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The Taxonomy, Morphology and Reproduction of the Myrionemaceae, Elachistaceae, Corynophlaeaceae and Giraudyaceae (Phaeophyceae) in southern Australia

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ABSTRACT

The work presented here is a taxonomic and morphological review of the 23 taxa of the Myrionemaceae, Elachistaceae and Corynophleaceae (Chordariales) and Giraudyaceae (Dictyosiphonales) of the Phaeophyceae (Phaeophyta) found in southern Australia, in marine and estuarine waters. In addition, culture studies have been attempted with many taxa, and life histories are presented of those taxa which were successfully grown.

The limits accepted for the Myrionemaceae are those of the tribe Myrionemeae of Loiseaux. Four species of *Myrionema* are described, including *M. strangulans* Greville and three species new to science, *M. latipilosum* sp. nov., close to *M. magnusii* (Sauv.) Loiseaux, *M. ramulans* sp. nov., close to *M. furcatum* Jaasund, and *M. myriodesmae* sp. nov., related to *M. siliquosum* Sauvageau. The life history of southern Australian *M. strangulans*, which lacks plurilocular sporangia on field plants, differs from that given by Loiseaux (1967c) for the French race of this species because the zooids from unilocular sporangia settle and germinate individually and do not regenerate the field form of the plant. The life history of *M. latipilosum* conforms closely with those of *M. magnusii* and *M. orbicularis* J. Ag. as described by Loiseaux (1967c). Recent collections of *"M. incommodum"* from Safety Cove, Tasmania, suggest that the plant previously recorded under that name from Tasmania is probably a member of the Streblonemaceae (Ectocarpales). One collection of *Myrionema compactum* Lindauer is also commented upon.

The Elachistaceae is represented in southern Australia by two species of *Elachista*, and one species in each of *Halothrix* and *Portphillipia*. *Elachista* (formerly *Gonodia*) *orbicularis* (Ohta) comb. nov. is a common epiphyte of *Ecklonia radiata* around the Fleurieu Peninsula in South Australia. *Elachista secundata* sp.nov. is an epiphyte on *Sargassum* in Port Phillip, Victoria, and is related to *E. scutulata* and *E. fucicola* from the north Atlantic. The life history of *E. orbicularis* is direct and asexual, agreeing with other members of this genus. *Halothrix ephemeralis* sp. nov., a short-lived seasonal epiphyte on *Heterozostera tasmanica*, is morphologically similar to *H. ambigua* from Japan. *Portphillipia australis* (J. Ag.) Silva, an epiphyte on species of *Xiphophora* in Victoria, Tasmania and New Zealand, was not successfully cultured.

The Corynophlaeaceae is divided into two tribes, the Myriactuleae containing *Strepsithalia* and *Myriactula*, and the Corynophlaeideae, containing the remaining genera. The presence is established of three species of *Strepsithalia*, a genus previously recorded only from the north Atlantic and Mediterranean. *Strepsithalia liagorae* Sauv. is found in *Liagora harveyiana* and *L. wilsoniana* in southern Australia. The results of cultures of this species were inconclusive, and not closely comparable to those for French plants by Sauvageau (1925a). *S. aemula* sp. nov. is similar to *S. curvata*, but has very large unilocular sporangia. *S. clavata* sp. nov., which is endophytic in *Caulocystis*, has the form of a reduced *Myriactula*. The genus *Myriactula* has two species in southern Australia. *Myriactula rivulariae* (Suhr) Feldmann is regarded as having three varieties, *M. rivulariae* var. *rivulariae*, *M. rivulariae* var. *chordae* and *M. rivulariae* var. *arabica*. *M. rivulariae* var. *arabica* shows a direct asexual life history from zooids of plurilocular sporangia. *Myriactula haydenii* (Gatty)

Levring is an uncommon endophyte of *Scytosiphon* in southern Australia.

Corynophlaea is shown to have three species in southern Australia. *C. cystophorae* J. Agardh is the commonest taxon, and the breadth of variation encompasses *C. longifila* (Reinbold) Lindr. *et al.* While this species was cultured from plants with either unilocular or plurilocular sporangia, no regeneration of the field form of the plant was achieved and so no life history can be given. *C. cristata* sp. nov. differs from *C. cystophorae* in the structure of the medulla and in the form of the plurilocular sporangia, which are lateral to the upper cells of the assimilatory filaments. *C. filiformis* sp. nov., a rare species, has assimilatory filaments similar to an *Elachista*. Both epiphytic and epilithic plants of *Leathesia difformis* (L.) Areschoug have been found in southern Australia, and the distribution of this species is extended to the Eyre Peninsula of South Australia. *Leathesia intermedia* Chapman is shown to have an extensive distribution and host range in southern Australia. Neither species of *Leathesia* responded well to culture. Comparison of *L. intermedia* with *L. spherocephala* from Japan showed that the two species are truly distinct. *Petrospongium rugosum* (Okam.) Setchell & Gardner is found in Victoria and New South Wales.

