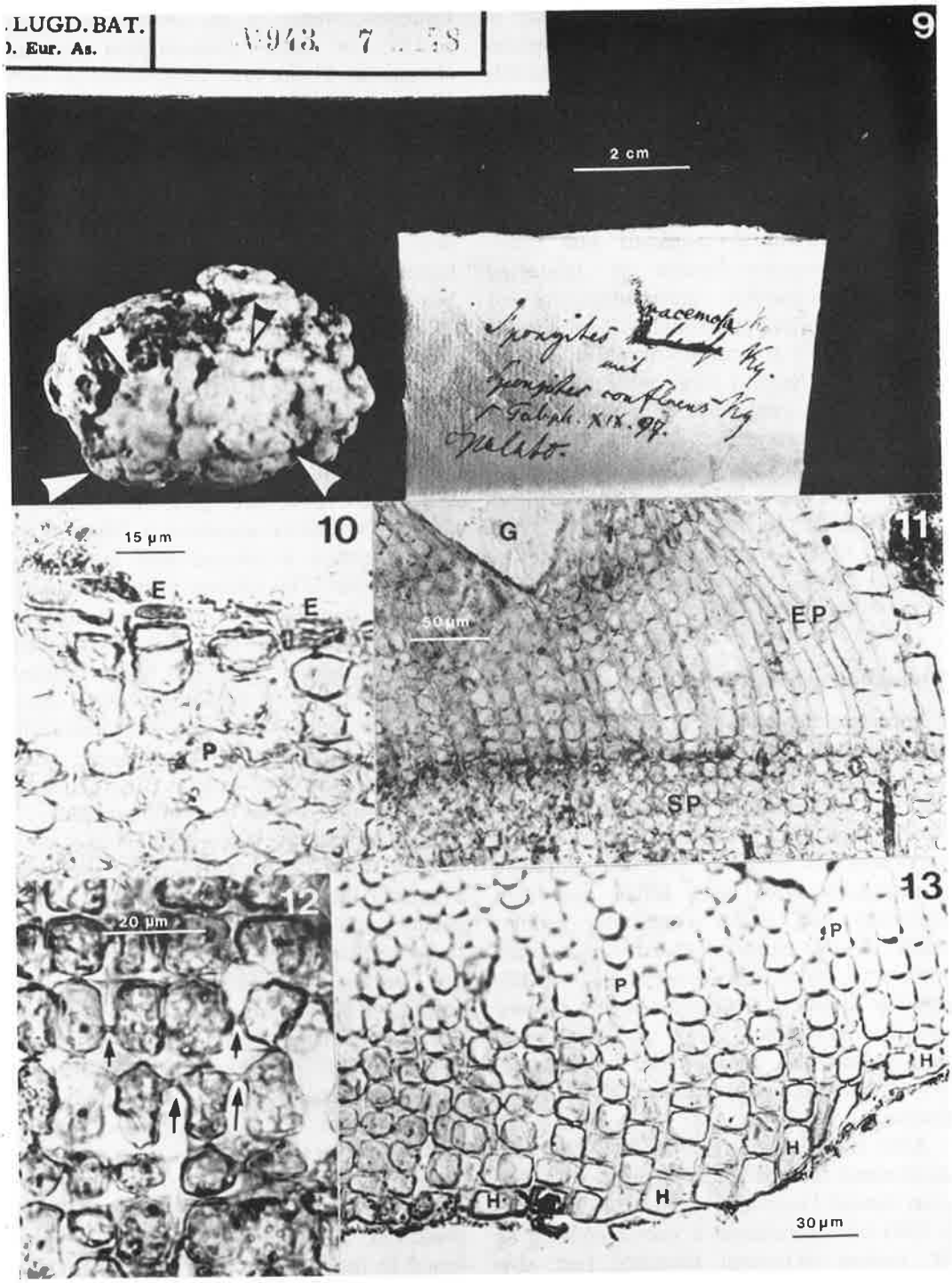
Holotype collection. The original collection of *S. confluens* Kützing (Fig. 9) consists of a single adnate crust up to 30 mm long, 20·5 mm broad, and 3·5 mm thick which is growing over the surface of the holotype collection of *S. racemosa* Kützing (q.v.). The upper surface appears to have a dull luster, is more or less undulate (contoured over the host surface), and bears a series of weakly protuberant mounds. Conceptacles were not apparent.

The vegetative anatomy of *S. confluens* (Figs 10–13) closely resembles that of *S. dentata* (Figs 3–8). Much of the unistratose epithallial layer appears damaged or lost (Fig. 10) and relatively few more or less transversely compressed epithallial cells were observed (H 3–8 μm, D 8–14 μm, H/D 0·3–0·8). The perithallium (Figs 11, 12) is multistratose and composed of cells that are mostly 8–14 μm long and 5–11 μm in diameter [L/D (0·7–) 1–2·2]. Occasional small groups of more elongate cells (L 14–41 μm, D 8–11 μm, L/D 1·5–4) occurred, but far less extensively than in *S. dentata*. Transitions between longer and shorter perithallial cells were quite abrupt (Fig. 11). Secondary pit connections (Fig. 12) were common between cells of adjacent filaments; cell fusions were not observed. Some tissue gaps comparable to those in *S. dentata* also were present (Fig. 11). A unistratose hypothallium (Fig. 13) of squarish to some elongate but not palisade-like cells [L 8–25 μm, D 11–19 μm, L/D (0·60) 1–1·7 (–2·3)] subtends the perithallium, and cells of adjacent hypothallial filaments also are interconnected with secondary pits. Attachment to the substrate is by hypothallial cellular adhesion; no rhizoids or haustoria were found.

The specimens appear to be sterile; no conceptacle like structures occurred in the material examined. Kützing's (1841, p. 32) reference to "Fruchthöhlen" which were smaller than in other species and which did not occur on the upper surface may concern tissue gaps rather than conceptacles.

Taxonomic disposition. Because the holotype collection of *S. confluens* Kützing appears to be sterile, the proper disposition of this taxon is attended by some uncertainty. The vegetative thallus, however, possesses seven characters which allow for proper generic assignment. These are: (1) the absence of geniculae; (2) the occurrence of secondary pit connections; (3) the absence of vegetative cell fusions; (4) rounded (not angular) epithallial cells; (5) a multistratose perithallium composed of cells that are not extremely elongate or aligned in conspicuous regular tiers (see Woelkerling, 1983a, fig. 15); (6) a non-palisade hypothallium; and (7) non-parasitic (no haustoria). The only currently recognized genus of Corallinaceae possessing the above combination of characteristics is *Lithophyllum* (see Woelkerling, 1983b).

While it is possible to place the holotype material of *S. confluens* into *Lithophyllum* with reasonable confidence, its status at the species level is less certain. In terms of vegetative morphology and anatomy, the lectotype specimens of *S. confluens* and *Lithophyllum incrustans* are so similar that they normally would be considered conspecific. Because the lectotype specimen of *S. confluens* is sterile, however, it may never be possible to determine whether these two taxa possess the same reproductive features. In these circumstances, two solutions are possible: (a) transfer *S. confluens* to *Lithophyllum* and maintain the taxon as a questionably distinct species; or (b) refer *S. confluens* to the synonomy of *Lithophyllum*



FIGS 9–13. Holotype of *Spongites confluens* Kützing (= *Lithophyllum incrustans* Philippi). Fig. 9. Holotype plant (arrow heads) and accompanying notes in Kützing's script (part of L 943..7..78). Fig. 10. L.S. showing several epithallial cells (E) and subtending perithallium (P). Fig. 11. Transition zone between a region of elongate perithallial cells (EP) and short perithallial cells (SP). Note portion of a tissue gap (G). Fig. 12. Secondary pit connections (arrows) between cells of adjacent perithallial filaments. Fig. 13. L.S. showing unistratose hypothallium (H) and lower portions of perithallium (P).

incrustans. The first solution would result in maintaining *S. confluens* as a dubious species in the algal literature, one of many currently assigned to *Lithophyllum*. The second solution would result in removing *S. confluens* from further consideration as an independent species and avoid making a new nomenclatural combination. Given that sterile plants of *S. confluens* and *Lithophyllum incrustans* cannot be delineated from one another morphologically or anatomically, and given that comparisons of reproductive structures may never be possible, the second solution seems preferable, and *S. confluens* Kützing is hereby considered conspecific with *Lithophyllum incrustans* Philippi. This arrangement follows that used by some earlier authors (e.g. Solms-Laubach, 1881; De Toni, 1905; Foslie, 1908; Lemoine, 1911). Nomenclatural details and related taxonomic data are summarized in Table I.

"*Spongites nodosa* Kützing"

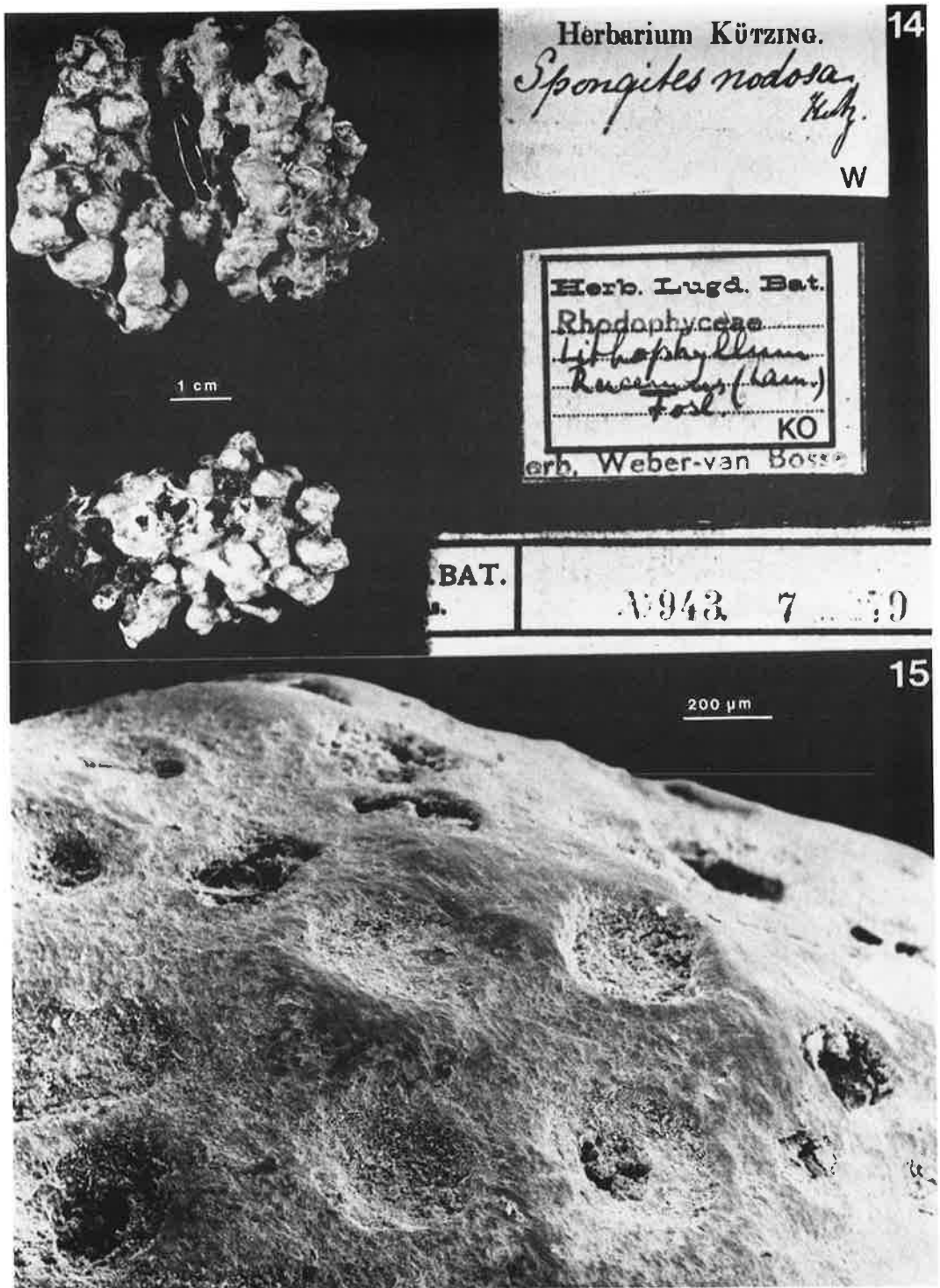
Nomenclatural history. Kützing (1841, p. 32) established *S. nodosa* for plants that formed branched nodular mounds up to the size of a fist, that possessed large nodular protuberances made up of smaller knobby protuberances which in turn bore very small papillate conceptacles often with pores, and that internally had starch containing cellular tissue. He also remarked that this is the only species to which Linnaeus' words "cellulis seriatus" apply in the diagnosis of *Cellepora spongites* (Linnaeus, 1767, p. 1286), when one understands thereby the conceptacles (Fruchthöhlen) in the crevices of the stony thallus.

After 1841, Kützing (1843a, b, 1849, 1869) maintained his species as *Spongites nodosa*, even though Decaisne (1842a, p. 126; 1842b, p. 114) had transferred it into *Melobesia* as *M. nodosa* (Kützing) Decaisne (see also Endlicher, 1843, p. 50), and Areschoug (1852, p. 525) had relegated it to the status of species inquirenda. Subsequently, *S. nodosa* has been placed into synonomy with *Lithothamnium racemus* Areschoug (Solms-Laubach, 1881, p. 18; Ardissone, 1883, p. 453) or with *Lithophyllum racemus* (Lamarck) Foslie (De Toni, 1905, p. 1779; Mazza, 1916–1922, p. 1135; 1917b, p. 205).

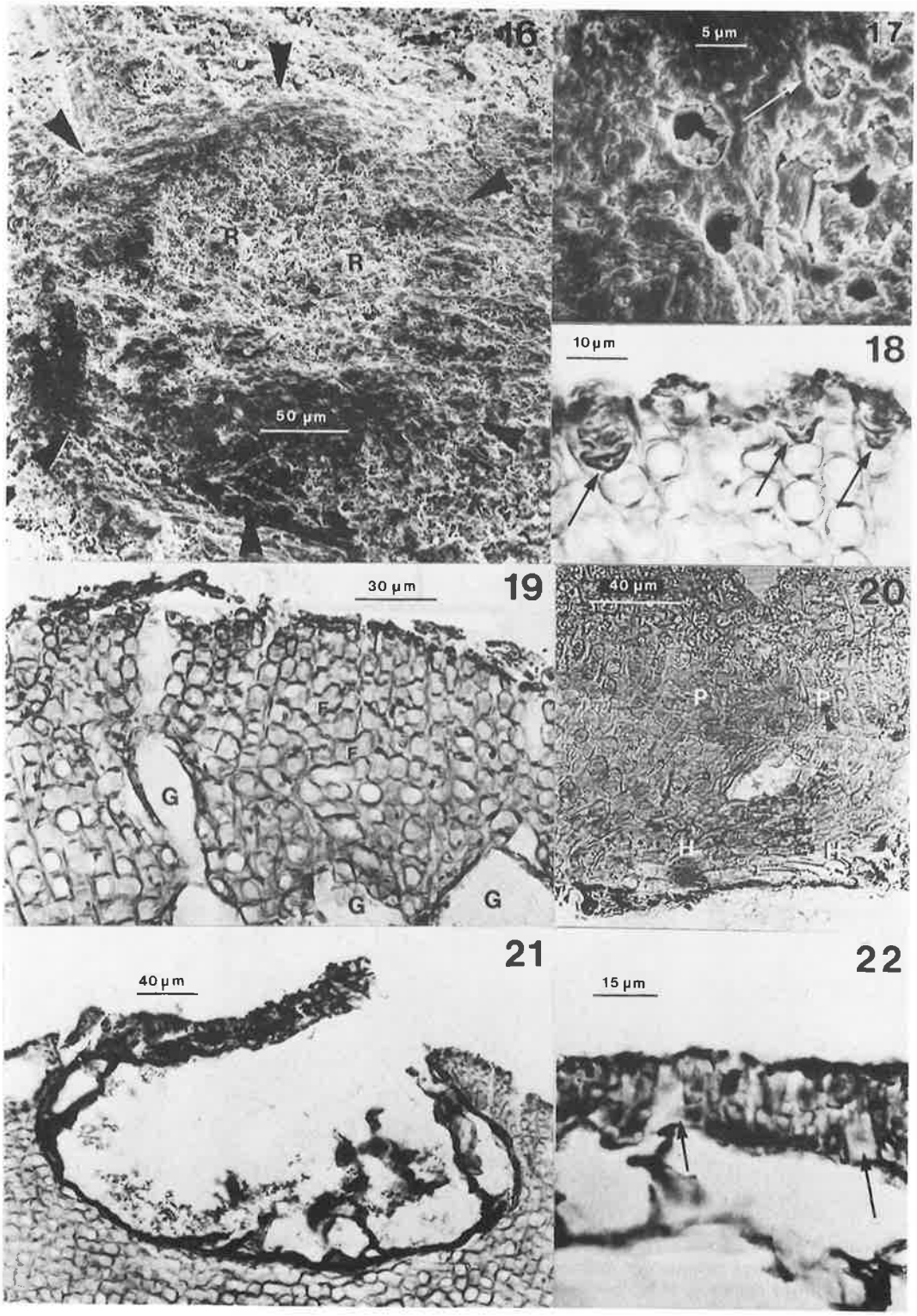
Lectotype collection. The original collection of *S. nodosa* Kützing (Fig. 14) survives as two fragments (designated here as the lectotype element); the larger is more or less box-like (up to 46 mm long, 40 mm broad, 27 mm thick) while the smaller is more or less compressed-torulose and up to 41 mm long, 25 mm broad, and 20 mm thick. Both specimens possess a number of irregularly knobby, more or less furcate excrescences 2–8 mm in diameter which protrude from the basal crust and give the thallus a coarsely verrucose appearance. Most of the thallus surface is covered with multiporate conceptacles (Fig. 15) but most conceptacle roofs are damaged or completely destroyed. Intact conceptacles are either somewhat sunken or are more or less frustoconiform (Fig. 16) and may protrude slightly above the surrounding tissues; the centrally flattened portions of conceptacle roofs contain a number of ostioles (Fig. 17), some of which are blocked by sporangial plugs.

Structurally, the lectotype material of *S. nodosa* (Figs 18–20) consists of numerous filaments firmly joined laterally to form a pseudoparenchymatous thallus. Although three types of tissue were identifiable, it was not possible to determine whether the vegetative system develops from one or two distinct meristems and thus the terms "perithallium" and "hypothallium" are used here (in quotes) in the older traditional sense (see Johansen, 1976) and do not imply a particular sort of tissue ontogeny (see Turner & Woelkering, 1982a).

The epithallium was in general poorly preserved, and only scattered cells were found in the material examined. These cells (H 3–4 μm, D 6–7 μm, H/D 0·5–0·6), however, were periclinally flattened in a sectional view (Fig. 18) and appeared angular in outline. The "perithallium" (Fig. 19) contains numerous layers of more



FIGS 14, 15. Lectotype collection of *Lithothamnion nodosum* (Kützing) comb. nov. (*Spongites nodosa* Kützing).
Fig. 14. Lectotype element (L 943 . . 7 . . 79) with accompanying labels of Koster (KO) and Weber van Bosse (W).
Fig. 15. Thallus surface showing multiporate conceptacles (most with damaged roofs).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or less quadrate to somewhat elongate cells [L 6–12 μm; D 6–11 μm; L/D (0·7–) 1·2]. Increase in thallus thickness presumably is effected from a subepithallial meristem and, judging from the size of cells derived from this meristem (Figs 18, 19), cellular elongation is confined largely to the meristem (see Adey & Johansen, 1972). Fusions (Fig. 19) occurred commonly between cells of contiguous filaments; secondary pit connections were not seen. Tissue gaps (Fig. 19) of various shapes and sizes also were evident in the "perithallium". The small portion of "hypothallium" observed (Fig. 20) was multistratose, non-coaxial and contained cells 11–19 μm long and 6–8 μm in diameter (L/D 1·4–3).

Few intact conceptacles were seen and none contained tetrasporangia (Fig. 21). Two conceptacle chambers measured were 131 and 163 μm high and 303 μm in diameter. Conceptacle roofs contained up to six layers of cells, and in one instance (Fig. 22) the remains of two tetrasporangial plugs were found in pores. Cells adjacent to the plugs showed no intense staining and fusions were evident between cells of adjacent roof filaments. Whether conceptacles become buried within the "perithallium" in time remains uncertain; only one possible conceptacle was encountered within "perithallial" tissue.

Taxonomic implications. The lectotype material of *S. nodosa* Kützing almost certainly belongs to the genus *Lithothamnion* as currently delineated by Johansen (1976) and by Woelkerling (1983a). Lectotype plants are non-geniculate, possess multiporate tetrasporangial conceptacles, and have fusions occurring between cells of contiguous vegetative filaments, an epithallium containing cells which appear more or less angular in section, a subepithallial meristem to which cellular elongation is largely confined, and a multistratose "perithallium" and multistratose, non-coaxial "hypothallium". Collectively, these characteristics distinguish *Lithothamnion* from other genera of Corallinaceae. Nomenclatural details and related taxonomic data on *Lithothamnion nodosum* (Kützing) comb. nov. are summarized in Table I.

The relationships of *Lithothamnion nodosum* to other species of *Lithothamnion* remain uncertain. At least 729 other taxa have been referred to *Lithothamnion*, and species concepts within the genus are poorly understood. Until comparative studies of relevant type collections can be undertaken and until species concepts have been re-evaluated in a modern context, it seems best to retain *Lithothamnion nodosum* as a distinct species to avoid making unsound taxonomic judgements and creating further potential confusion nomenclaturally or taxonomically.

"*Spongites fruticulosa* Kützing"

Nomenclatural history. Kützing (1841, p. 33) established *S. fruticulosa* for plants which formed cushion-like, spongy, stalactite-like calcareous masses consisting of racemose aggregates of fruticose branchlets which are anastomosed to one another to form a sponge-like thallus. He provided no details of internal structure.

After 1841, Kützing (1843a, b, 1849, 1869) retained *S. fruticulosa* within *Spongites*, while Decaisne (1842a, b) transferred it to *Melobesia* [as *M. fruticulosa* (Kützing) Decaisne] and was followed by Endlicher (1843). Areschoug (1852, p. 525), in contrast, listed *S. fruticulosa* as a species inquirenda, and Solms-Laubach (1881,

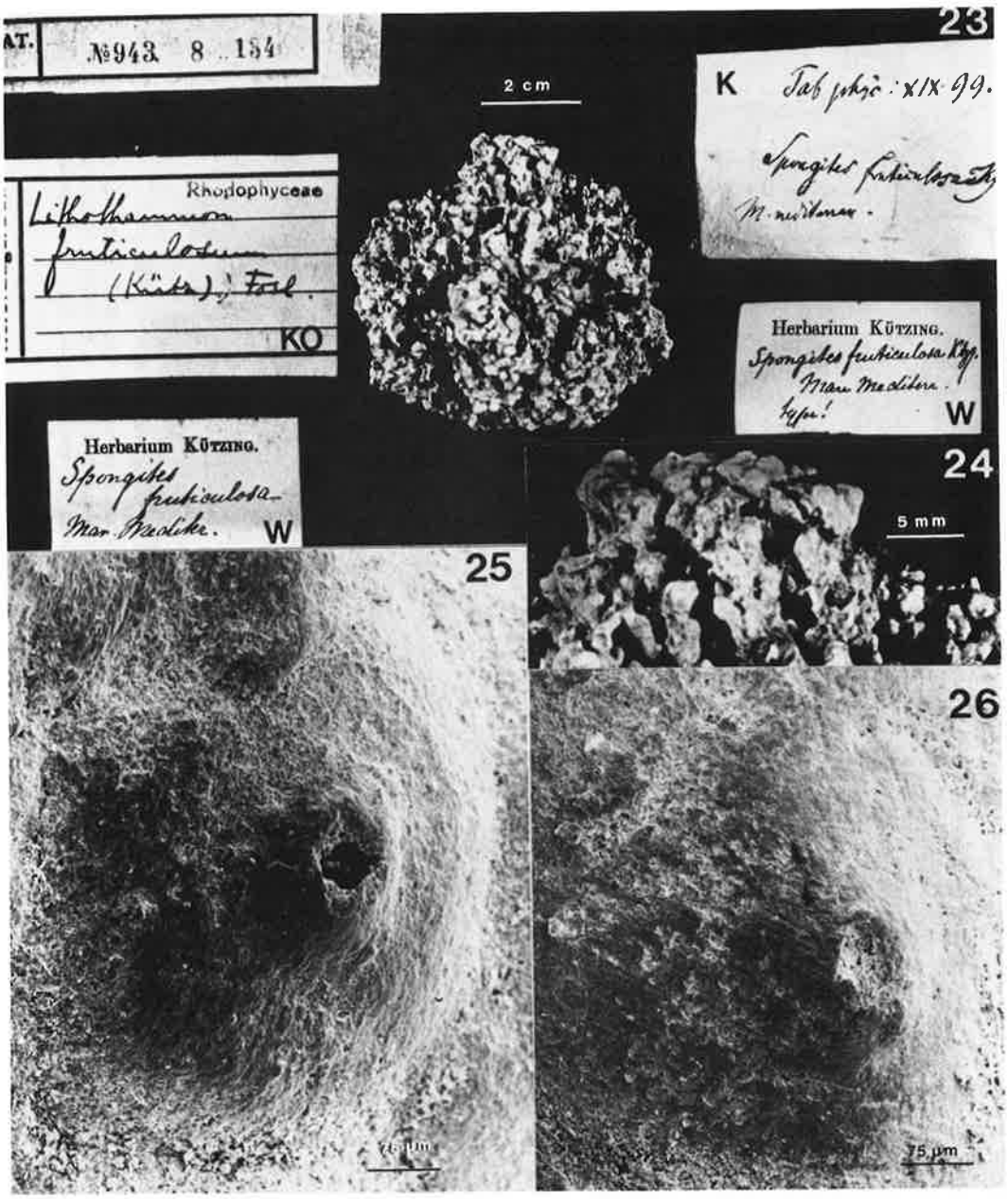
FIGS 16–22. Lectotype collection of *Lithothamnion nodosum*. Fig. 16. Frustoconiform multiporate conceptacle with intact roof (R). Arrow heads indicate margin of conceptacle roof. Fig. 17. Ostioles of conceptacle roof. Note plug blocking one ostiole (arrow). Fig. 18. L.S. of thallus showing several angular epithallial cells (arrows). Fig. 19. L.S. of thallus showing upper portion of "perithallium", fusion (F) between cells of adjacent filaments, and portions of several tissue gaps (G). Most epithallial cells are missing. Fig. 20. L.S. of thallus showing poorly preserved "hypothallium" (H) and lower portion of "perithallium" (P). Fig. 21. Tetrasporangial conceptacle at thallus surface. Fig. 22. Portion of conceptacle roof showing remains of two tetrasporangial plugs (arrows) in ostioles.

p. 19) considered it to be conspecific with *Lithothamnium ramulosum* Philippi. Hauck (1883, p. 274), however, and later Vinassa (1892), treated Kützing's taxon as *Lithothamnium fasciculatum* (Lamarck) Areschoug f. *fruticulosum* (Kützing) Hauck. Foslie (1895, p. 46) then raised it to species level as *Lithothamnium fruticulosum* (Kützing) Foslie, a judgement accepted by most subsequent authors (e.g. Debray, 1897; De Toni, 1905, 1924; Preda, 1908; Lemoine, 1915, 1920, 1964; Funk, 1927, 1955; Printz, 1929; Hamel & Lemoine, 1953; Dawson, 1960; Bressan, 1974; Cinelli *et al.*, 1976). At first Heydrich (1897a, b) accepted Foslie's placement, but subsequently Heydrich (1900, 1908) placed Kützing's taxon in *Paraspora* Heydrich as *Paraspora fruticulosa* (Kützing) Heydrich. *Paraspora fruticulosa* is the type species of *Paraspora* (see Silva in Farr *et al.*, 1979); the genus has not been recognized by subsequent authors, and it is a later homonym of *Paraspora* Grove (1884).

Holotype collection. The original collection of *S. fruticulosa* (Fig. 23) consists of a single more or less globose calcareous mass of conjoined excrescence-like branches; the specimen, up to 62 mm in diameter, agrees nicely with Kützing's protologue account. Excrescences (Fig. 24) are mostly 1·5–4 mm in diameter and variously irregularly furcate. Some excrescences are reasonably intact, but others are broken or eroded and most of the thallus surface appears worn. Uniporate conceptacles (Fig. 25) are scattered over the excrescences; conceptacle roofs are more or less domoid (sometimes with a slightly conoid peak) and protrude to varying degrees above the thallus surface. Ostioles of immature conceptacles (Fig. 26) appear to be blocked by some sort of plug-like material which is not associated with the sporangia.

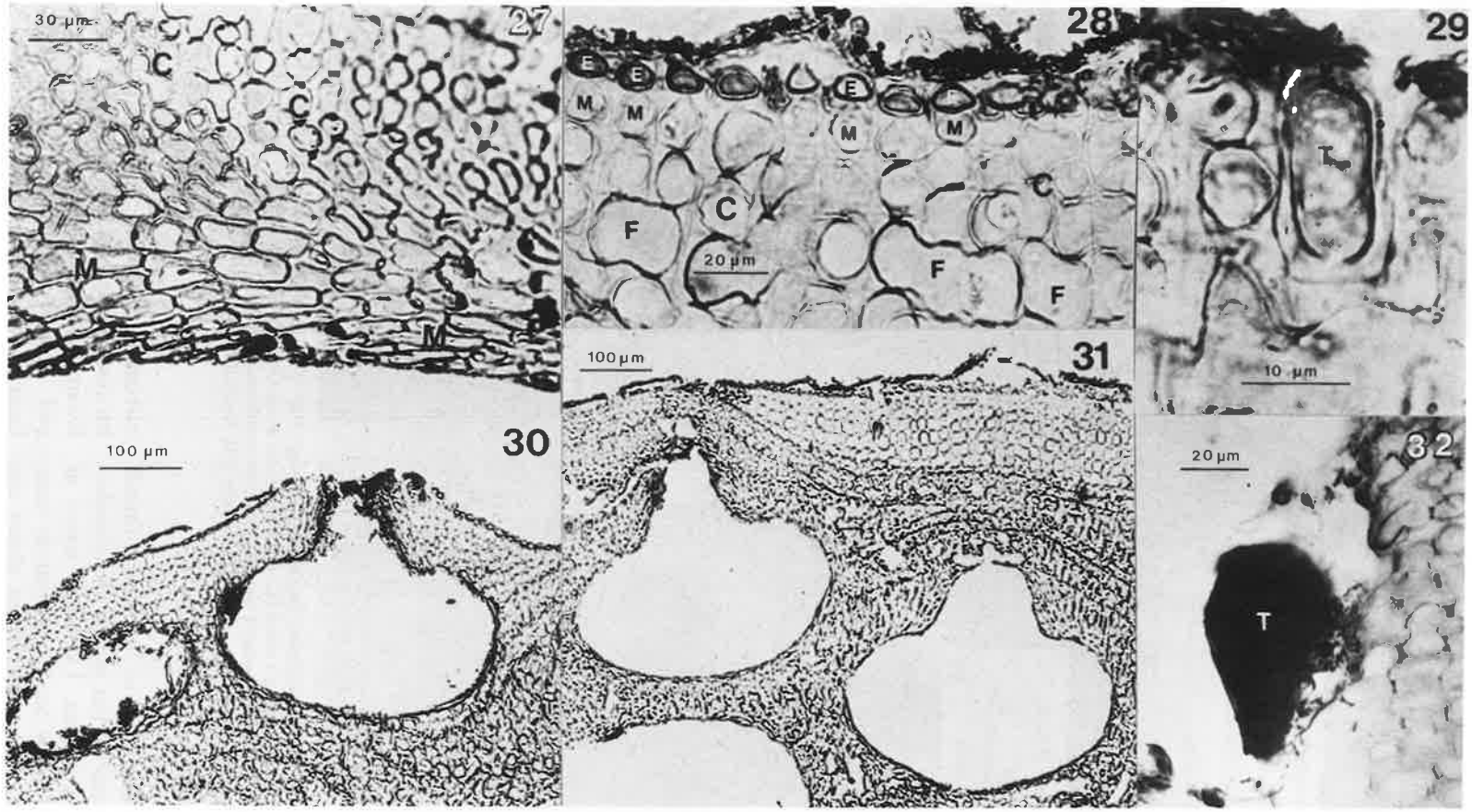
Anatomically, the thallus consists of numerous contiguous filaments (Figs 27–31) more or less firmly united into a pseudoparenchymatous mass in which three regions are recognizable. The number of meristems involved in vegetative thallus development is uncertain, but because individual filaments can be traced readily through all three regions, it seems likely that only a single meristem is present, and thus the internal regions will be referred to as medulla and cortex rather than hypothallium and perithallium. (For detailed discussions of meristem and tissue terminology, see Turner & Woelkerling, 1982a; Woelkerling, 1980a.) Older portions of filaments form a non-coaxial, multistratose medulla (Fig. 27) in which the axes of most cells [L 11–38 µm; D 6–11 µm; L/D 1·4–4 (–4·8)] lie more or less parallel with the thallus surface. Medullary filaments which become displaced towards the ventral thallus surface are not involved in further tissue development (Fig. 27). Filaments displaced dorsally, however, become oriented with long axes more or less perpendicular to the thallus surface, and collectively these filaments may be divided into two further regions: the epithallium and the cortex. The epithallium (Fig. 28) is unistratose, occurs at the thallus surface, and is composed of rounded or transversely compressed cells 5–8 µm high and 8–14 µm in diameter (H/D 0·4–0·8). The subtending cortex (Figs 28, 30, 31) contains numerous layers of cells (8–) 11–20 (–25) µm long and 8–16 µm in diameter (L/D 1·0–1·8). Thallus growth probably results from a meristematic layer situated just beneath the epithallium and cellular elongation appears to be confined largely to the meristem, the cells of which resemble their immediate basipetal derivatives (Fig. 28). Fusions between cells of contiguous filaments are common in the cortex (Fig. 28), occasional in the medulla, but are absent in the epithallium. Some cortical cells also contain floridean starch granules. Thick-walled solitary trichocytes (Fig. 29) up to 27 µm long and 14 µm broad occurred occasionally at the thallus surface but were not observed within the cortex. Secondary pit connections were not observed.

Conceptacles (Figs 30, 31) possess more or less ovoid chambers up to 385 µm in diameter and 222 µm in height and are uniporate. Ostioles up to 111 µm long with a



FIGS 23–26. Holotype of *Spongites fruticulosa* Kützing. Fig. 23. Holotype specimen (L 943 . . 8 . . 134) with accompanying label in Kützing's script (K) and subsequent annotations by Koster (KO) and Weber van Bosse (W). Fig. 24. Portion of holotype specimen showing fruticose excrescences. Fig. 25. Mature uniporate conceptacle with open ostiole. Fig. 26. Immature uniporate conceptacle with blocked ostiole.

surface diameter of up to 74 µm were found; ostiole diameter at the top of the chamber ranged up to 148 µm. Up to 10 layers of cortical cells have been observed in conceptacle roofs which protruded above the surrounding thallus surface; cell fusions between contiguous filaments were common. Eventually conceptacles become overgrown and buried within the cortex (Fig. 31). Details of conceptacle formation are



FIGS 27–32. Holotype of *Spongites fruticulosa*. Fig. 27. L.S. of thallus showing medulla (M) and lower portion of cortex (C). Fig. 28. L.S. showing epithallium (E), subtending cortex (C), subepithallial meristem cells (M), and fusions (F) between cells of adjacent cortical filaments. Fig. 29. L.S. showing trichocyte (T) at thallus surface. Fig. 30. Uniporate conceptacle at thallus surface. Fig. 31. Uniporate conceptacle buried within the thallus cortex. Fig. 32. Remnants of probable tetrasporangium (T) in a buried conceptacle.

uncertain, but no evidence for the occurrence of a columella could be found. In one conceptacle, remnants of a probable tetrasporangium (Fig. 32) were present.

Taxonomic implications. The holotype specimen of *S. fruticulosa* is referrable to the genus *Neogoniolithon* as delineated by Hamel & Lemoine (1953), Adey (1970), Cabioch (1972), and Johansen (1976, 1981), but it does not conform to the original concept of *Neogoniolithon* put forth by Setchell & Mason (1943). The status and circumscription of *Neogoniolithon* and its relationships to the genus *Spongites* are considered in detail in the Discussion, and since these matters affect the disposition of *S. fruticulosa*, its generic placement will be considered at that time.

Since at least 1883, Kützing's epithet "fruticulosum" has been misapplied widely to a species with far different characteristics than those evident in the lectotype specimens of *S. fruticulosa*. Hauck (1883, p. 274, pl. 3, figs 10, 11, pl. 5, figs 4, 5) reported multiporate tetrasporangial conceptacles in plants he referred to Kützing's taxon [as *Lithothamnion fasciculatum β fruticulosa* (Kützing) Hauck]. Foslie (1895, p. 46), who examined some of Hauck's specimens, also reported multiporate tetrasporangial conceptacles and raised Kützing's taxon to species rank [as *Lithothamnium fruticulosum* (Kützing) Foslie]. Neither Hauck nor Foslie ever examined Kützing's specimens; nevertheless since 1900 nearly all authors (e.g. Foslie, 1904; De Toni, 1905; Pilger, 1908; Funk, 1927, 1955; Printz, 1929; Hamel & Lemoine, 1953; Dawson, 1960; Bressan, 1974) have followed Foslie (1895) and have applied Kützing's name to specimens with multiporate conceptacles. Dixon & Irvine (1976, p. 534) noted, however, that *Lithothamnion fruticulosum* required nomenclatural reinvestigation. Results from the present study provide unequivocal evidence that the modern concepts of Kützing's "fruticulosum" in no way agree with the lectotype specimens of *S. fruticulosa* Kützing. Thus considerable confusion exists over the use of Kützing's name in the literature, and caution must be exercised when referring to published records of this taxon. The correct name for the taxon to which Kützing's epithet "fruticulosum" has been misapplied has not been determined. If (as seems to be the case judging from the account of Hamel & Lemoine, 1953), this taxon belongs to *Lithothamnion* [as circumscribed by Johansen (1976) and Woelkerling (1983a)], then over 700 possibilities for names already exist; however, a comparison of relevant type collections with specimens erroneously referred to "fruticulosum" to determine which epithet is correct is beyond the scope of the present study.

"*Spongites racemosa* Kützing"

Nomenclatural history. Kützing (1841, p. 32) established *S. racemosa* for plants with the following characteristics: (1) thallus forming nodules of various sizes; upper thallus surface covered by prominent warty protuberances; (2) protuberances as large as a pea, separated from one another by distinct cavities but occurring in racemose clusters; (3) protuberances possessing small papillae (the protruding conceptacles); (4) internal structure less well-organized than in *S. confluens* and cells lacking lateral (secondary) pit connections; and (5) cell fusions present. Kützing also remarked that his plants bore resemblance to those figured by Ellis & Solander (1786, pl. 41, fig. 4) and that perhaps *Lithothamnium crassum* Philippi was the same as *S. racemosa*.