The Giraudyaceae is extended to contain a new species of *Giraudya* and a new genus and species, *Flabellonema codii* gen. et sp. nov. *F. codii* is an epiphyte on the lower utricles of *Codium mamillosum* with a fan-like basal disc and erect axes with three cells/tier. *Giraudya sphacelarioides* Derbés & Solier, which corresponds very closely with the European plants of the same species, is found commonly on seagrasses in South Australia. *Giraudya robusta* sp. nov. differs from *G. sphacelarioides* by possessing a stalk of medullary filaments below the erect axes, and having unilocular

sporangia, unbranched basal plurilocular sporangia, and individual lateral plurilocular sporangia. Cultures of both species show an asexual cycle which is either direct or involves a myrionemoid prothallus. The form of the stages is similar to those obtained for *Striaria* and *Stictyosiphon*.

DECLARATION

This is to certify that the material contained in this thesis is the work of the author, except where otherwise acknowledged, and has not been accepted for the award of any other degree or diploma.

STEPHEN SKINNER.

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CHAPTER I

TAXONOMIC CONCEPTS, WITH A HISTORICAL REVIEW OF PULVINATE PHAEOPHYTA

1.1 Introduction

The four families examined here contain many taxa which are semi-microscopic and are thus very easily passed over by collectors. Other taxa, not always so much larger, can be locally very numerous and conspicuous. They show contrasting colour with the host (for example *Myrionema strangulans* Greville covers the lettuce green lamina of *Ulva* plants with conspicuous brown spots, and the very dark brown tufts of *Elachista orbicularis* (Ohta) comb. nov. contrast markedly with the mid brown of the laterals of the kelp, *Ecklonia radiata* (C. Agardh) J. Agardh), or the habit of the epiphyte breaks up the normally regular outline of the host (for example the crowded hemispherical tufts of *Corynophlaea cystophorae* J. Agardh obscure the form of the ramuli of various *Cystophora* species, and the tufts of species of *Giraudya* break up the outline of leaf blades of *Posidonia*). As such epiphytes are obscure, often seasonal or erratic in occurrence, and appear to play no major ecological role, their study in southern Australia has been neglected. Seven conspicuous species have received some attention (Harvey in Hooker 1860; Lucas 1936; Womersley 1967). They are *Myrionema strangulans*, *Portphillipia australis* (J. Ag.) Silva, *Corynophlaea cystophorae*, *Leathesia difformis* (L.) Areschoug, *L. intermedia* Chapman, *Petrospongium rugosum* (Okamura) Setchell & Gardner, and *Giraudya sphacelarioides* Derbes & Solier. With rare exceptions (MacLennan 1956, on *P. rugosum*) the treatment has involved a short description, with or without a figure, and notes on distribution and nomenclature. The need, therefore, for a complete treatment of the four families and their occurrence in southern Australia is clear.

1.2 Taxonomic concepts

A biological species is usually defined as a group of populations of organisms which share the same discrete pool of genetic information, and are able to successfully exchange that information. This hypothesis has the corollary that each biological species involves a suite of morphological forms, and the name is based on a designated type specimen. For cryptogamic plants, where there may be two or more free-living and morphologically distinct phases in the life history of a species, the populations of organisms which constitute such a biological species conform to one life history. Where a species reproduces asexually, i.e. where spores are formed by mitotic division in specialized reproductive organs or where vegetative budding initiates new individuals within a population, the populations of the species share the same discrete pool of genetic information and form a suite of morphological (phenotypic) variations as well as having the same life history.

A subspecies is considered to be a subsection of the populations of a biological species which is in some manner prevented from exchanging genetic information with the rest of the species population, but which would do so if existing barriers could be circumvented. A variety is considered to be a subsection of the species population in which some phenotypic characters are consistently associated. A genus is a group of species with related phenotypic (and thus genotypic) morphology and which share a generalized pattern of similar life history.