Although Kützing (1843a, b, 1845, 1849) subsequently continued to recognize his taxon as *S. racemosa*, Decaisne (1842a, b) transferred it to *Melobesia* as *M. racemosa* (Kützing) Decaisne and was followed by Endlicher (1843, p. 49). Areschoug (1852, p. 521), in contrast, placed *S. racemosa* into synonymy with *Lithothamnium racemus* (Lamarck) Areschoug, a judgement accepted by Solms-Laubach (1881, p. 18) and Ardissone (1883, p. 453). *Spongites racemosa* also has been placed into synonomy with *Lithophyllum racemus* (Lamarck) Foslie

FIGS 33, 34. Lectotype of *Spongites racemosa* Kützing. Fig. 33. Lectotype element (part of L 943 . . 7 . . 78) with accompanying labels in Kützing's script (K) and subsequent annotations by Koster (KO) and Weber van Bosse (W). Fig. 34. Portion of thallus surface showing two uniporate conceptacles.

(Mazza, 1916–1922, p. 1135; 1917b, p. 205), with *Lithophyllum incrustans* Philippi (De Toni, 1905, p. 1786; Preda, 1908, p. 24; Mazza, 1916–1922, p. 1143; 1917b, p. 213), with *Lithothamnion incrustans* (Philippi) Foslie (Foslie, 1895, p. 123) and with *Lithothamnion crassum* Philippi (Piccone, 1889, p. 51). None of these taxonomic opinions were based on studies of the relevant type collections.

Lectotype collection. The original collection of *S. racemosa* Kützing (Fig. 33) includes one large, more or less ovoid specimen up to 55 mm long and 44 mm in diameter and five small fragments all less than 16 mm in

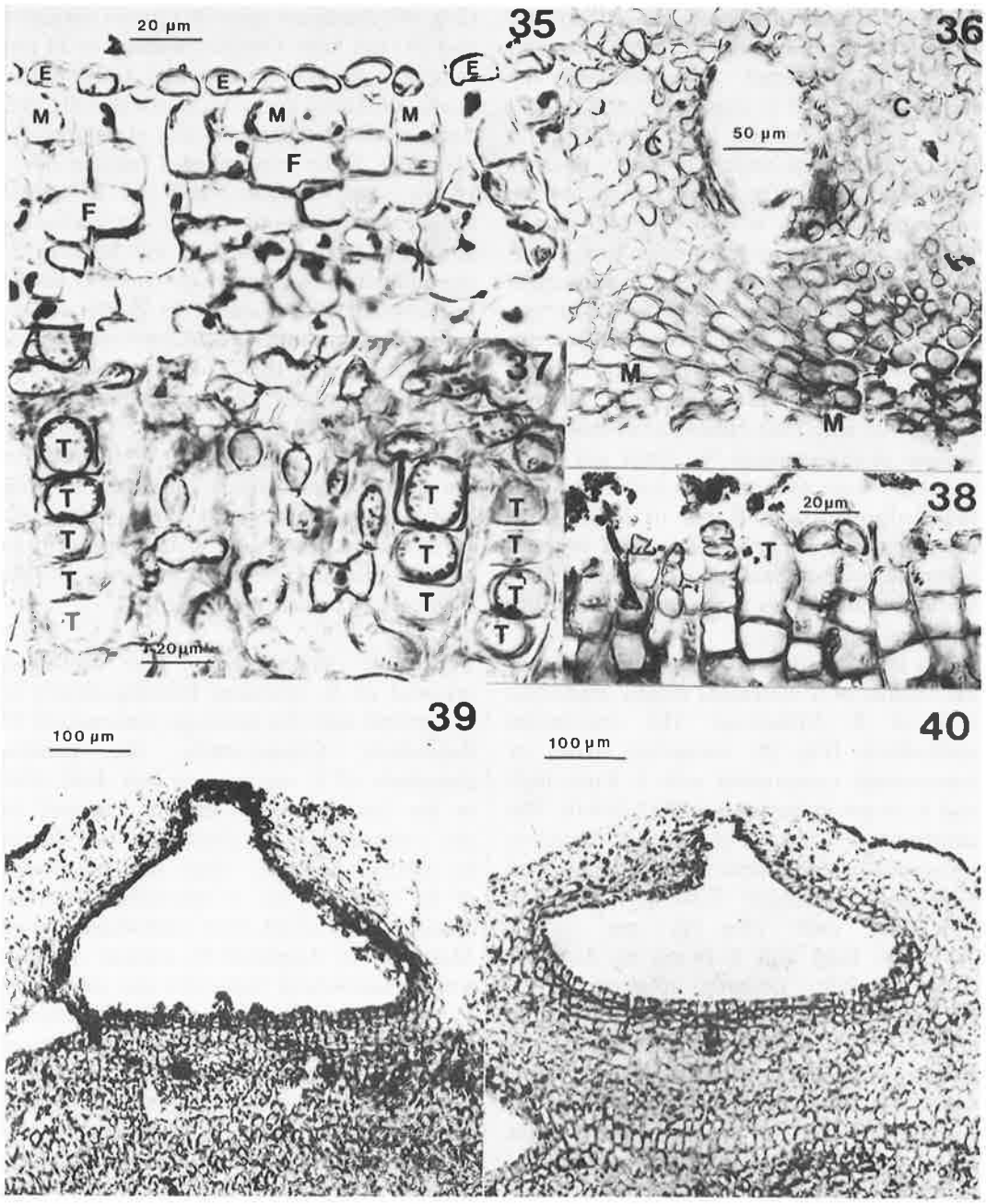
greatest dimension. These collectively are designated here as the lectotype element. The large specimen also contains the lectotype plant of *S. confluens* Kützing, and both taxa appear to have overgrown a central calcareous nodule (possibly another coralline alga). The large plant of *S. racemosa* consists of a series of mostly unbranched, more or less verruciform excrescences (3–) 4–8 mm in diameter and up to 8 mm high which arise from a basal crust. Adjacent excrescences commonly are conjoined and collectively form a variously furrowed spongiate appearing thallus. Numerous uniporate conceptacles cover the surface of excrescences but most are badly damaged from natural wear and erosion of the thallus surface. Roofs of intact conceptacles (Fig. 34) are more or less domoid, protrude somewhat above the thallus surface, and possess a single ostiole within an apical depression.

The internal structure and organization of the thallus of *S. racemosa* closely resembles that of *S. fruticulosa*. The unistratose epithallium (Fig. 35) comprises ovoid or transversely compressed cells 6–8 μm high and 8–16 μm in diameter (H/D 0·5–1·0). The subtending cortex (Figs 35, 36) contains numerous layers of cells 11–27 μm long and 8–16 μm in diameter [L/D (0·7–) 1–2·5]. Medullary cells (Fig. 36) are mostly 14–27 μm long and 8–16 μm in diameter (L/D 1·1–2·8). Growth appears to be effected from a subepithallial meristem (Fig. 35). Cell fusions are common in the cortex, occasional in the medulla, but absent from the epithallium, and secondary pit connections were not found. In the sections of *S. racemosa* examined, individual filaments in the cortex commonly were more difficult to identify than in *S. fruticulosa*, and because portions of medulla were missing, a coaxial arrangement was not as evident. Trichocytes (Figs 37, 38) were present both at the thallus surface and within the cortex, with the latter sometimes occurring in vertical series.

The uniporate conceptacles had flask-shaped (Fig. 39) or somewhat fusiform (Fig. 40) chambers up to 488 μm in diameter and 215 μm high. Ostioles were up to 81 μm long and 89 μm in diameter. Conceptacle roofs contained up to 10 layers of cells and fusions occurred between cells of contiguous filaments. Older conceptacles become overgrown and buried, and a columella apparently does not occur. Reproductive structures were not found, but because of the differences in conceptacle chamber shape in plants of *S. racemosa* (Figs 39, 40) and *S. fruticulosa* (presumed to be tetrasporangial; see Figs 30, 31), those of *S. racemosa* are likely to be gametic, and comments provided by Kützing (1841, p. 31) suggest that the plants probably are female. Differences in the shape of conceptacle chambers between gametic and tetrasporic plants also are known for other taxa of Corallinaceae (e.g. see Woelkerling, 1980a; Johansen, 1981; Turner & Woelkerling, 1982b).

Taxonomic implications. The lectotype material of *S. racemosa* Kützing clearly is congeneric with the lectotype specimen of *S. fruticulosa*. Consequently, the generic placement of *S. racemosa* is best dealt with in the Discussion for reasons outlined in the treatment of *S. fruticulosa*. It should be noted, however, that the placement of *S. racemosa* (as a synonym of other species) into *Lithophyllum*, *Lithothamnion*, or *Melobesia* as suggested by various authors (see nomenclatural history) is not supported by results from this study. *Spongites racemosa* lacks secondary pits (unlike taxa of *Lithophyllum*—see Woelkerling, 1983b), lacks epithallial cells which are angular in section (unlike taxa of *Lithothamnion*—see Woelkerling, 1983a), and produces a multistratose medulla ("hypothallium") and cortex ("perithallium") (unlike taxa assigned to *Melobesia*—see Johansen, 1976).

Because the vegetative anatomy of *S. racemosa* is virtually identical to that of *S. fruticulosa*, there is a strong possibility that the two taxa are conspecific. Morphologically, however, the lectotype specimens of *S. racemosa* (Fig. 33) and *S. fruticulosa* (Fig. 23) look different, and the excrescences



FIGS 35–40. Lectotype of *Spongites racemosa*. Fig. 35. L.S. showing epithallium (E), subepithallial meristem cells (M), upper portion of cortex, and fusions (F) between cells of adjacent cortical filaments. Fig. 36. L.S. showing lower part of cortex (C) and a portion of the medulla (M). Fig. 37. L.S. of cortex showing several vertical series of trichocytes (T). Fig. 38. Remnants of solitary trichocyte (T) at thallus surface. Figs 39, 40. L.S. of conceptacles with flask shaped (Fig. 39) and fusiform (Fig. 40) chambers.

of the latter are much more highly developed and generally smaller in diameter. Further studies are needed to determine whether these two specimens represent distinct species or merely growth forms of a single variable species. Pending the results of such studies (and also because the lectotype specimens come from different localities), the

two taxa are maintained as distinct species for the present.

"*Spongites stalactitica* Kützing"

Nomenclatural history. Kützing (1841, p. 33) established *S. stalactitica* for plants forming irregular stalactite-like, racemose nodules whose protuberances usually were the size of a hemp seed but occasionally were also larger or smaller. He also remarked that his specimens were partially overgrown by several other organisms.

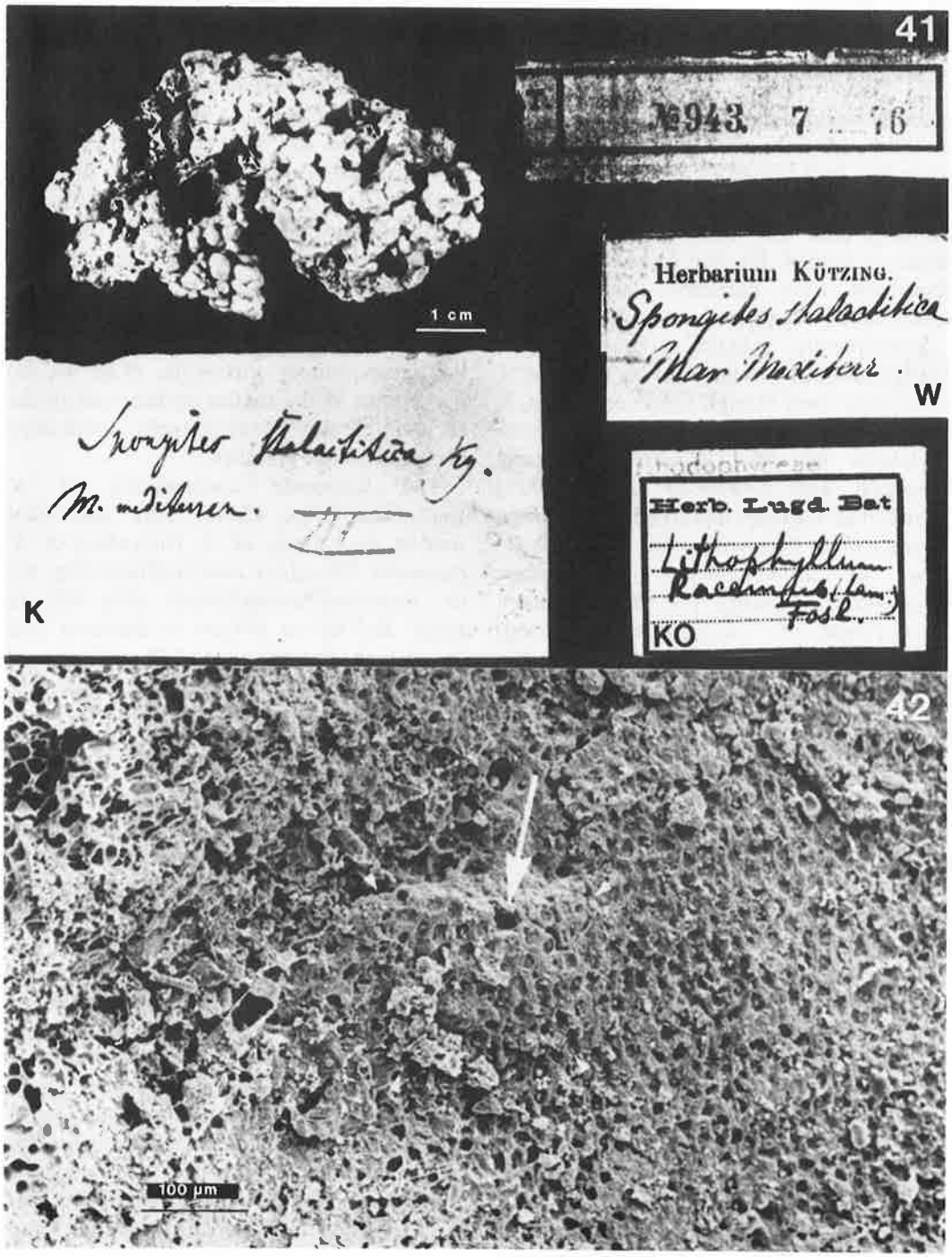
Subsequently, Kützing (1843a, b, 1849, 1869) continued to recognize his taxon as *S. stalactitica*, even though Decaisne (1842a, b; see also Endlicher, 1843) transferred it into *Melobesia* [as *M. stalactitica* (Kützing) Decaisne], and Areschoug (1852, p. 525) treated it as a species inquirenda. Since then, *S. stalactitica* has been listed as a distinct form of *Lithothamnion polymorphum* (Linnaeus) Areschoug [i.e. *Lithothamnion polymorphum* f. *stalactitica* (Kützing) Vinassa, 1892, p. 59; Foslie, 1900b, p. 19], and has been considered synonymous with *Lithothamnion racemus* (Lamarck) Areschoug (e.g. Solms-Laubach, 1881, p. 18; Ardissone, 1883, p. 453) or with *Lithophyllum racemus* (Lamarck) Foslie (e.g. De Toni, 1905, p. 1779; Mazza, 1916–1922, p. 1135; 1917b, p. 205).

Holotype collection. The original collection of *S. stalactitica* (Fig. 41) comprises a single irregularly torulose specimen up to 65 mm long and 39 mm in diameter and is composed of a series of more or less nodular, moderately branched mostly conjoined excrescences 1–4·5 mm in diameter which give the thallus a fruticose–spongiose appearance. In external form, the specimen is intermediate to *S. fruticulosa* and *S. racemosa* (compare Figs 23, 24, 33, 41). Much of the thallus surface is pitted or worn and many excrescences are partially eroded or broken off. Inconspicuous, uniporate conceptacles (Fig. 42) occur on some excrescences, but conceptacle roofs barely protrude above the thallus surface.

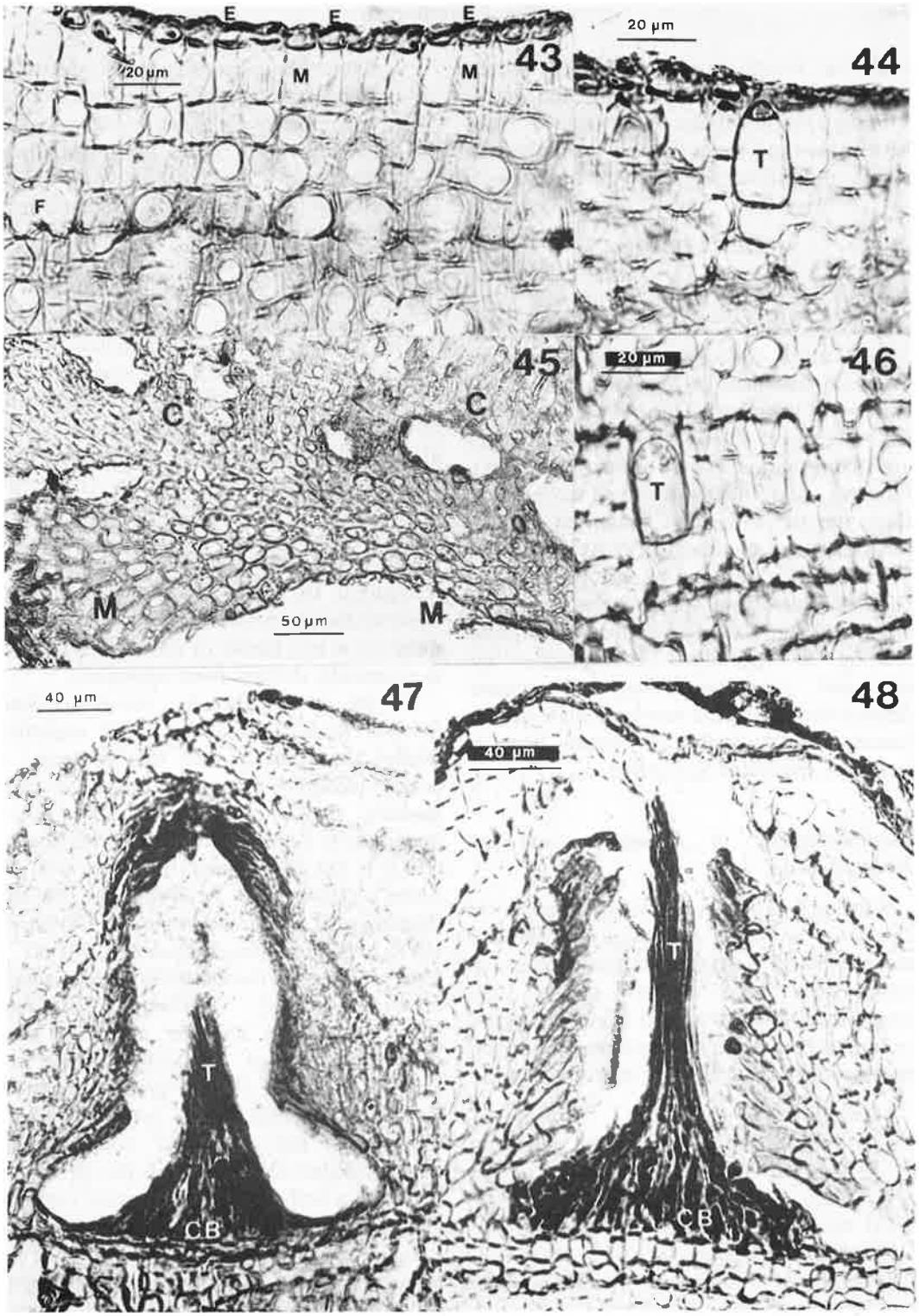
The vegetative anatomy of *S. stalactitica* (Figs 43–46) is essentially the same as that of *S. fruticulosa* and *S. racemosa*. A unistratose epithallium (Fig. 43) of rounded or compressed cells (H 5–8 μm; D 8–11 μm; H/D 0·5–0·8) is underlain by a multilayered cortex (Figs 43, 45) composed of cells 11–27 μm long and 8–16 μm in diameter (L/D 0·9–2·0). The medulla (Fig. 45) contains cells 11–27 μm and 8–16 μm in diameter (L/D 1·0–2). Growth occurs via a subepithallial meristem (Fig. 43), cell fusions occur in the cortex and medulla (Figs 43, 45), and secondary pit connections were not seen. Solitary trichocytes (Figs 44, 46) occur both at the thallus surface and in the cortex. Some cortical cells contained floridean starch granules.

The uniporate conceptacles of *S. stalactitica* (Figs 47, 48) were somewhat smaller than those of *S. fruticulosa* or *S. racemosa*. Chambers were fusiform (Fig. 47) to depressed-hemispherical (Fig. 48) in shape and up to 164 μm in diameter and 38 μm high. Ostioles up to 125 μm long and 27 (–74) μm in diameter were observed. Conceptacle roofs often contained 10–15 or more layers of cells with fusions occurring between cells of contiguous filaments. In a number of conceptacles (Figs 47, 48), the entire floor was lined with relatively poorly preserved carpogonial branches bearing carpogonia with long trichogynes protruding into the ostiole. Postfertilization stages were not observed in the material examined.

Taxonomic implications. The holotype specimen of *S. stalactitica* Kützing is congeneric with both *S. fruticulosa* and *S. racemosa* and all remarks made about generic placement of *S. racemosa* also apply to *S. stalactitica* (see general Discussion for further comments). Moreover, the vegetative anatomy of *S. stalactitica* is the same as that of *S. fruticulosa* and *S. racemosa*, and morphologically the lectotype specimen of *S. stalactitica* is intermediate to the lectotype specimens of the latter two species. It seems likely that all three lectotype specimens probably belong to the same species, but



FIGS 41, 42. Holotype of *Spongites stalactitica* Kützing. Fig. 41. Holotype specimen (L 943 . . 7 . . 76) with accompanying label in Kützing's script (K) and subsequent annotations by Koster (KO) and Weber van Bosse (W). Fig. 42. Uniporate conceptacle barely protruding above thallus surface. Arrowheads indicate approximate margin of conceptacle roof. Note ostiole (arrow).



FIGS 43–48. Holotype of *Spongites stalactitica*. Fig. 43. L.S. of thallus showing epithallium (E), subepithallial meristem (M), and upper part of cortex with fusions (F) between cells of adjacent filaments. Fig. 44. Solitary trichocyte (T) at thallus surface. Fig. 45. L.S. showing lower part of cortex (C) and a portion of medulla (M). Fig. 46. Solitary trichocyte (T) buried in the cortex. Figs 47, 48. Female conceptacles with fusiform (Fig. 47) or depressed hemispherical (Fig. 48) chambers and remnants of carpogonial branches (CB) and trichogynes (T). Both conceptacles are becoming buried in the cortex.

until the morphological variability within freshly collected male, female, and tetrasporangial populations referrable to these taxa is assessed more fully, it seems best to maintain all three taxa as distinct entities.

DISCUSSION

Lectotypification of *Spongites*

Kützing (1841 *et seq.*) provided no firm indication as to which of the six species originally assigned to *Spongites* best fit his concept of the genus. Three of the six species (*S. fruticulosa*, *S. racemosa*, *S. stalactitica*) are congeneric in a modern context, however, and of the six type collections, these are the three best preserved. Of the three, the type specimens of *S. racemosa* and *S. stalactitica* appear to be gametangial plants, while that of *S. fruticulosa* is apparently tetrasporangial. Because criteria relating to sporangial conceptacles are employed more extensively in generic delineation among the non-geniculate Corallinaceae, *S. fruticulosa* is chosen here as lectotype species of *Spongites*.

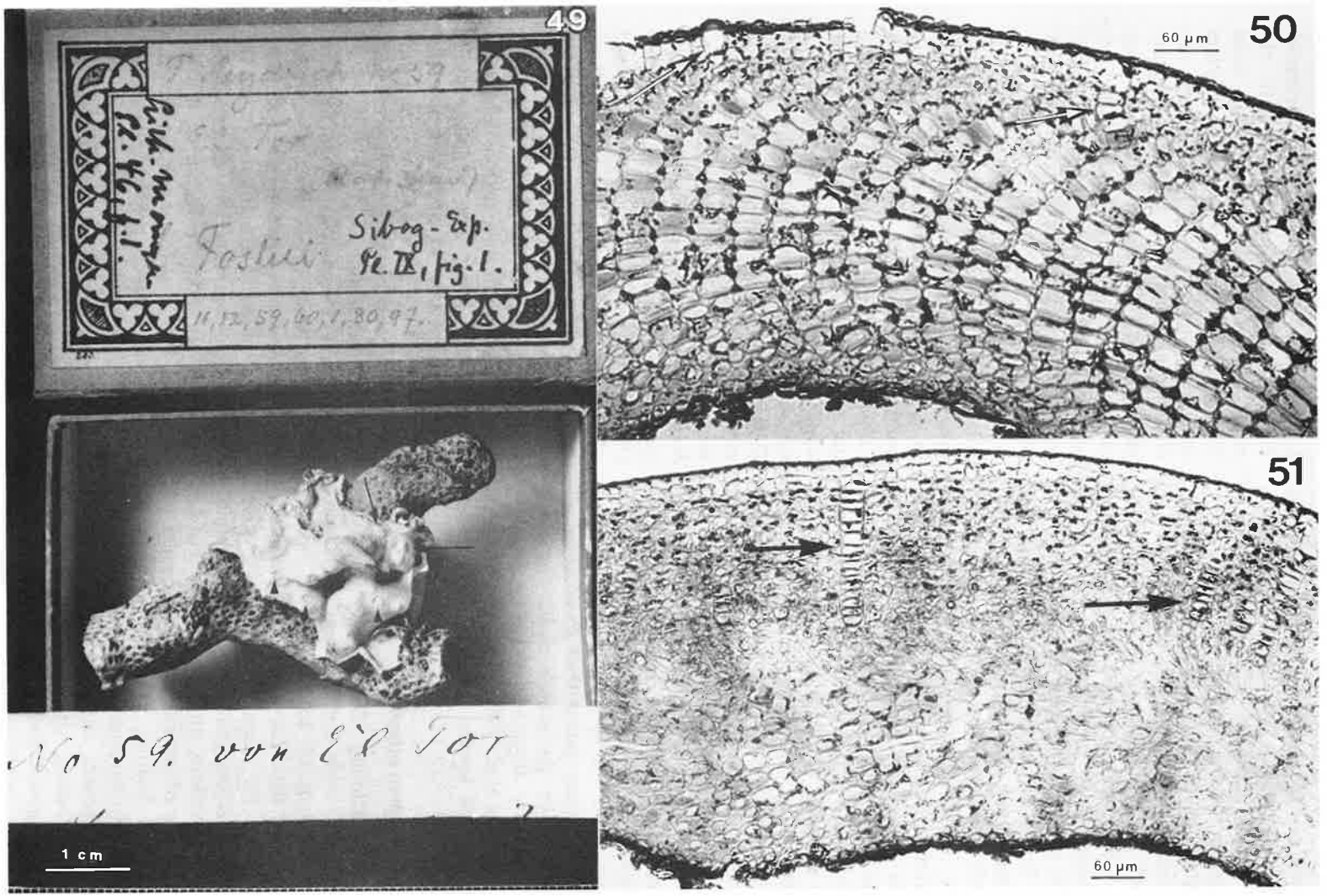
Circumscription of *Spongites* and of *Neogoniolithon*

Kützing's (1841) original description of *Spongites* is based entirely on superficial morphological characters and thus is meaningless in a modern context. As circumscribed in the present study, *Spongites* includes those taxa of Corallinaceae which possess all of the following characteristics:

(1) thallus non-geniculate;
(2) tetrasporangial conceptacles uniporate and tetrasporangia devoid of apical plugs;
(3) thallus filaments organized into definable tissues;
(4) cells of contiguous filaments interconnected by cell fusions;
(5) medulla ("hypothallium") multistratose, non-coaxial (i.e. devoid of arching recumbent tiers of cells) and non-palisade like (i.e. devoid of a single conspicuous layer of vertically elongate cells which appear more or less obliquely arranged within filaments as seen in longitudinal section);
(6) cortex ("perithallium") multistratose, present throughout the thallus; and
(7) trichocytes (megacells), when present, solitary or in a vertical series.

This combination of characteristics is evident in the generitype specimen of *Spongites* (i.e. the type of *S. fruticulosa*); however, *Spongites*, as circumscribed here, also largely encompasses the genus *Neogoniolithon* [Setchell & Mason (1943) as delineated by Hamel & Lemoine (1953), Adey (1970), Cabioch (1972), and Johansen (1976, 1981)], and were a single genus to be recognized, the name *Spongites* would have nomenclatural priority. This raises the question as to whether or not *Neogoniolithon* is generically distinct from *Spongites*.

In the protologue for *Neogoniolithon*, Setchell & Mason (1943, p. 89) explicitly limited the genus to taxa that possessed a coaxial medulla ("hypothallium"). A coaxial medulla does not occur in the genus *Spongites* as defined here. Setchell & Mason (1943, p. 88) also typified the genus with *N. fosliei* (Heydrich) Setchell & Mason [Basionym: *Lithothamnion fosliei*, Heydrich, 1897b, p. 58], and they included (p. 90) a "... large number of incompletely known series of forms [species] ...". Hamel & Lemoine (1953, pp. 72, 73), however, concluded that the species placed in *Neogoniolithon* by Setchell & Mason showed greater variation than was indicated in the original circumscription of the genus and, consequently, they extended the limits of the genus to encompass both taxa with a coaxial medulla ("hypothallium") and taxa with a non-coaxial medulla ("hypothallium"). This broader concept of the genus was accepted by Adey (1970), Cabioch (1972), and Johansen (1976, 1981). The problem, then, is whether taxa with a coaxial tissue should be considered generically distinct from taxa which lack a coaxial tissue as Setchell &



FIGS 49–51. Lectotype of *Neogoniolithon fosliei* (Heydrich) Setchell & Mason. Fig. 49. Lectotype specimen from TRH. Note two uniporate conceptacles (arrows) and broken conceptacles (arrow heads). No. 59 is Heydrich's collecting number; other numbers refer to collecting stations on Siboga Expedition (see Foslie, 1904). Fig. 50. Longitudinal section near thallus margin showing a coaxial medulla ("hypothallium") and several trichocytes (arrows). Fig. 51. Somewhat oblique section of central region of thallus showing vertical series of trichocytes (arrows). Coaxial nature of medulla partly obscured as a result of the angle of sectioning.

Mason (1943) have done and, indeed, as Lemoine (1928; see also Hamel & Lemoine, 1953) has done in the case of *Mesophyllum*, or whether taxa of both sorts should be placed in the same genus.

Although the original specimens (Heydrich, 1897b, pl. III, figs 9–11) upon which the protologue of *N. fosliei* is based are considered to have been destroyed (Koster, 1969, p. 553; Stafleu & Cowan, 1979, p. 187), an isotype (Fig. 49) occurs in the Foslie herbarium (TRH); this has been chosen (Adey, Townsend & Boykins, 1982, p. 25) to serve as lectotype of the species and thus the generitype of *Neogoniolithon*. Sections of the lectotype (Figs 50, 51) clearly show a distinct coaxial medulla which is quite different in structure from that of *S. fruticulosa* (Fig. 27). Given that coaxial and non-coaxial development appear to represent two distinct types of growth (see Johansen, 1981, p. 39), and given that among taxa of the subfamily Melobesioideae, *Mesophyllum* is delineated primarily on the basis of possessing a coaxial type of development, it seems best at present to recognize *Neogoniolithon* for taxa with a coaxial tissue and *Spongites* for taxa without a coaxial tissue rather than to combine all entities under the generic name *Spongites*. The recently described genus *Paragoniolithon* (Adey *et al.*, 1982, p. 12) also has been characterized by the occurrence of coaxial tissue.

Relationships to other Corallinaceae

In considering the relationships of *Spongites* to other Corallinaceae, the classification system of Johansen (1981, p. 10, tables 3, 4) has been selected to provide a framework for discussion. In this system *Spongites* is assignable to the subfamily Mastophoroideae, which is characterized by the absence of geniculae, the occurrence of lateral cell fusions, and the presence of uniporate bi-/tetrasporangial conceptacles.

Of the genera currently placed in the Mastophoroideae, six [*Hydrolithon* Foslie, 1909, *Neogoniolithon* Setchell & Mason, 1943, *Paragoniolithon* Adey *et al.*, 1982, *Porolithon* Foslie, 1909, *Pseudolithophyllum* Lemoine, 1913 (*sensu* Adey, 1970), *Spongites* Kützing, 1841] are characterized by the occurrence of cortical (perithallial) tissue throughout the vegetative thallus [certain species assigned to *Pneophyllum* by Chamberlain (1983) are similarly characterized]. The bases upon which these genera presently are delineated from one another (Table II) appear to be attended by some uncertainties which require further comment.

The genus *Hydrolithon* (see Adey, 1970; Johansen, 1976, 1981 for descriptions) presumably differs from *Spongites* (Table II) in possessing a unistratose rather than a multistratose medulla ("hypothallium"). Cabioch (1972, pp. 228, 269), however, did not regard this difference to be of generic significance and listed *Hydrolithon* as a subgenus of *Neogoniolithon* (*sensu* Cabioch). Detailed studies of thallus ontogeny of taxa referrable to *Hydrolithon* and to *Spongites* are needed to help clarify the situation. Based on studies of five other genera of non-geniculate Corallinaceae [*Lithophyllum* (Woelkerling, 1983b), *Lithoporella* and *Mastophora* (Turner & Woelkerling, 1982a, b), *Mastophoropsis* (Woelkerling, 1978), *Metamastophora* (Woelkerling, 1980a, b)], however, it seems likely that thallus ontogeny in taxa with a unistratose hypothallium may be fundamentally different from that in taxa with a multistratose medulla ("hypothallium"), and such a difference probably provides a sound basis for generic delineation.

The genera *Pseudolithophyllum* Lemoine, 1913 (*sensu* Adey, 1970), *Porolithon* Foslie, 1909, and *Spongites* presently are delineated from one another on differences in the occurrence and arrangement of trichocytes (see Table II). Adey (1970, pp. 7, 12), has noted, however, that the presence or absence of trichocytes presents problems when used as a generic character; he included some taxa in *Neogoniolithon* (*sensu* Adey) in which trichocytes could not be found and noted (based on reports of Masaki, 1968) that some species of *Pseudolithophyllum* (charac-

TABLE II. Attributes presently used to delineate *Hydrolithon*, *Neogoniolithon*, *Paragoniolithon*, *Porolithon*, *Pseudolithophyllum*, and *Spongites* as genera. (Data based on this paper and Adey, 1970; Johansen, 1976; Adey *et al.*, 1982)

		Trichocytes	
	Medulla ("hypothallium")	Occurrence	Arrangement
Hydrolithon	Unistratose	Present	Solitary or in vertical rows
Porolithon	Multistratose, non-coaxial	Present	In horizontal rows
Pseudolithophyllum	Unistratose or multistratose	Absent (?)	—
Spongites	Multistratose, non-coaxial	Present	Solitary or in vertical rows
Neogoniolithon	Multistratose, coaxial	Present	Solitary or in vertical rows
Paragoniolithon	Multistratose, coaxial	Present	Loosely grouped in horizontal fields of two to three

terized by the absence of trichocytes) sometimes can produce small trichocytes. Cabioch (1972, p. 228; see also Johansen, 1981, p. 222) has reported that intermediate forms occur between *Porolithon* (trichocytes arranged in horizontal rows) and *Neogoniolithon* (*sensu* Cabioch) (trichocytes solitary or arranged in vertical rows), thus raising the question of whether trichocyte arrangement is a reliable character for delineating these two genera. Obviously, further studies also are required to resolve these matters, especially since trichocyte occurrence and arrangement are known to vary among other taxa assigned to the Mastophoroideae. In taxa of the *Pneophyllum* (syn. *Heteroderma*)–*Foslie-lla* complex (Chamberlain, 1983; Jones & Woelkerling, 1984), for example, trichocytes may be present or absent in individuals of a population depending upon abiotic conditions in the field or upon the experimental regime used in culture. In *Mastophora* and *Lithoporella* (Turner & Woelkerling, 1982a), trichocyte arrangement can vary considerably within and among plants of a population under field conditions. Similar types of data from field populations and culture experiments are needed for taxa referable to *Spongites*, *Porolithon*, and *Pseudolithophyllum* in order to assess properly the taxonomic reliability of trichocyte occurrence for purposes of generic delineation.

At present (Table II), *Spongites* is delineated from *Neogoniolithon* (and from *Paragoniolithon*) by the absence of a coaxial medulla (hypothallium). Further studies are needed to determine the extent to which

TABLE III. The disposition of specified taxa hitherto referred to *Neogoniolithon* and *Spongites* based on studies of relevant type collections

Taxon and basionym	Reference	Generic disposition
Neogoniolithon fosliei (Heydrich) Setchell & Mason (*Lithothamnion fosliei* Heydrich)	This paper	*Neogoniolithon*
Spongites confluens Kützing	This paper	*Lithophyllum*
S. crassa (Philippi) Kützing (*Lithothamnium crassum* Philippi)	Woelkerling (1983a)	*Lithophyllum*
S. dentata Kützing	This paper	*Lithophyllum*
S. fruticulosa Kützing	This paper	*Spongites*
S. incrustans (Philippi) Kützing (*Lithophyllum incrustans* Philippi)	Woelkerling (1983b)	*Lithophyllum*
S. nodosa Kützing	This paper	*Lithothamnion*
S. racemosa Kützing	This paper	*Spongites*
S. ramulosum (Philippi) Kützing (*Lithothamnium ramulosum* Philippi)	Woelkerling (1983a)	*Pseudolithophyllum*
S. stalactitica Kützing	This paper	*Spongites*

coaxial development can vary within a taxon and whether or not coaxial development can be defined in a consistent manner. Adey (1970), for example, characterized some species of *Mesophyllum* as weakly coaxial or as irregularly coaxial, thus suggesting that possible variation occurs in this character. Similarly, Adey *et al.* (1982, p. 20) characterized the medulla (hypothallium) of *Neogoniolithon rufum* Adey, Townsend & Boykins as simple to coaxial. Should further study provide unequivocal evidence that coaxial and non-coaxial development occur interchangeably in the same thallus, the generic distinctions between *Spongites*, *Neogoniolithon*, and/or *Paragoniolithon* would no longer hold and one or both of the latter genera would have to be relegated to the synonymy of *Spongites*.

Other nomenclatural and taxonomic aspects

Since 1841 at least 19 taxa have been referred to *Spongites*, and since 1943 at least 63 taxa have been put into *Neogoniolithon*. How many of these 82 taxa belong to these two genera as circumscribed in this paper remains uncertain, as does the real number of species these 82 names represent. Based on direct examination of the type collections of 10 of these taxa, three are referrable to *Spongites*, one to *Neogoniolithon* and six to other genera (Table III). Selected nomenclatural and taxonomic data on the three species of *Spongites* examined during the present study are summarized in Table IV. The generic disposition of the remaining 72 taxa will have to await the re-examination of relevant type collections, a task beyond the scope of the present study.

Studies still are needed to assess the variability occurring in attributes of potential taxonomic importance at the species level, to determine how many species should be recognized and how they are delineated from one another, and to elucidate the geographic distribution of *Spongites* and its included species. It would appear from extant data that a number of species might occur and that the genus is represented in most geographic regions. Once necessary studies have been carried out, it also will be possible to determine whether *S. racemosa* and/or *S. stalactitica* are conspecific with *S. fruticulosa*, and whether *S. fruticulosa* is the oldest available name for the taxon it currently represents.