It is often difficult to establish the validity of a taxon on the basis of genetic discreteness, because the number and characters of the taxon's chromosomes may not be successfully obtained. This difficulty was encountered in the present study. Therefore the naming of the organisms studied is based upon the examination of TYPE descriptions, and TYPE material or authenticated material where available, and on life history studies and comparison of the results obtained with those of other workers.

A taxonomic study of any group within the Phaeophyta involves examination of suites of morphological and reproductive variations upon

one or more basic patterns. The study involves grouping those organisms which share morphological characters and which have similar reproductive patterns. Recognition of the smaller taxa in the class Phaeophyceae of the Phaeophyta necessarily involves both types of study, as very many of them have life histories with, usually, two distinct morphological life forms and one or other of these life forms can be very similar to microthalli stages of other members of the class with much larger macrothallial stages. The morphology of such organisms is intimately associated with their reproductive behaviour.

When the life history of a species has been determined and is in agreement with one group of species, with which it also shares morphological similarity, it can be considered as a valid member of that group, or genus. When a group of morphologically similar species is found to have two divergent life history patterns, the two subgroups may be referable to two different genera or the generic concepts may be recast, e.g. the redistribution of the genus *Ascocyclus* between *Myrionema* and *Hecatonema* (Loiseaux 1967a).

Nomenclatural difficulties may arise when the microthallial stage (or stages) of a species may have been discovered, typified and named independently of the macrothallial stage, and placed in a widely separated genus. Here the International Code of Botanical Nomenclature (1978) is followed in clearing up the difficulty.

It is with the above in mind that the four families, Myrionemaceae, Elachistaceae, Corynophloeaceae and Giraudyaceae are reviewed here.

1.3 General Introduction to the Four Families

1.3.1 The pulvinate families in the Chordariales

Most taxa in the Myrionemaceae, Elachistaceae and Corynophlaeaceae are epiphytes. The macrothallus, usually the unilocular sporangiate stage, is the commonly found form in field collections. This happens because of the inconspicuousness of the microthallus, which is seldom recognised in field collections, and also because microthalli of various taxa are very similar. The macrothallial stages are often pronouncedly seasonal, and there are few known cases where the two phases share the same hosts. Therefore the systematics of these three families of the Chordariales has been based very

largely on the morphological characters of the conspicuous macrothallus. An increasing emphasis is being placed on life histories of the various taxa, as refinement of unialgal culture has progressed.

1.3.2 The Myrionemaceae

The Myrionemaceae[1] as treated by Papenfuss (1951) are a large assemblage of discoid and pseudodiscoid small brown algae. Much discussion of the limits of the group has occurred in recent years, with the expansion in interest in life history studies. Loiseaux (1967a) excluded the Streblonemaceae, since Hamel (1939) had included these in the Ectocarpales (close to Ectocarpaceae), and divided the remaining genera among three tribes:-

i. Myrionemeae, with a regular monostromatic disc; all cells of disc producing erect structures; determinate growth in the erect filaments; and uni- or biseriate plurilocular organs (*Myrionema; Ulonema?*).

ii. Hecatonemeae, with a more or less regular, partly distromatic disc; regionalization of erect structure production; indeterminate growth of erect filaments; and multiseriate plurilocular organs (*Hecatonema, Compsonema, Chilionema?* and *Protectocarpus?*).

and iii. Ralfsieae, with a strictly regular, multistromatic disc; all cells could produce erect structures; determinate growth of erect filaments; and various plurilocular organs (*Ralfsia, Lithoderma* and their allies).

Recent accounts (Abbott & Hollenberg 1976; Nakamura 1972; Wynne & Loiseaux 1976) have favoured separation of the *Ralfsia* group, as a separate family or even a distinct order, both because of the morphological distinctness of this group, and because of the frequent association of ralfsioid microthalli with taxa of the Dictyosiphonales and Scytosiphonales. Species of *Hecatonema* and *Compsonema* have also been implicated in the life histories of Dictyosiphonales and Scytosiphonales (Clayton 1974; Clayton & Ducker 1970; Loiseaux 1969, 1970a). Clayton (1974) included *Hecatonema maculans* (Collins) Sauv.

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1. The spelling Myrionemataceae, used by some authors, does not seem really justified on linguistic grounds, see Art. 18 of the I.C.B.N.

in the Ectocarpaceae. Thus the Myrionemaceae, sensu stricto, consists of *Myrionema* (including *Ulonema*) and *Compsonema*.