TABLE IV. Selected nomenclatural and taxonomic data on *Spongites fruticulosa*, *S. racemosa*, and *S. stalactitica* (retained here in the genus *Spongites*)

S. fruticulosa Kützing, 1841, p. 33
Synonyms:
Lithothamnion fruticulosum (Kützing) Foslie, 1895, p. 46
Melobesia fruticulosa (Kützing) Decaisne, 1842a, p. 126
Paraspora fruticulosa (Kützing) Heydrich, 1900, p. 315
Lithothamnion fasciculatum β fruticulosum (Kützing) Hauck, 1883, p. 274
Type locality: Mediterranean Sea
Lectotype specimen: L 943 . . 8 . . 134 (see Fig. 23)
S. racemosa Kützing, 1841, p. 32
Synonym: *Melobesia racemosa* (Kützing) Decaisne, 1842, p. 126
Type locality: Spalato (Adriatic Sea), Italy
Lectotype specimen: L 943 . . 7 . . 78 (see Fig. 33), growing with lectotype specimen of *S. confluens* Kützing
S. stalactitica Kützing, 1841, p. 32
Synonyms:
Melobesia stalactitica (Kützing) Decaisne, 1842, p. 126
Lithothamnium polymorphum f. *stalactiticum* (Kützing) Vinassa, 1892, p. 59
Type locality: Medittanean Sea
Lectotype specimen: L 943 . . 7 . . 76 (see Fig. 41)

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(783) Proposal to conserve **Lithothamnion** against *Lithothamnium* (Rhodophyta: Corallinaceae).

Lithothamnion Heydrich, Ber. Deutsch. Bot. Ges. 15: 412. 1897, *nom. cons. prop.* LT.: *L. muelleri* Lenormand ex Rosanoff, Mém. Soc. Imp. Sci. Nat. Math. Cherbourg 12: 101, pl. 6, figs. 8–11. 1866 (vide Woelkerling, 1983: 190).

(H) *Lithothamnium* R. A. Philippi, Arch. Natuurgesch. 3: 387. 1837, *nom. rej. prop.* LT.: *L. ramulosum* R. A. Philippi (vide Mason, 1953: 322). [RHODOPH.: CORALLIN.]

Lithothamnium Philippi (1837), as noted by Woelkerling (1983), was established for five species and was circumscribed solely using characteristics of the vegetative thallus. *Lithothamnion* Heydrich (1897), in contrast, was characterized in part by the occurrence of multiporate tetrasporangial conceptacles, a characterization which has been adopted by all subsequent authors. Heydrich (1897) and subsequent investigators [including Mason (1953) who lectotypified *Lithothamnium* Philippi] all have presumed that the lectotype or at least one of the species originally included in *Lithothamnium* Philippi possessed multiporate tetrasporangial conceptacles. Results published by Woelkerling (1983), however, have shown this presumption to be erroneous; all of the taxa originally included in *Lithothamnium* Philippi possess uniporate tetrasporangial conceptacles. Thus Heydrich (1897) unknowingly excluded all of Philippi's taxa from his genus. *L. ramulosum* Philippi, the type species of *Lithothamnium* Philippi, was not explicitly included in *Lithothamnion* by Heydrich (1897), and subsequently Heydrich (1908, p. 53) explicitly excluded *Lithothamnium ramulosum* Philippi from *Lithothamnion* Heydrich by placing it in *Paraspora* Heydrich [non *Paraspora* Grove] while simultaneously continuing to rec-

ognize his (Heydrich's) genus *Lithothamnion.* The net result is that *Lithothamnion* Heydrich must be considered a later homonym (Art. 48.1) of *Lithothamnium* Philippi.

Unless conserved (Art. 14.8), the name in the sense of Heydrich cannot be retained. Although, as noted by D. H. Nicolson (personal communication), it might be technically more correct to propose conservation of *Lithothamnion* Woelkerling, 1983, it seems preferable to propose conservation of *Lithothamnion* Heydrich so as to have an earlier date and recognize Heydrich's important work. Moreover, the retention of *Lithothamnion* Heydrich appears highly desirable since the Heydrich concept or various modifications of it have been used widely and persistently in the botanical and geological literature ever since 1897 and the generic name has become associated with nearly 700 taxa of Corallinaceae.

If *Lithothamnion* Heydrich (1897) is not conserved against *Lithothamnium* Philippi (1837), the stability of nomenclature (Art. 14.1) would be markedly and adversely affected, and considerable confusion would result. Thus the name *Lithothamnium* Philippi (type species *L. ramulosum*) would have to be used (barring another conservation proposal) for taxa now referred to *Pseudolithophyllum* (sensu Adey, 1970), a genus characterized by uniporate tetrasporangial conceptacles, and a new name would have to be employed for all taxa now referred to *Lithothamnion* Heydrich. The end result would necessitate hundreds of nomenclatural changes for taxa now referred to *Lithothamnion* Heydrich, thereby destabilizing the nomenclature of a name and concept entrenched in the botanical and geological literature since 1897. Further confusion would result, moreover, if the name *Lithothamnium* Philippi were retained and applied to a taxon with uniporate conceptacles because two quite different concepts and usages of a single generic name would become a part of the botanical and geological literature. To avoid these undesirable consequences approval is sought to conserve *Lithothamnion* Heydrich against *Lithothamnium* Philippi.

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A taxonomic and nomenclatural reassessment of *Tenarea, Titanoderma* and *Dermatolithon* (Corallinaceae, Rhodophyta) based on studies of type and other critical specimens*

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WM. J. WOELKERLING, Y.M. CHAMBERLAIN AND P.C. SILVA. 1985. A taxonomic and nomenclatural reassessment of *Tenarea, Titanoderma* and *Dermatolithon* (Corallinaceae, Rhodophyta) based on studies of type and other critical specimens. *Phycologia* **24:** 317–337.

The taxonomy and nomenclature of genera of the *Tenarea/Dermatolithon* complex has been reassessed on the basis of a study of generitype and other critical specimens. The type specimen of *Millepora tortuosa* Esper, which is the type of *Tenarea* Bory 1832, proves to be conspecific with the specimen on which Bory based his description of the genus. *Tenarea undulosa* Bory is an illegitimate name for *T. tortuosa* (Esper) Lemoine rather than an independent species. Since 1898, *M. tortuosa* has been incorrectly associated with the alga that is the principal component of the 'trottoirs' (coralline pavements) of the western Mediterranean. This alga is referable to *Lithophyllum lichenoides* Philippi. *Titanoderma* Nägeli 1858 is an earlier homotypic synonym of *Dermatolithon* Foslie 1898, both being based on *Melobesia pustulata* Lamouroux. *Titanoderma,* in view of its clear record, is adopted in preference to proposing *Dermatolithon* for conservation. *Tenarea* comprises a single species of Lithophylloideae in which the thallus is composed of erect or ascending lamellae whose vegetative tissues are organized in an isobilateral manner and include a medulla of two layers of palisade cells. *Titanoderma* (syn. *Dermatolithon*) encompasses those Lithophylloideae in which the thallus consists largely or entirely of a prostrate crust whose tissues are organized in a dorsiventral manner and include a unistratose hypothallium composed of palisade-like cells. *Titanoderma* includes at least 16 species.

INTRODUCTION

The circumscription and naming of genera in the *Tenarea/Dermatolithon* complex (Corallinaceae, Rhodophyta) has been attended by uncertainties as is indicated by Johansen (1981, pp. 42, 217, 223, 225, 226) in his recent survey of coralline algae. In addition to differences in taxonomic opinion, two factors are responsible for these uncertainties. First, it has been a long-standing controversy whether a generic name must be typified with material in the hands of the author (that is, material upon which the generic description was primarily based) or, alternatively, with the type of a cited species, whether or not the citation proves to be correct taxonomically. The controversy was settled in favour of the second alternative (in the absence of an overwhelming case for conservation) in 1981 by the Nomenclature Section of the International Botanical Congress at Sydney and is incorporated in Articles 10.2 and 10.3 of the current International Code of Botanical Nomenclature (ICBN—see Voss 1983). Second, no attempt has been made to examine the type specimens of these generic names and thus the nomenclature of this complex has lacked the foundation that is essential to stability.

During the course of studies on the nongeniculate Corallinaceae of the British Isles (by Y.M.C.) and of southern Australia (by W.J.W.), independent visits were made by these authors to CN (Université de Caen, France) in 1979 and 1980 to examine Lamouroux's specimens of *Melobesia pustulata,* on which the generic name *Dermatolithon* is based. Subsequently (1981), Y.M.C. and W.J.W. concurrently studied material on

* Dedicated to the memory of Mme Marie Lemoine (1887–1984) in recognition of her generous help over 76 years (1909–1984) to all people interested in corallines.

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which Bory based his description of *Tenarea,* housed at PC (Laboratoire de Cryptogamie, Muséum National d'Histoire Naturelle, Paris). The whereabouts of Esper's specimen of *Millepora tortuosa,* on which the concept of *Tenarea* must be based in accordance with the Sydney decision, remained unknown until 1983 when one of us (Y.M.C.) discovered that it was at FR (Forschungsinstitut Senckenberg, Frankfurt, Germany). [Dr M. Grasshoff from FR has indicated in correspondence (with W.J.W.) that it was transferred from ER (Botanisches Institut der Universität Erlangen, Germany) to FR in 1970.] Comparative examination of the Lamouroux, Bory, and Esper specimens together with studies of more recently collected materials enabled us to resolve various uncertainties in the *Tenarea/Dermatolithon* complex at the generic level. Type specimens have been designated and relevant historical background data are provided.

MATERIALS AND METHODS

Data were obtained from type and other critical specimens housed at CN, FR, L (Rijksherbarium, Leiden, Netherlands) and PC and from additional collections housed at LTB (Department of Botany, La Trobe University, Bundoora, Victoria, Australia). Microtechnique follows Jones & Woelkerling (1984) and permanent slides have been retained at LTB. Fractures for scanning electron microscopy were prepared by breaking small pieces of thallus, mounting these on aluminium stubs with 'Fotobond' acrylic adhesive (Agfa-Gevaert Limited), and double-coating the specimens with carbon and then with gold prior to viewing in a Siemens ETEC Autoscan microscope. Wherever cell measurements are given, 'L' denotes length, 'D' denotes diameter, and 'L/D' denotes the ratio of length to diameter. Measurements include the cell walls. Herbarium abbreviations are taken from Holmgren *et al* (1981).

HISTORICAL BACKGROUND

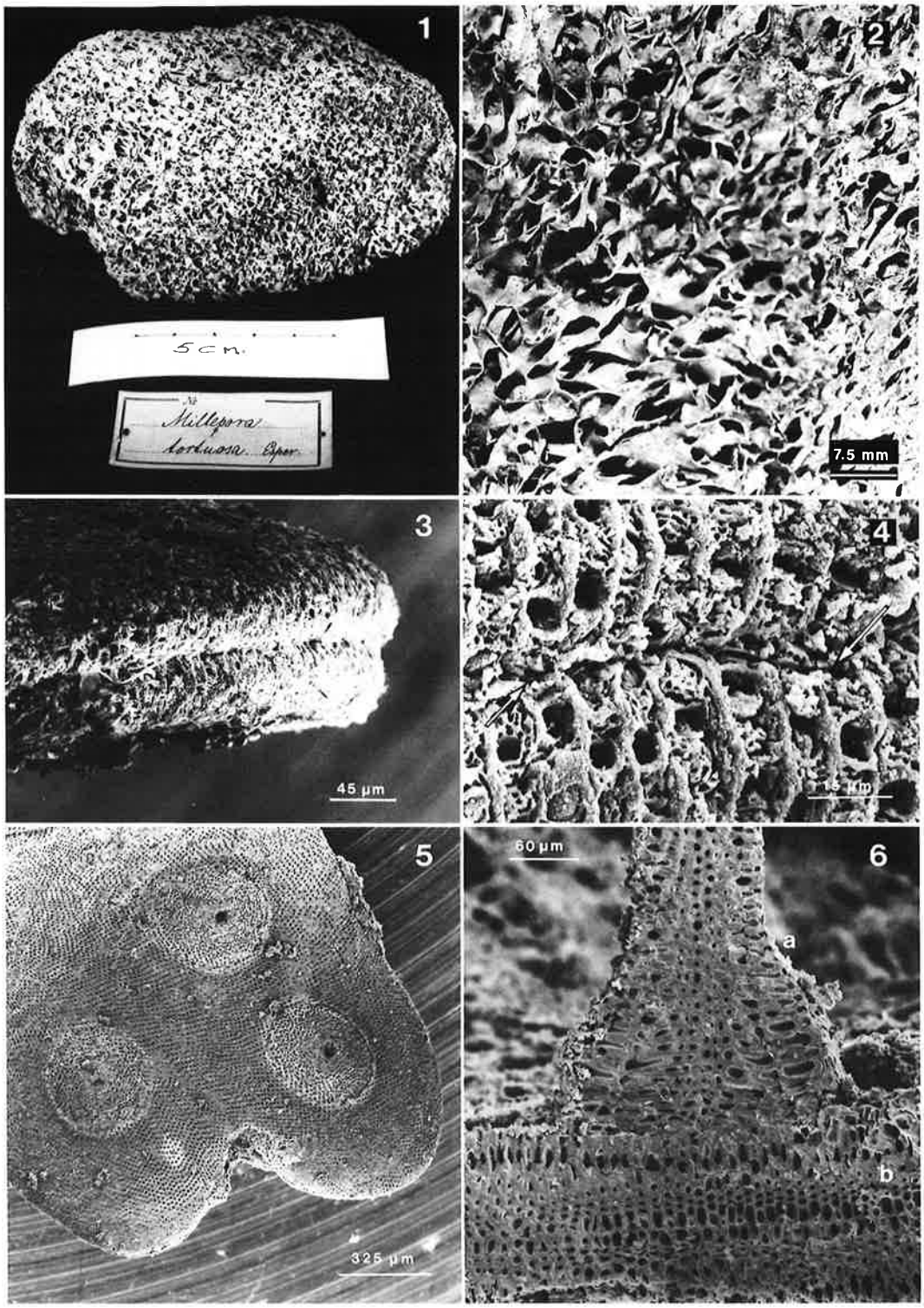
Tenarea

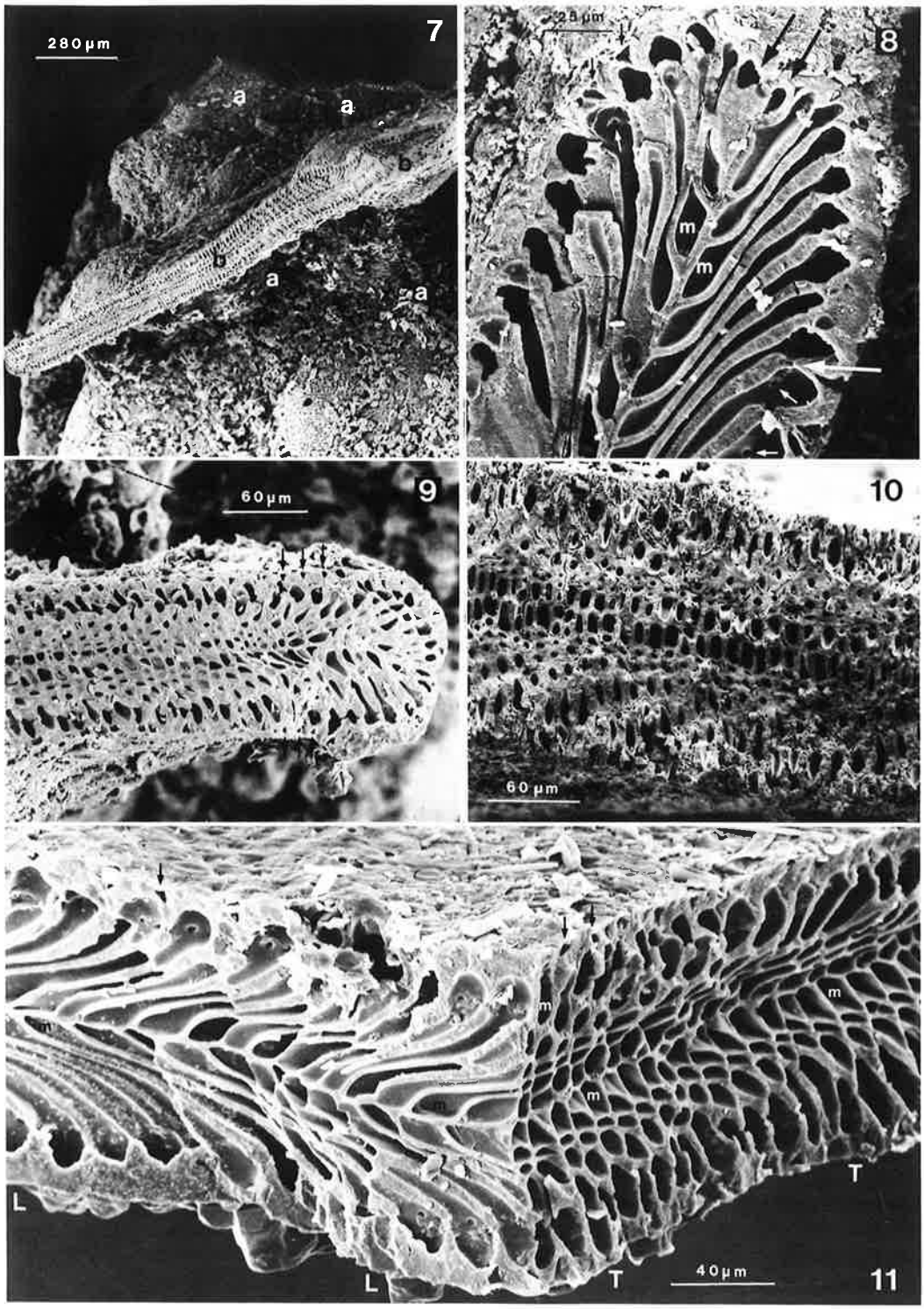
Bory (1832, p. 207, pl. 54, fig. 3) established the genus *Tenarea* to accommodate a 'polypier' (plant-like animal) collected at Cap Ténare (Cape Taínaron), Greece. The organisms were described as calcareous, canary yellow when growing but bleached when dry and composed of lamellae that were undulate-tortuouse, anastomosing, and folded together. Bory was explicit in indicating that it was not new to science at the species level and cited *Millepora tortuosa* Esper (1796, p. 118, Millepora pl. xxii) in synonymy. This name had been applied by Esper to a more or less globular calcareous organism with thin, ascending, variously twisted lamellae which were closely united with one another and which had scattered hemispherical 'pores' (conceptacles). Esper's specimen presumably came from the Mediterranean, and he compared his organism with several others, including *Corallina officinalis* Linnaeus and *Millepora lichenoides* (Ellis) Ellis & Solander. Unfortunately, in an action that complicated subsequent nomenclature, Bory (1832) changed the specific epithet to *undulosa.* The ICBN always has proscribed unnecessary changing of epithets and if Bory had not established a new genus at the same time that he changed the epithet, no problem would have arisen. Establishing a new genus, however, allowed for the interpretation of *Tenarea undulosa* as a new species and the type of its genus, an interpretation which has been held by many botanists but which was ruled out by the Sydney decision in 1981 (ICBN, Arts 10.2, 10.3; see Voss 1983).

Tenarea was overlooked until Hariot (1895)

→

Figs 1–6. Lectotype of *Tenarea tortuosa* (Esper) Lemoine.
Fig. 1. Lectotype specimen (housed at FR).
Fig. 2. Surface of lectotype showing numerous, tortuouse, intertwined, branched lamellae.
Fig. 3. Apex of lamella showing characteristic groove.
Fig. 4. Close-up of portion of groove (arrows). Note distinct cell row on opposite sides of groove.
Fig. 5. Surface of lamella showing early stage of branch development, three conceptacles, and numerous concavities denoting the positions of epithallial cells.
Fig. 6. Fracture showing one lamella (a) abutting against the surface of another lamella (b). Both lamellae are fractured in a transverse plane.


1
5 cm.
Millepora
horbusa. Espr.
2
7.5 mm
3
45 µm
4
5
325 µm
6
50 µm
a
b



Figs 7–11. *Tenarea tortuosa.* Lectotype, Figs 7–10; LTB 14645, Fig. 11.
Fig. 7. Penetration of one lamella (a) by another lamella (b); the latter is transversely fractured above the region of penetration.

re-examined Bory's specimen and confirmed that it was a nongeniculate coralline alga. He noted Bory's citation of Esper's diagnosis of *Millepora tortuosa,* but chose to retain the epithet *undulosa.* Considering mainly external morphology, Hariot concluded that *Tenarea* Bory (1832) was congeneric with and had priority over *Lithophyllum* Philippi (1837). He did not examine Philippi's collections, however, and the first modern account of this critical material was not published until 88 years later (Woelkerling 1983).

Without examining the type collections, both Foslie (1895, p. 178, footnote; 1898d) and Kuntze (1898, p. 433) accepted Hariot's conclusion, and although Kuntze adopted *Tenarea* over *Lithophyllum,* Foslie rejected *Tenarea* on the grounds that *Lithophyllum* ". . . has been accepted and applied for about 60 years . . ." (Foslie 1898d, p. 5). Foslie (1898b, p. 9; 1898d, p. 5), however, adopted the epithet *tortuosa* over the epithet *undulosa,* believing that the two taxa were conspecific (as originally indicated by Bory).

Subsequently, Lemoine (1910, p. 368; 1911, pp. 5, 62, 169) undertook an anatomical examination of the alga which forms the 'trottoirs' (coralline pavements) commonly seen on western Mediterranean shores (Lemoine 1911; Feldmann 1937; Lewalle 1961). She concluded that this alga, which was then generally known as *Lithophyllum tortuosum* (Esper) Foslie, differed from other members of *Lithophyllum* (*sensu* Lemoine) in having a multistratose but noncoaxial hypothallium and a perithallium composed of more or less juxtaposed filaments. She adopted the generic name *Tenarea* for the 'trottoir' alga without examining Bory's specimen anatomically. Had she done so, she would have found that the two entities were not congeneric, as did Huvé (1957). After studying Bory's specimen and recently collected material from the original locality, Huvé concluded:

(1) that Bory's alga (for which she retained the name *Tenarea undulosa*) is characterized by a hypothallium that is unistratose and palisade-like (i.e. with vertically elongate, more or less obliquely arranged cells) and thus generically distinct from *Lithophyllum*; and

(2) that plants identified by Lemoine and others as *Tenarea tortuosa* are truly referable to *Lithophyllum,* belonging to the species *L. tortuosum* (Esper) Foslie. Huvé's concept of *Lithophyllum tortuosum,* however, was not based on an examination of Esper's type.

Dermatolithon

This name was applied by Foslie (1898b, p. 11) to his emended concept of *Melobesia* (Foslie, 1898a, p. 6). This genus was characterized by uniporate conceptacles in which sporangia occur around or between a bundle of cylindric-clavate paraphyses. He typified *Dermatolithon* with *Melobesia pustulata* Lamouroux (1816, p. 315, pl. 12, fig. 2; see also Lamouroux 1821, p. 46, pl. 73, figs 17, 18). This 'polypier' was said by Lamoroux to grow on red algae along the coast of France, and to take the form of convex orbicular plates with ostioles (of the conceptacles) visible to the naked eye.

Subsequently, Foslie (1904, p. 3) reduced *Dermatolithon* to a subgenus of *Lithophyllum,* but later (1909, p. 57) again elevated it to generic rank, distinguishing it from *Lithophyllum* on the basis that thalli of *Dermatolithon* have a unistratose, palisade-like hypothallium whereas those of *Lithophyllum* have a multistratose, nonpalisade-like hypothallium. Foslie, however, apparently never examined relevant generitype specimens.

Between 1909 and 1957, some authors (e.g. Rosenvinge 1917; Newton 1931; Feldmann 1939; Suneson 1950) treated *Dermatolithon* as a subgenus of *Lithophyllum* while other authors (e.g. Svedelius 1911; Mazza 1917; De Toni 1924; Funk 1927, 1955; Hamel & Lemoine 1953; Mason 1953; Dawson 1955; Kylin 1956; Huvé 1957) considered *Dermatolithon* to be a distinct genus,

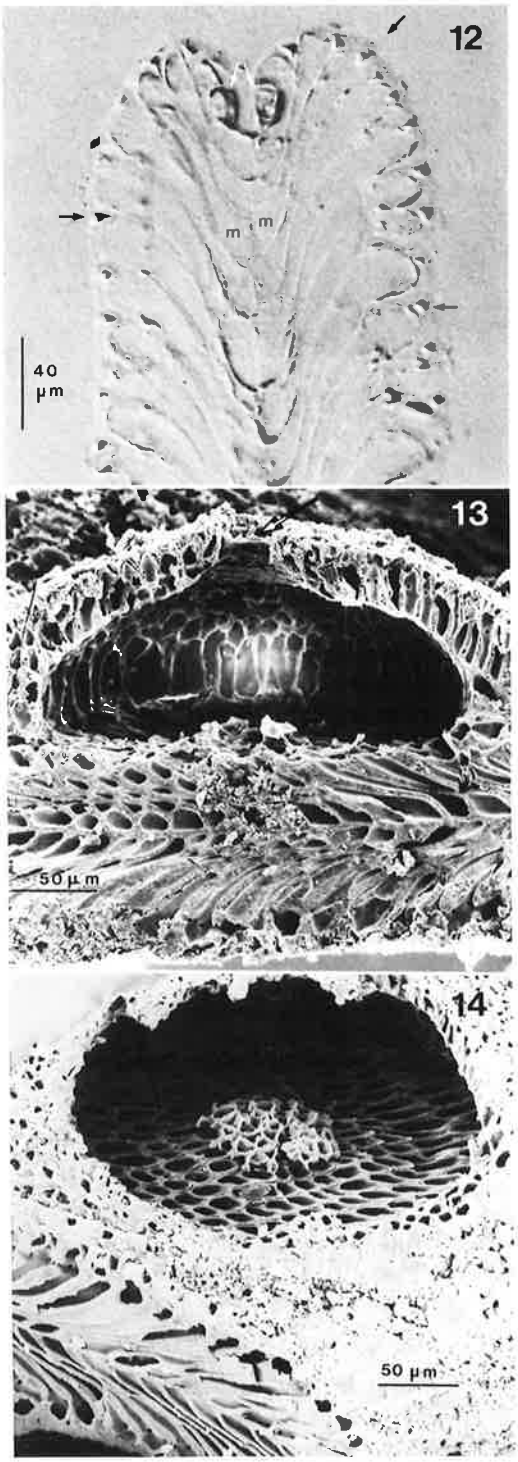
←

Fig. 8. Longitudinal fracture through apex of a lamella. Note minute epithallial cells (small black arrows), elongate medullary cells (m), meristem cells at the apex (large black arrows), primary pit connection between cells of the same filament (large white arrow), and position of secondary pit connections between cells of contiguous filaments (small white arrows).

Fig. 9. Transverse fracture of margin of a lamella. Epithallial cells are indicated with small arrows; remaining layers are composed of medullary cells viewed 'end on'.

Fig. 10. Transverse fracture of central portion of older lamella. All cells are medullary cells; epithallial cells have not been preserved.

Fig. 11. Fracture showing relationships of tissues as seen in transverse (T) and longitudinal (L) views. Note epithallial cells (small black arrows) and cells of medulla (m).



Figs 12-14. *Tenarea tortuosa.*
Fig. 12. Interference contrast view of longitudinal section through apex of a lamella showing two densely stained meristem cells (white arrows) situated in the lamellar groove, two rows of medullary cell derivatives (m), each with a minute epithallial cell (black arrows). LTB 14645.
Fig. 13. Fracture through a uniporate conceptacle of the lectotype specimen. Note pore (arrow) and inside of empty chamber.
Fig. 14. Conceptacle of lectotype specimen with part of roof removed to show remains of a central columella.

based on the occurrence of a unistratose hypothallium. Huvé (1957), after concluding that Bory's alga was generically distinct from *Lithophyllum,* differentiated it from *Dermatolithon* on the presence or absence of erect lamellae—present in *Tenarea,* absent in *Dermatolithon.* Subsequently, some authors (e.g. Cabioch 1972; Bressan 1974; Johansen 1981) have accepted this distinction while others (Adey 1965, 1970; Littler 1971; Adey & Adey 1973; Adey & MacIntyre 1973; Notoya 1974; Johansen 1976a, 1976b; Townsend 1981) have recognized only one genus (*Tenarea*), in which they include all nongeniculate Corallinaceae with secondary pit connections and a palisade-like hypothallium. Still other authors (e.g. Mason 1953; Dawson 1955, 1960; Masaki 1968) place all Lithophylloideae (see Johansen 1981, p. 11, for subfamily characteristics) with a unistratose, palisade-like hypothallium in one genus, which they call *Dermatolithon.* Finally, Adey (1965, p. 78) suggested that Esper's plant represented an unnamed genus. None of these concepts and opinions, however, were based on studies of relevant generitypes.

OBSERVATIONS

Millepora tortuosa Esper

Lectotypification

The Esper collections of *Millepora* at FR include a single unnumbered specimen (Fig. 1) labeled *Millepora tortuosa* Esper. According to Dr M. Grasshoff (personal communication with W.J.W.), the label is not in Esper's handwriting, but apparently all original labels have been replaced. The specimen, whose dimensions and other attributes are concordant with those mentioned in the protologue (Esper 1796, p. 118), is chosen here as lectotype.

Morphology and anatomy

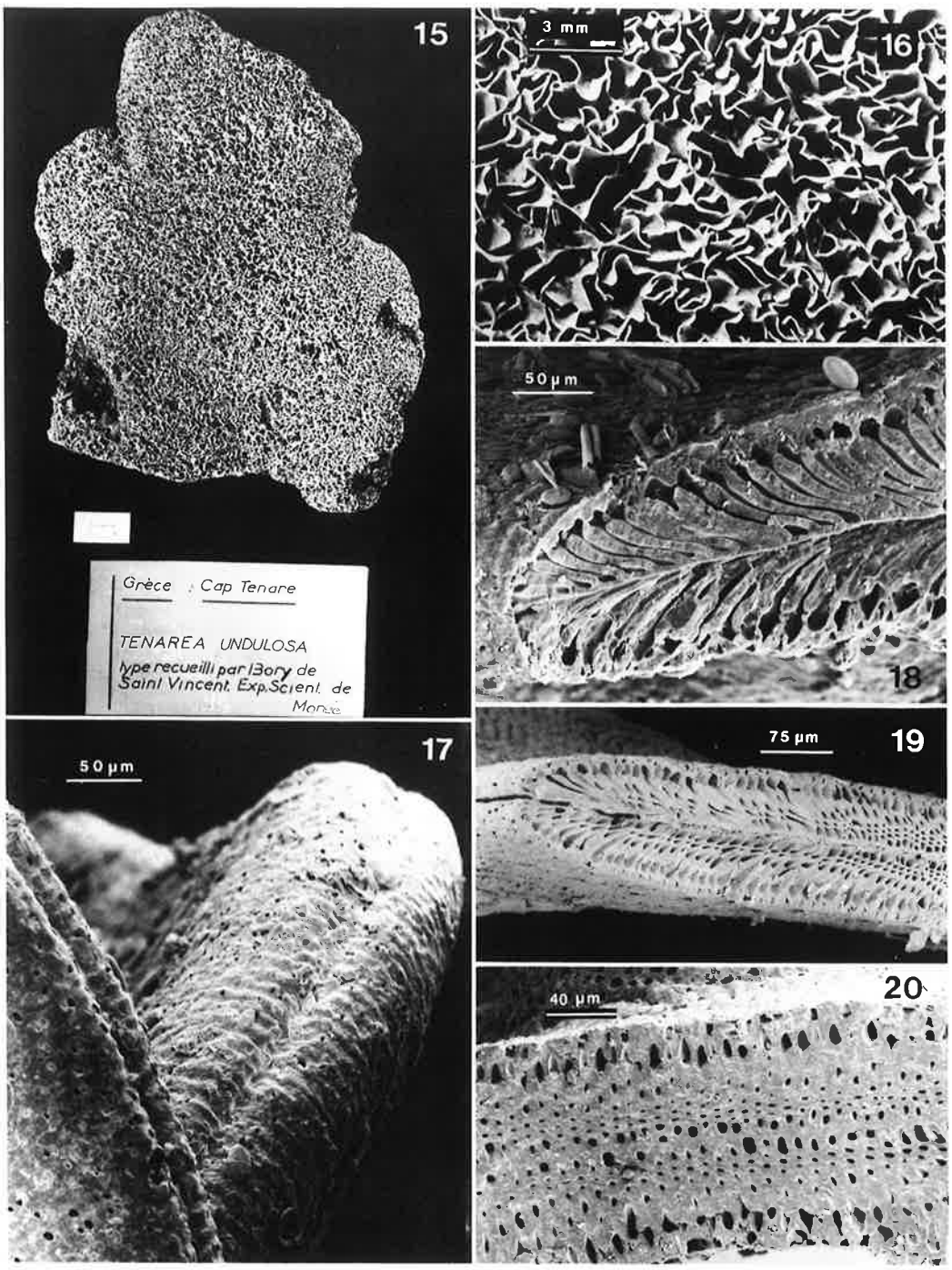
The lectotype (Fig. 1) is a somewhat elongate conglomerate of intertwined lamellae 120 mm long, 91 mm broad, and 53 mm thick. Esper listed the dimensions as approximately 4 inches (102 mm) long and broad. The lower surface is flat, more or less dull white, and contains a cylindrical hole *c.* 11.5 mm in diameter and *c.* 25 mm deep. Whether Esper's fig. 3 is based on material taken from this hole is uncertain. Remaining surfaces vary from dull white to sooty grey, the latter colour probably due to long accumulation of dust.

The lectotype lacks any conspicuous holdfast, prostrate system, or other evidence of attachment and is composed almost entirely of erect or ascending lamellae (Fig. 2) which are moderately to heavily calcified, flattened, variously twisted, irregularly branched to differing degees, and densely intertwined or interlocked. Most lamellae are 1–5 mm broad, and while some apices remain intact, many have been damaged. A fairly distinct groove occurs around the lateral and apical edges of most lamellae (Fig. 3), and the cell rows on the two sides of the groove tend to be aligned oppositely (Fig. 4). Branches appear to result from continued growth of lobes formed at the apex of a lamella (Fig. 5), probably caused by differential activity of meristem cells in a manner analogous to that found in *Mastophora* (Turner & Woelkerling 1982). Branches commonly abut one another, or in some cases one branch penetrates another (Figs 6, 7). Where abutment occurs, the two lamellae become firmly adherent to one another (Fig. 6).

Anatomically, the lamellae are organized in an isobilateral manner, and their appearance in longitudinal and transverse views is quite different (Figs 8–10). Except near conceptacles, each lamella usually consists of four cell layers (two medullary and two epithallial) when seen in longitudinal view (Fig. 8). The central two rows of cells are vertically elongate (L 75–130 μm; max. D 12–25 μm; L/D 4–7) and slanted towards the apex. Some authors (e.g. Huvé 1957; Cabioch 1972; Bressan 1974; Johansen 1981) have used the term 'hypothallium' or 'palisade hypothallium' when referring to the tissue comprising these cells, but it must be remembered that this tissue is in the center of an isobilaterally organized lamella and thus is more properly termed a medulla. [See Turner & Woelkerling (1982, pp. 214–215), and Woelkerling (1980a, p. 221) for further comments on these terms.] Each palisade-like medullary cell bears a small epithallial cell (Figs 8, 9). Collectively these cells form a unistratose epithallium on each lamellar surface, but this layer is poorly preserved in the lectotype, and when lamellae are examined in surface view (Fig. 5), numerous concavities denoting the position of epithallial cells are evident. Within a given filament, medullary cells are joined by primary pit connections (Fig. 8). Medullary cells of laterally contiguous filaments may be joined by secondary pit connections (Fig. 8), but pit connections across the midline were not observed. Cell fusions do not occur. In transverse sections of lamellae (Figs 9, 10), the palisade-like nature of the oblique medullary cells and the isobilateral organization of the thallus are obscured. For comparison, the relationship between tissue appearance in transverse and longitudinal sections is shown in Fig. 11, which was prepared from recently collected material (LTB 14645, leg. E. Coppejans, South Coast, Isle of Sikinos, Cyclades, Greece, August 1972).

Detailed data on lamellar ontogeny and on meristems were not obtainable from the lectotype, and only limited information was gleaned from recently collected specimens. It appears that the palisade cells comprising each medullary cell row are derived basipetally from anticlinal–transaxial divisions of a terminal meristem cell (Figs 8, 12) which lies in the groove (Fig. 3) at the lamellar apex. Cell elongation occurs only in the basipetal derivative, the meristem cell never becoming greatly elongated. Soon after formation, each medullary cell undergoes a single asymmetric, periclinal or somewhat oblique division to produce a small epithallial cell acropetally. Medullary cells apparently do not undergo further divisions except in association with conceptacle production, but details on this aspect are uncertain.

Further studies, based on liquid-preserved specimens and on cultured plants, are needed to determine just how the lamellar meristem is formed. In more mature lamellae, the meristem appears to be composed of two rows of contiguous cells situated in the lamellar groove (Figs 3, 4, 12). Each row gives rise to one of the two layers of subtending medullary cells (Figs 8, 12), and it *appears* that cell division activity within the two rows of meristem cells is more or less equal in rate, resulting in the isobilateral organization of tissues (Figs 8–12). What remains unknown is whether the two rows of meristem



Figs 15-20. Bory's specimen of *Tenarea undulosa.*
Fig. 15. Bory's specimen housed at PC.
Fig. 16. Surface of specimen showing apices of numerous intertwined lamellae.
Fig. 17. Apices of two lamellae showing characteristic groove.
Fig. 18. Longitudinal fracture through apex of a lamella. Compare with Fig. 8.
Fig. 19. Transverse fracture of margin of a lamella. Compare with Fig. 9.
Fig. 20. Transverse fracture of central portion of a lamella. Compare with Fig. 10.

cells originate independently or are derived from a single row during very early stages of lamellar formation. If we consider Cabioch's comments and figure (1972, p. 209, pl. 5, fig. 6), the second course seems more probable, a single row of meristem cells at some stage undergoing a synchronous periclinal–coaxial division.

Uniporate conceptacles are scattered over both surfaces of the lamellae in the lectotype (Fig. 5). Conceptacles are solitary or in groups, and the more or less domoid roofs are up to 350 μm across and protrude up to 130 μm above the lamellar surface. Conceptacles (Figs 13, 14) presumably arise from derivatives of medullary cells and possess more or less ovoid chambers up to 305 μm broad and 90 μm high. The remains of a central columella (Fig. 14) suggest that the lectotype is (bi-) tetrasporangial, but sporangia were not seen. Details of conceptacle roof formation are uncertain; at maturity the roof consists mostly of one or two layers of cells which appear to be interconnected by secondary pits. Cell fusions between roof cells were not seen.

Tenarea undulosa sensu Bory

Morphology and anatomy

The specimen on which Bory based his description of *Tenarea* (Fig. 15), as noted by Hariot (1895, p. 113) and Huvé (1957, p. 136), is preserved at PC. It consists of numerous intertwined, erect or ascending lamellae which form an irregularly shaped conglomerate up to 215 mm long and 155 mm broad. The specimen does not have a holdfast or other conspicuous attachment mechanism.

Morphologically and anatomically, Bory's specimen (Figs 15–26) and Esper's specimen (Figs 1–14) are concordant, and there is no doubt that Bory was correct in concluding that the two entities were conspecific. All of the features described in Esper's material are equally apparent in Bory's collection.