The important taxonomic characters for the Myrionemaceae include the pattern of branching and general form of the disc; the determinate or indeterminate nature of the erect filaments; and whether the plurilocular sporangia, on the macrothallus, are uniseriate or pluriseriate. The presence or absence of ascocysts[1] may be of subsidiary taxonomic value. The life history, while often complex, involves the occurrence of discoid and streblonemoid phases, with or without an alternation of haploid and diploid generations. The general form of the thallus is shown in Fig. IC.

1.3.3 The Elachistaceae

The Elachistaceae are a neatly circumscript group of taxa, united by the presence of two forms of erect filaments arising from the medulla in the macrothallus. There are no hairs present at any stage in the life cycle. This family has only three genera (*Elachista* (incl. *Symphoricoccus*); *Halothrix;* and *Portphillipia*). The previous inclusion of *Giraudya*, although supported by Fritsch (1945), had been reassessed by Kylin (1933) and Hygen (1934) and consequently placed in the Dictyosiphonales. A repositioning, into the Dictyosiphonales, was proposed for *Leptonematella* by P.M. Pedersen (1978), following comparative culture studies with *Pogotrichum (Litosiphon) filiforme* Reinke. Another genus, *Herpodiscus*, has been included in the Elachistaceae (South 1974) but the life history is in marked contrast with other demonstrated life histories in the family.

All three of the remaining genera, *Elachista*, *Halothrix* and *Portphillipia*, show the same basic plan of construction (cf. Fig. 1D). There is a basal layer, which may be disclike or diffuse, and cells of

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1. Ascocysts are cells in which much of the normal cytoplasm has been replaced by physodes which contain tannin-like compounds.

this layer may develop rhizoidal pegs. The medulla is filamentous, sometimes reduced (in *Halothrix*), and varies from compact to diffuse. A corona of short determinate cortical assimilatory filaments forms above the usually hemispherical medullary zone. These filaments are often referred to as "paraphyses" as the sporangia are distributed between them. With their meristematic zones in the region of the corona, the long assimilatory filaments, which characterize this family, grow indeterminately and may extend beyond the corona up to four times its depth. Differences between genera are based largely on variations in these features, as well as on the form and position of sporangia.

The life history proposed for those few species of *Elachista* which have been cultured to date (Blackler & Katpitia 1963; Hoek *et al.* 1972; Koeman & Cortel Breeman 1976; Kylin 1934, 1937; Sauvageau 1933b· Wanders *et al.* 1972) involves a direct asexual cycle and a macrothallial/ microthallial stage, with no clear confirmation of sexuality in the latter.

1.3.4 The Corynophlaeaceae

The Corynophlaeaceae are characterized by having a plan of construction similar to the Elachistaceae but with hairs rather than long assimilatory filaments protruding beyond the cortex, and the cortical filaments are more developed to take over the role of the major photosynthetic region (Fig. 1A). Five to eight genera (*Strepsithalia*, *Myriactula* including *Gonodia*, *Corynophlaea*, *Leathesia*, *Microcoryne*, *Cylindrocarpus* and *Petrospongium*) are recognized. *Strepsithalia* Bornet ex Sauvageau is variously placed in this family, or the Streblonemaceae or Myrionemaceae, and the validity of placing the genera *Petrospongium*, *Microcoryne*, and *Cylindrocarpus* in the family Corynophlaeaceae

will be discussed below. Generic characters are based on variations in the general plan of construction, as well as on the habit of the macrothallus, for the taxa include minute endophytes, various epiphytes and even semiperennial lithophytes.

Little is known of the life histories displayed by this family, with the exception of *Leathesia difformis* (L.) Areschoug. For this taxon a rather complex life history is suggested by Dangeard (1965a, 1969), involving an alternation of generations with macrothallial and microthallial stages, derived from the spores of unilocular sporangia, and a complex asexual cycle, from spores from plurilocular organs.

1.3.5 The Giraudyaceae (Dictyosiphonales)

To date the Giraudyaceae has been a monogeneric, monospecific family, with a grade of construction similar to the Striariaceae in the Dictyosiphonales. The thallus is pulvinate, but with multicellular erect axes, the cells of which are all assimilatory (except those in the basal meristematic zone), and are arranged in tiers - there is no medulla in the axis. A terminal hair or fascicle of hairs is often evident in undamaged axes, and there may also be lateral hairs. The thallus shows a basal layer, but the peripheral axes show rhizoidal development. The life history of *Giraudya sphacelarioides* Derbes & Solier was studied in detail by Sauvageau (1927), although he was not satisfied that he had completed the cycle. It was sufficiently different from that of the then known Chordariales for Kylin (1933) to suggest the establishment of a separate family in the Dictyosiphonales. Dangeard (1965b) proposed a genus *Giraudyopsis*, but Loiseaux (1967b) showed that this alga belonged in the Xanthophyceae, because its pigments agreed with that class rather than the Phaeophyta.