Melobesia pustulata Lamouroux

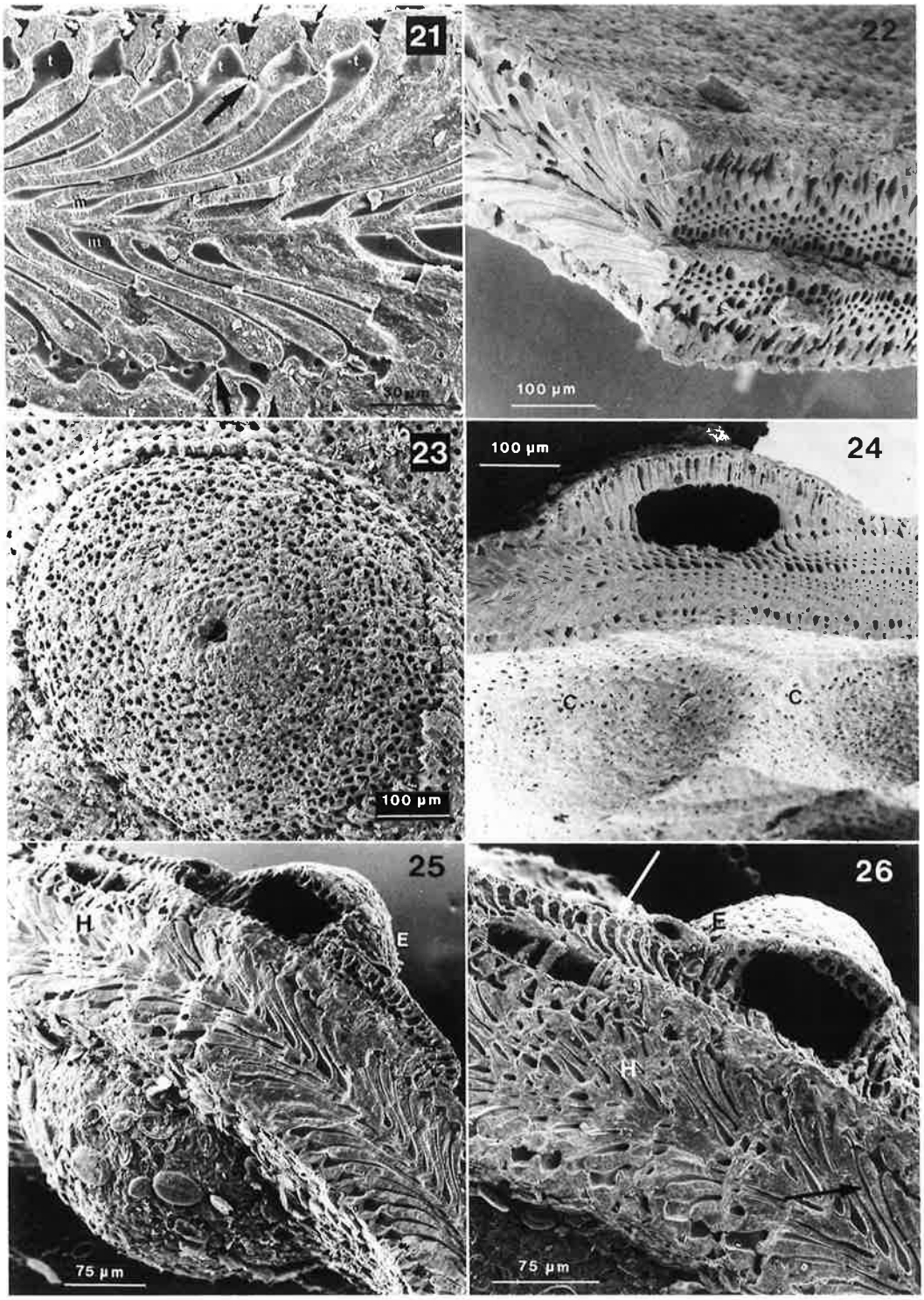
Lectotypification

Lamouroux (1816, p. 315) did not designate a type specimen. His herbarium at CN contains a single unnumbered collection (Fig. 29) labeled *Melobesia pustulata* in his handwriting, which is chosen here as lectotype. The collection consists of a few plants of the coralline growing on *Chondrus* (Rhodophyta), but the host does not agree closely with Lamouroux's rather stylized drawing (1816, pl. 12, fig. 2). Collection data are lacking.

Morphology and anatomy

Plants in the lectotype collection form a series of flattened, irregularly shaped crusts less than 1 mm thick on both sides of the compressed surface of the host. Adjacent crusts abut (Fig. 30) but do not overgrow one another, and most or all of the central surface of each plant is firmly attached to the host, as evidenced by cellular remains on the host surface where portions of the epiphyte have become detached (Fig. 30). Excrescent and ascending lamellae do not occur, and except for concavities which mark the position of epithallial cells (Figs 30, 32), the dorsal surface of the vegetative thallus is smooth. Uniporate conceptacles occur in a scattered fashion on some crusts; conceptacle roofs protrude only slightly above the thallus surface and are more or less domoid or have slightly flattened tops (Figs 37–39).

Anatomical examination of the lectotype shows that the thallus is organized dorsiventrally; the appearance of perithallial and epithallial cells is similar in longitudinal and transverse views (Figs 34, 35). In young plants or near the crust margin (Figs 31, 32), the thallus consists of a unistratose hypothallium composed of palisade cells (L 40–85 μm; D 10–23 μm; L/D 2–6). These hypothallial cells arise basipetally from a primary marginal meristem (Fig. 31) and each hypothallial cell, in turn, gives rise dorsally to a small, noncalcified epithallial cell (Fig. 36). Epithallial cells are not apparent on much of the lectotype, but their positions are delineated on the dorsal surface by concavities. In older portions of the lectotype plants, perithallial filaments up to five cells deep also occur (Figs 34, 35). In these portions of the thallus, hypothallial cells appear to be obliquely slanted when viewed longitudinally (Fig. 34), but appear more upright when viewed transversely (Fig. 35). The production of perithallial filaments in this species is similar to that in *Metamastophora* (Woelkerling 1980a) and in *Lithoporella* (Turner & Woelkerling 1982). First, a secondary meristem is formed as a result of a series of periclinal, transaxial divisions of hypothallial cells (Figs 32, 33). These meristem cells undergo further periclinal divisions and give rise basipetally to additional perithallial cells (Figs 33–35) which are quadrate to vertically elongate


21
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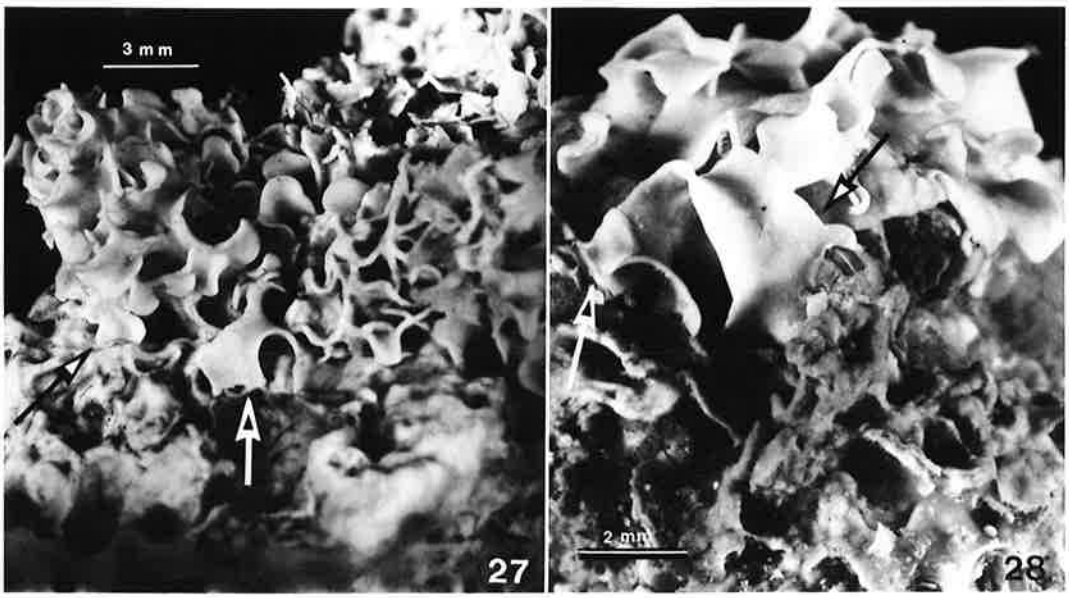

Figs 27, 28. Substrate relations of *Tenarea tortuosa* (LTB 14646).
Fig. 27. Interface between lamellae of *T. tortuosa* and a host coralline alga. Note how lamella abut the substrate (arrows).
Fig. 28. Erect portions of lamellae (arrows) arising from prostrate portions adherent to substrate.

(L 34–123 μm; D 18–29 μm; L/D 1.1–4.6) and may be aligned in more or less regular rows. Within a given hypothallial or perithallial cell row, adjacent cells are connected by primary pits; contiguous cell rows may be interconnected by secondary pits (Fig. 36). Cell fusions were not observed.

Two conceptacles from lectotype material were examined anatomically (Figs 38, 39). These possessed more or less ovoid chambers which were up to 400 μm across and 130 μm high and were devoid of contents. Two to four layers of cells occurred beneath the conceptacle floor and two or three layers of cells occurred in the roof; secondary pits were evident but cell fusions were not observed.

'Trottoir' alga

Specimens in PC from Banyuls (Mediterranean France) identified by Lemoine as *Lithophyllum tortuosum* and a more recent similarly named collection by Coppejans from La Dromont (Mediterranean France) have been examined to determine the correct name for this alga. We

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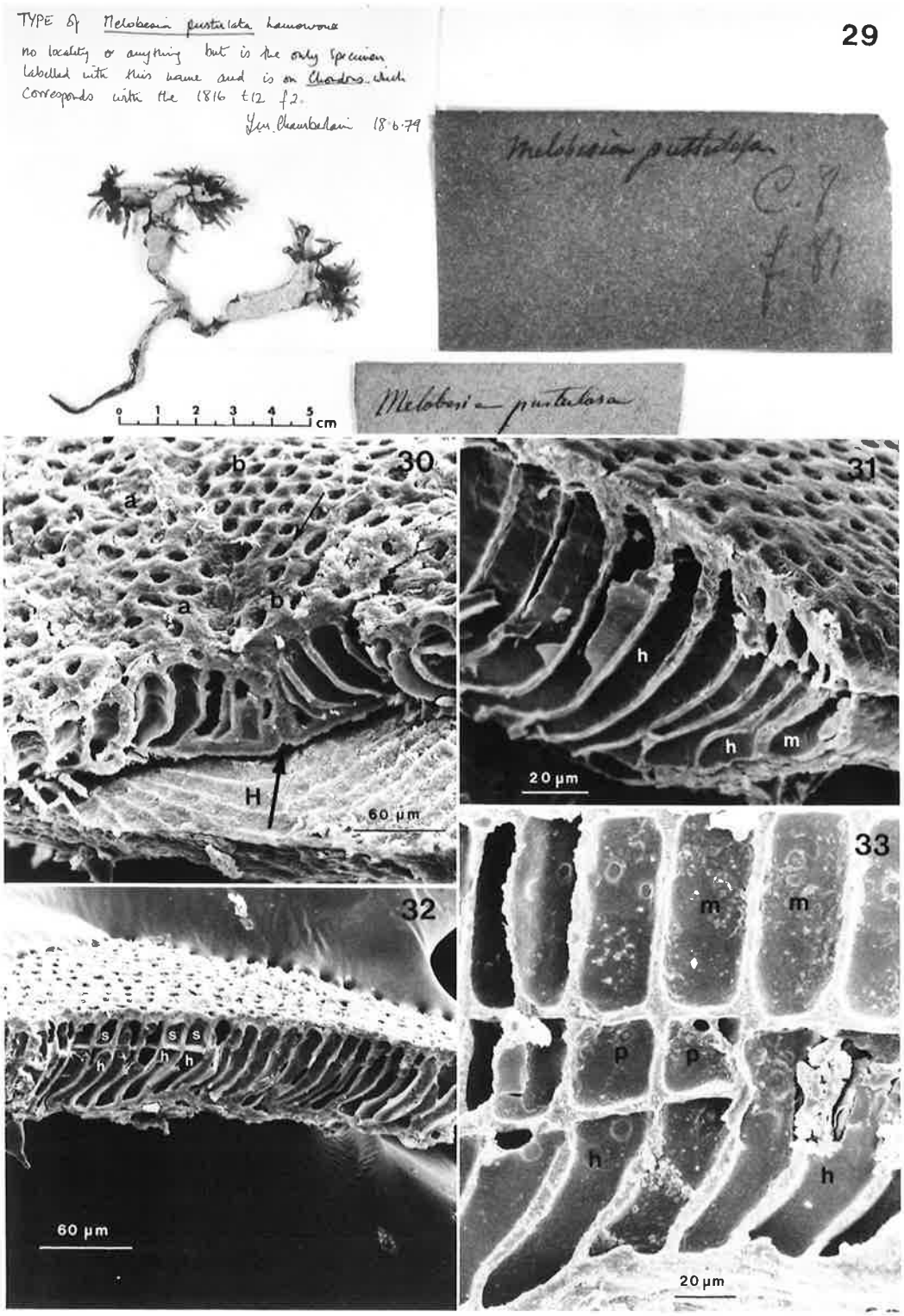
Figs 21-26. Bory's specimen of *Tenarea undulosa.*
Fig. 21. Longitudinal fracture through portion of a lamella showing minute epithallial cells (small black arrows), elongate medullary cells (m) with swollen tips (t), primary pit connections between cells of the same filament (large black arrows) and position of secondary pit connections between cells of contiguous filaments (small white arrows).
Fig. 22. Fracture showing relationships of tissues as seen in transverse (T) and longitudinal (L) views. Compare with Fig. 11.
Fig. 23. Surface view of uniporate conceptacle.
Fig. 24. Fracture through a uniporate conceptacle showing structure of roof. Pore not shown. Note parts of two intact conceptacles (C) on lower surface of lamella.
Fig. 25. Portion of a host (H) *Tenarea* lamella with an epiphytic plant (E) of *Titanoderma.* Note size difference in conceptacles of the host (lower surface) and the epiphyte (upper surface).
Fig. 26. Longitudinal fracture of a host (H) *Tenarea* lamella and a *Titanoderma* epiphyte (E). Note size difference between hypothallial cells (white arrow) of the epiphyte and the corresponding medullary cells (black arrow) of the host.


TYPE of Melobesia punctulata Lamouroux
no locality or anything but is the only specimen labelled with this name and is on Chondrus crispus which corresponds with the 1816 t12 f2.
Jean Chamberlain 18.6.79
29
Melobesia punctulata C.7 f11
Melobesia punctulata
0 1 2 3 4 5 cm
30
a
b
H
60 µm
31
h
m
20 µm
32
s
h
60 µm
33
m
p
h
20 µm

have found that these specimens are conspecific with the type specimen of *Lithophyllum lichenoides* Philippi (1837, p. 389) from Sicily, a detailed account of which has been published elsewhere (Woelkerling 1983, p. 317, figs 24–32). It is of interest to note that Lemoine (1911, p. 169) listed *L. lichenoides* Philippi as a synonym of *Tenarea tortuosa,* the name that she incorrectly applied to the 'trottoir' alga.

DISCUSSION AND CONCLUSIONS

Nomenclatural implications

The discovery of the type specimen of *Millepora tortuosa* Esper together with the fixing of procedures for typifying generic names permits clarification of the status of *Tenarea* and thus removes an extremely bothersome uncertainty from the nomenclature of nongeniculate Corallinaceae. Demonstrating the conspecificity of the type of *M. tortuosa* and the specimen upon which Bory based his description of *Tenarea* was an important and satisfying result of the present study. Had the two specimens proved to belong to different genera, there would have been the possibility of conserving the name *Tenarea* as typified by Bory's specimen, an exceptional procedure which is allowed by the ICBN (Art. 10.3) but which might engender controversy. As it is, there is only one possible application of the name—the one determined by the type specimen of the type species, *Millepora tortuosa* Esper.

Tenarea undulosa Bory must be considered an illegitimate name for the type species, sharing its type specimen in accordance with Arts 63.1, 63.2, and 7.11 of the ICBN. All names based on *Millepora tortuosa* and all those based on *Tenarea undulosa* share the same type (Table 1). The 'trottoir' alga, to which the name *Tenarea tortuosa* has generally been misapplied since the time of Lemoine (1910, 1911)*, is referable to *Lithophyllum* (see Woelkerling 1983, p. 324) rather than to its own genus as thought by Lemoine, and moreover is referable to *L. lichenoides* Philippi.

An examination of the type specimen of *Me-*

* The misapplication of the epithet *tortuosa* was initiated by Foslie (1898b, p. 9), who placed Esper's species in the genus *Goniolithon* [as *G. tortuosum* (Esper) Foslie]. Foslie circumscribed Esper's species to include *Lithophyllum cristatum* Meneghini (1840), based on specimens from the Ligurian Sea, and *L. crassum* Rosanoff (1866, p. 93, pl. 7, figs 5, 7), based on specimens from Atlantic France. The former synonym was recognized as forma *cristatum,* the latter as forma *crassum.* Subsequently, Foslie's (1898c, p. 15) stated that "*M. tortuosa* Esp. without any doubt represents an old specimen of *L. cristatum* f. *crassa.*" *Lithophyllum crassum* Rosanoff [not to be confused with *L. crassum* (Philippi) Heydrich] had been treated previously as a form of *L. cristatum* by Hauck (1883, p. 271, pl. 2, fig. 5, pl. 3, fig. 9) and as a variety of *Tenarea undulosa* Bory by Hariot (1895). Two years after having proposed the genus *Goniolithon,* Foslie (1900a) remodeled it in such a way as to exclude *Millepora tortuosa,* which he removed to *Lithophyllum* [as *L. tortuosum* (Esper) Foslie]. De Toni (1905, p. 1792) adopted Foslie's treatment and was followed by Lemoine (1910, 1911), who, however, perceived a generic distinction between the 'trottoir' alga and *Lithophyllum* and therefore applied to it the name *Tenarea,* making the combination *T. tortuosa* (Esper) Lemoine. The subsequent accounts of *Tenarea tortuosa* (or *Lithophyllum tortuosum*) provided by Mazza (1917), De Toni (1924), Funk (1927, 1955), Feldmann (1939), Hamel & Lemoine (1953), Masaki (1968), Ardré (1970, 1971), Bressan (1974), and Boudouresque & Perret (1977), among others, are almost certainly based on plants referable to *Lithophyllum lichenoides* Philippi.

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Figs 29–33. Lectotype of *Titanoderma pustulata* (Lamouroux) Nägeli.

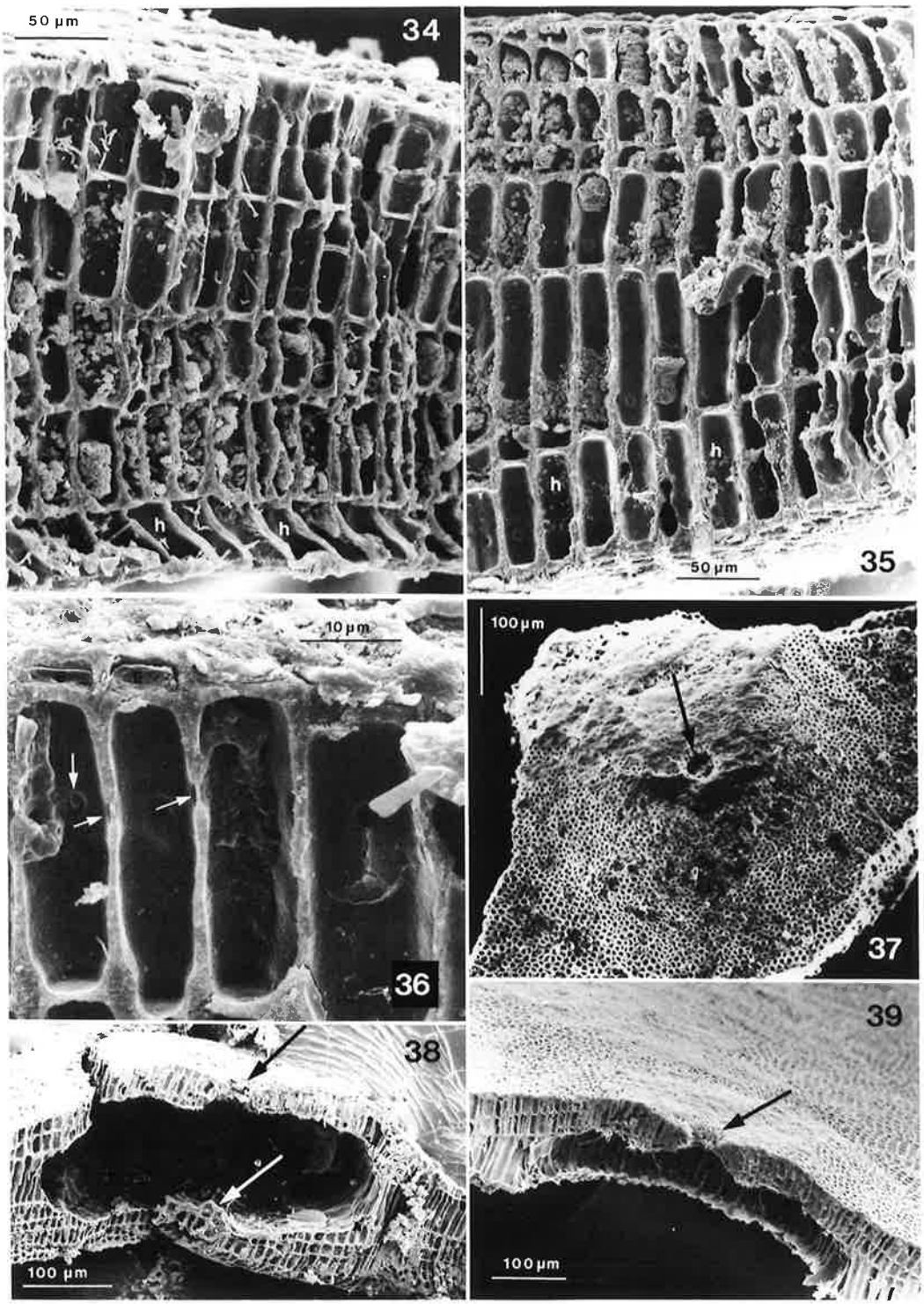
Fig. 29. Lectotype collection housed at CN. A number of plants cover the host thallus (*Chondrus*). Data on annotation label of Chamberlain refer to Lamouroux 1816. Other labels are in Lamouroux's script.

Fig. 30. Abutment of two adjacent crusts (a, b) in lectotype collection. Note juncture line (large arrow), concavities (small arrow) marking position of epithallial cells, and cellular remains on surface of host (*Chondrus,* H) where portions of the epiphyte have become detached.

Fig. 31. Longitudinal fracture of crust margin showing terminal primary meristem cell (m), hypothallial cell derivatives (h) and concavities marking position of epithallial cells on dorsal surface.

Fig. 32. Longitudinal fracture of crust showing formation of secondary (s) meristem cells as a result of periclinal transaxial divisions of hypothallial cells (h).

Fig. 33. Longitudinal fracture showing early development of perithallial cells (p). Note hypothallium (h) and perithallial meristem (m).



Figs 34–39. Lectotype of *Titanoderma pustulata* (Lamouroux) Nägeli.
Fig. 34. Longitudinal fracture of older portion of crust. Note oblique hypothallial cells (h).
Fig. 35. Transverse fracture of older portion of crust. Note more or less upright hypothallial cells (h).

lobesia pustulata Lamouroux, which is the type of *Dermatolithon,* has shown that it agrees with the concept of that genus held by recent authors (e.g. Cabioch 1972; Bressan 1974; Johansen 1981).

Having cleared up much of the uncertainty in the *Tenarea/Dermatolithon* complex, we now must introduce a slightly discordant note. In a work that has been almost completely overlooked, Nägeli (1858, p. 532) established the genus *Titanoderma* to receive *Melobesia pustulata* Lamouroux, distinguishing it from *Melobesia* by its production of bispores rather than tetraspores. Nägeli included only one species in the genus. To our knowledge, the only subsequent appearance of this name in literature is its listing by Silva in the *Index Nominum Genericorum (Plantarum)* (Farr *et al* 1979, p. 1764). *Titanoderma* is clearly an earlier homotypic synonym of *Dermatolithon.* Although it would be possible to propose conservation of *Dermatolithon,* this name has undergone such vicissitudes that it seems better to adopt *Titanoderma,* a name with a completely clear record.

The genus *Tenarea*

CHARACTERIZATION: *Tenarea,* as delineated here, encompasses those nongeniculate Corallinaceae which have uniporate (bi-) tetrasporangial conceptacles, secondary pit connections between cells of adjacent filaments, and a thallus composed of erect or ascending lamellae whose vegetative tissues are organized in an isobilateral manner and include a central region of two layers of palisade-like cells. Nomenclatural and taxonomic data relating to *Tenarea* are summarized in Table 1.

COMMENTS: The above circumscription of *Tenarea* is most closely associated with the concept of the genus provided by Huvé (1957), Cabioch (1972), Bressan (1974) and Johansen (1981), but several points require emphasis. Firstly, the isobilateral lamellae appear to be integral structures which, as shown by Cabioch (1972, p. 209b, pl. V, fig. 6), can arise as single units from one surface of a parent lamella. No evidence was found in support of Huvé's hypothesis (1957, p. 134; see also Adey 1965, p. 79, 1970, p. 6; Cabioch 1972, pp. 209, 270; Johansen 1981, p. 43, fig. 3B) that erect lamellae form when two prostrate crusts come into contact and then grow upright back to back. Indeed, ascending lamellae can arise directly as intact units from portions of the thallus which adhere to an underlying substrate (Figs 27, 28). Moreover, when *Tenarea* lamellae become forked (Fig. 5), the resulting branches always retain an isobilateral organization, providing further evidence that functionally the lamellae are integral units. In no case was an intact lamella found which lacked an isobilateral organization or looked like a monostromatic crust. Adey (1970, p. 6) noted in relation to his concept of *Tenarea* that ". . . the characteristic of thallic upgrowing base to base is a common and apparently largely fortuitous feature in many crustose corallines . . ." and that ". . . it is not warranted to consider this a generic feature." In view of evidence that the lamellae of *Tenarea* can arise and function as single, integral units, and do not form by the fortuitous union of independent crusts, this argument of Adey's no longer appears tenable.

Secondly, Cabioch (1972) and Johansen (1981) incorrectly characterized *Tenarea* by the occurrence of a unistratose, palisade hypothallium, a characterization probably based on data provided by Huvé (1957, p. 134, fig. 8). Huvé reported that in "young plants" of *Tenarea tortuosa* (as *T. undulosa*) the thallus was prostrate and possessed a unistratose hypothallium whose cells were 40–50 μm long and 5–10 μm broad. These characteristics contrast with those of the lamellae (Huvé 1957, fig. 4), which were erect and possessed two layers of "hypothallial" cells, each 80–100 μm long. Huvé makes no mention of seeing erect lamellae arising from the "young" plants, and while the "young" plants appear (Huvé 1957, fig. 3) to be largely affixed to an unidentified substrate, the older plants (Huvé 1957, p. 133) are stated to be attached to the substrate only in several places and removed very easily.

During the present study, plants corresponding to those described as "young" thalli by Huvé were encountered as epiphytes on lamellae of Bory's specimen of *Tenarea tortuosa* (Figs 25,

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Fig. 36. Fracture of upper portion of crust showing remains of two epithallial cells (E) and secondary pit connections (arrows) between cells of contiguous filaments.
Fig. 37. Surface view of uniporate conceptacle. Note ostiole (arrow).
Figs 38, 39. Fractures of two conceptacles. Note ostiole (black arrows) and remnants of columella (white arrow).

Table 1. Nomenclatural and taxonomic data relating to *Tenarea* and *Titanoderma* and their type species

Tenarea Bory 1832, p. 207

Type species: *Tenarea tortuosa* (Esper) Lemoine 1910, p. 368 (only as to binomial).

Basionym: *Millepora tortuosa* Esper 1796, p. 118, *Millepora* Tab. XXII.

Nomenclatural synonyms:

Crodelia incrustans f. *tortuosa* (Esper) Heydrich 1911, p. 13 (only as to trinomial)

Goniolithon tortuosum (Esper) Foslie 1898b, p. 9 (only as to binomial)

Lithophyllum tortuosum (Esper) Foslie 1900a, p. 20 (only as to binomial)

Superfluous substitute names:

Tenarea undulosa Bory 1832, p. 207

Goniolithon tortuosum f. *undulosum* (Bory) Foslie 1898b, p. 9 ('*undulosa*')

Lithophyllum cristatum f. *undulosum* (Bory) Heydrich 1901, p. 537 ('*undulosa*')

Lithophyllum tortuosum f. *undulosum* (Bory) Foslie 1900a, p. 20 ('*undulosa*')

Tenarea tortuosa f. *undulosa* (Bory) Lemoine 1910, p. 368

Type locality: Mediterranean Sea (Esper 1796, p. 118).

Lectotype specimen: FR (Fig. 1)

Additional references (all as *Tenarea undulosa*):

Bressan 1974, p. 105, fig. 30; Cabioch 1972, p. 208, pl. V, figs 6–11; Coppejans 1974, p. 399; Huvé 1957, 1963, p. 150.

Titanoderma Nägeli 1858, p. 532

Nomenclatural synonym: *Dermatolithon* Foslie 1898b, p. 11

Type species: *Titanoderma pustulatum* (Lamouroux) Nägeli 1858, p. 532.

Basionym: *Melobesia pustulata* Lamouroux 1816, p. 315

Nomenclatural synonyms:

Dermatolithon pustulatum (Lamouroux) Foslie 1898b, p. 11

Epilithon pustulatum (Lamouroux) Lemoine 1921, p. 10*

Lithophyllum pustulatum (Lamouroux) Foslie 1904, p. 8

Tenarea pustulata (Lamouroux) Adey 1965, p. 88 (comb. invalid)

Type locality: France (Lamouroux 1816, p. 315)

Lectotype specimen: CN (Fig. 29)

Additional references: Hamel & Lemoine 1953, p. 59, text fig. 22, pl. IX, figs 1, 2 (as *Dermatolithon*); Kornmann & Sahling 1977, p. 206, Abb. 115 (as *Dermatolithon*).

* Mme Lemoine (pers. comm.) has indicated that this combination was made by mistake; elsewhere on the same page the intended binomial *Lithophyllum pustulatum* was used.

26) as well as on more recently collected specimens (LTB 14645). The epiphytes are prostrate and have a unistratose, palisade hypothallium whose cells are much smaller than the corresponding palisade cells of the lamellae of *Tenarea tortuosa* (Fig. 26). Moreover, the epiphyte possesses conceptacles which are considerably smaller than those of *T. tortuosa* (Fig. 25). The occurrence of this epiphyte, combined with the facts that Huvé makes no mention of erect lamellae arising from her "young" plants and that the cellular dimensions of Huvé's young plants are only half those of the lamellae, suggests to us that what Huvé considered to be "young" plants of *T. tortuosa* may really represent a species of *Titanoderma*.

Finally, Bressan (1974, p. 106) noted that *Tenarea* could be distinguished from *Dermatolithon* (≡ *Titanoderma*) by the occurrence of triangular epithallial cells. We have observed triangular epithallial cells in longitudinal sections of the generitype specimen of *Tenarea* (Fig. 9) and more or less rounded-rectangular epithallial cells in the generitype specimen of *Titanoderma* (Fig. 38). Further studies are required before the generic significance of this difference can be assessed, especially since Littler (1971) recorded triangular cells in *Titanoderma tessellata* [as *Tenarea*].

Since 1832, at least 32 specific and infraspecific taxa have been referred to *Tenarea*. Based on studies of several type collections and on a survey of the extant literature relating to these taxa, it would appear that *Tenarea* as circumscribed here includes only one species, namely *T. tortuosa*. Most other taxa placed in *Tenarea* by recent authors (e.g. Adey 1970) belong to *Titanoderma* while most taxa referred to *Tenarea* by earlier authors (e.g. Kuntze 1898; Lemoine 1911, 1929; Airoldi 1936; Feldmann 1939) probably represent taxa of *Lithophyllum*. The proper disposition of these *Lithophyllum*-like taxa, however, can be determined only after examination of the relevant type collections, a task beyond the scope of the present study.

At present, *Tenarea tortuosa* is known only from the Aegean and parts of the north-eastern Mediterranean Sea (Huvé 1957, p. 133).

The genus *Titanoderma*

CHARACTERIZATION: *Titanoderma*, as delineated here, encompasses those nongeniculate Corallinaceae which have uniporate (bi-) tetrasporangial conceptacles, secondary pit connections between cells of adjacent filaments, and a

thallus consisting largely or entirely of a prostrate crust whose tissues are organized in a dorsiventral manner and include a unistratose hypothallium composed of palisade cells.

This characterization is concordant with the concept of *Dermatolithon* presented by Cabioch (1972), Bressan (1974), and Johansen (1981), except that our circumscription emphasizes the dorsiventral organization of thallus tissues. Nomenclatural and taxonomic data relating to *Titanoderma* are summarized in Table 1.

COMMENTS: Only one species (*T. pustulatum*) has been referred to *Titanoderma.* Since 1898, however, at least 67 specific and infraspecific taxa have been placed in *Dermatolithon,* a homotypic synonym of *Titanoderma.* The proper disposition of many of these taxa will have to await reexamination of the relevant type collections. During the course of studies on the Foslie herbarium, however, Adey (1970) examined a number of type specimens of taxa which he referred to *Tenarea.* Because Adey's concept of *Tenarea* is equivalent to *Titanoderma* as delineated here, those species that he recognized can be transferred into *Titanoderma.* Similarly, published accounts (protologues) of several other taxa provide unequivocal evidence that they also belong to *Titanoderma.* The necessary nomenclatural changes are summarized in Table 2. Further studies of taxa referred here to *Titanoderma* are needed to clarify taxonomic limits and relationships at the species level; some of these taxa ultimately may be demonstrated to be conspecific.

The genus *Titanoderma,* as represented by the taxa listed in Table 2, appears to be widespread, but the geographic distributions of individual species are less certain and require checking of specimens upon which published records are based.

Table 2. Associated nomenclatural data for taxa transferred to *Titanoderma* Nägeli

(a) *Taxa whose type specimens were examined by Adey (1970, pp. 6, 7)*

Titanoderma ascripticium (Foslie) comb. nov.
Basionym: *Lithophyllum pustulatum* f. *ascripticium* Foslie 1907a, p. 34

Titanoderma bermudense (Foslie & Howe) comb. nov.
Basionym: *Lithophyllum bermudense* Foslie & Howe 1906, p. 132

Titanoderma canescens (Foslie) comb. nov.
Basionym: *Melobesia canescens* Foslie 1900b, p. 6

Titanoderma conspectum (Foslie) comb. nov.
Basionym: *Lithophyllum conspectum* Foslie 1907b, p. 29

Titanoderma dispar (Foslie) comb. nov.
Basionym: *Lithophyllum tumidulum* f. *dispar* Foslie 1907b, p. 29

Titanoderma polycephalum (Foslie) comb. nov.
Basionym: *Lithophyllum polycephalum* Foslie 1905, p. 16

Titanoderma polyclonum (Foslie) comb. nov.
Basionym: *Lithophyllum polyclonum* Foslie 1905, p. 18

Titanoderma prototypum (Foslie) comb. nov.
Basionym: *Lithothamnion prototypum* Foslie 1897, p. 18

Titanoderma rasile (Foslie) comb. nov.
Basionym: *Lithophyllum rasile* Foslie 1907a, p. 34

Titanoderma tumidulum (Foslie) comb. nov.
Basionym: *Lithophyllum tumidulum* Foslie 1901, p. 5

(b) *Other taxa*

Titanoderma corallinae (P. Crouan & H. Crouan) comb. nov.
Basionym: *Melobesia corallinae* P. Crouan & H. Crouan 1867, p. 150

Titanoderma cystoseirae (Hauck) comb. nov.
Basionym: *Melobesia cystoseirae* Hauck 1883, p. 266

Titanoderma mutabile (Lemoine) comb. nov.
Basionym: *Lithophyllum mutabile* Lemoine 1930, p. 70

Titanoderma stephensonii (Lemoine) comb. nov.
Basionym: *Dermatolithon stephensonii* Lemoine 1971, p. 558

Titanoderma tessellatum (Lemoine) comb. nov.
Basionym: *Lithophyllum tessellatum* Lemoine 1930, p. 68

Relationships of *Tenarea* and *Titanoderma* to other Corallinaceae

In considering the relationships of *Tenarea* and *Titanoderma* to other Corallinaceae, the classification system of Johansen (1981, p. 10, tables 3, 4) has been selected to provide a framework for discussion. In this system, both *Tenarea* and *Titanoderma* are assignable to the Lithophylloideae, which is characterized by the absence of geniculae, the presence of secondary pit connections between cells and the occurrence of uniporate tetrasporangial conceptacles.

In addition to *Tenarea* and *Titanoderma* (syn. *Dermatolithon*), Johansen includes four other genera in the Lithophylloideae: *Ezo, Goniolithon, Lithophyllum,* and *Metamastophora. Tenarea* is readily set apart from these genera in

possessing a thallus whose tissues are organized in an isobilateral manner. In the remaining genera, the thallus is organized in a dorsiventral manner or in a dorsiventral/radial manner (the latter occurring in excrescences). *Titanoderma* is distinctive in possessing a prostrate thallus with a unistratose hypothallium composed of palisade-like cells interconnected by secondary pits. This structure contrasts with that of *Ezo* (a parasitic genus; Adey *et al* 1974) and *Lithophyllum* (Woelkerling 1983) which lack a palisade hypothallium, and with *Metamastophora* (Woelkerling 1980a, 1980b) in which the thallus is an erect, branched, taeniform structure with both secondary pit connections and cell fusions. Further study is needed to clarify the relationships between *Titanoderma* Nägeli (1858) and *Goniolithon* Foslie (1898a). Huvé (1962) provided an extensive account of *Goniolithon papillosum* (Zanardini ex Hauck) Foslie (as *Lithophyllum*), the type species of *Goniolithon,* and further studies were undertaken by Cabioch (1970, 1972). Based on these studies, Cabioch characterized *Goniolithon* by the occurrence of numerous layers of palisade-like cells which in excrescences are aligned in coaxial tiers. The young thallus is considered (Cabioch 1972, pp. 210, 270) to have a *Titanoderma*-like structure, including a unistratose palisade-like hypothallium. Whether *Goniolithon* should be treated as a distinct genus remains uncertain.

Finally, the relationships between *Tenarea* and the fossil genus *Distichoplax* require comment. Pia (1934, p. 18) established the genus for *D. biserialis* (Dietrich) Pia [Basionym: *Lithothamnium biserialis* Dietrich 1927, p. 461, pl. 2, fig. 1] and characterized it by the occurrence of calcified thalli which formed free-standing plates composed of two rows of cells. Keij (1963, 1964) recorded possible conceptacles in fossil specimens from Borneo, and Denizot & Massieux (1965) concluded, after studying additional material, that *Distichoplax* was most closely related to *Tenarea.* Although no material has been examined during the present study, it is obvious from the accounts and illustrations of the above authors that *Distichoplax,* like *Tenarea,* is organized in an isobilateral manner. Formal judgement as to whether these two taxa are related or even possibly congeneric, however, must await further study of *Distichoplax,* especially of the reported occurrence of trichocytes (Denizot & Massieux 1965), of the *possible* occurrence of cell fusions (Denizot & Massieux 1965, p. 388, pl. 7, fig. 5), and of the relationships of tissues as seen in longitudinal and transverse views (compare Denizot & Massieux 1965, text fig. 2B and Pia 1934, fig. 8 with our Figs 11, 22). Cell fusions are unknown in *Tenarea,* and the tissues of *Tenarea* in transverse view show a more complex organization than is thought to occur in *Distichoplax.* Confirmation of the occurrence of conceptacles in *Distichoplax* also is needed.

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