1.4 History of systematic classification of the pulvinate Phaeophyceae

1.4.1 From J. Agardh to Kjellman (1842-1911)

From the recognition of the Chordarieae[2] by J. Agardh (1842) and Harvey (1842), as an order of brown algae characterized by "Fronde filis contexta; axi filis radiantibus peripheric is vestitio",[3] to the delineation of five sections for the Chordariaceae by Kjellman (1897), and separation of the Elachistaceae as a separate family, the common taxa which make up the pulvinate Chordariales have been reviewed in descriptions of the whole order. Table 1a shows the development, from 1842 to 1897, of the various groupings within the pulvinate taxa, later to become the families Myrionemaceae, Elachistaceae and Corynophlaeaceae, as they were organized in the principal treatises.

There were three "centers" for clustering of pulvinate taxa:-

(i) *Myrionema* - *Ralfsia*, with an essentially discoid habit;

(ii) *Elachista* - *Myriactis*, with a truly pulvinate habit;

and (iii) *Corynophlaea* - *Leathesia*, with a subglobose, spongiose habit.

Harvey (1842, 1846), J. Agardh (1842, 1848) and Kützing (1843, 1845, 1849) all associated *Ralfsia* with *Myrionema*, on similarity of form, although they variously distributed these genera in either Ectocarpeae or Chordarieae (= Mesogloeaceae of Kützing). Their concepts were followed, with little dissent, by Meneghini (1843), Crouan & Crouan (1867) and Hauck (1885).

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2. Greville (1830) proposed a family of this name, with only one genus, *Chordaria*.

3. J. Agardh (1848); p.5. "a frond of contiguous filaments, the axis dressed with radiating peripheral filaments".

Thuret (1849) grouped *Leathesia*, *Elachista* and *Myriactis* together (with *Myrionema*) in a family, Myrionemées, immediately before the Chordariées. J. Agardh (1882) discussed *Myrionema* and *Ralfsia* together, as well as *Herponema*. Kjellman (1897) recognizes Section I, the Myrionemaeae, in the Chordariaceae, including *Herponema*, *Phaeosphaerium* and *Microspongium*, the latter two now usually associated with *Ralfsia;* however, he placed *Ralfsia* in a separate family. Kjellman and Svedelius (1911), in the revision of the Kjellman 1897 work, included *Ulonema*, *Compsonema* and *Strepsithalia* in the Myrionemeae, but retained *Ascocyclus* in the Ectocarpaceae, as Kjellman (1897) had. Sauvageau (1897) presented a monographic treatment of the Myrionemaceae, which included these latter genera, but excluded the ralfsioid forms.

The *Elachista*-like group, where long, straight filaments (with pigmented cells) protrude from a compact hemispherical medulla (Fig. 1D) is an example of how rigorous limits for the groups developed gradually. Harvey (1846) and J. Agardh (1842, 1848) recognized two genera, *Elachista* and *Myriactis*, the former truly epiphytic, while the latter had a partly endophytic thallus. Kützing (1843, 1845, 1849), while accepting the two genera as distinct, limited *Myriactis* to one species, *Elachista* to a very few species, and described an intermediate genus, *Phycophila*, with a large number of indistinct forms, based on *E. fucicola* (Velley) Aresch. J. Agardh (1882) and Hauck (1885) combined all taxa into an expanded and unworkable genus, *Elachista*. Kjellman (1897) made a clear break, creating a family Elachistaceae, with Kützing's *Phycophila* in synomony with *Elachista*, and placing a monospecific genus, *Myriactis*, in Section III (Mesogloieae) of the Chordariaceae. He was the first to separate the families on the presence or absence of hairs, although he included *Giraudya* in the

Elachistaceae, interpreting the terminal hair filaments as separated filaments of the main axis (see Kjellman 1897: Fig. 152D).

The *Corynophlaea-Leathesia* group varied in the number of genera accepted, depending mainly on the limits given to *Leathesia*. Thus Harvey (1846) and Kützing (1849) included *Petrospongium berkeleyi* (Grev.) Naegeli as *L. berkeleyi* Greville, while Kützing (1858) separated it, and the Crouan brothers (1867) included it in *Cylindrocarpus*, which they placed in the Ectocarpiées, separately from *Leathesia* in the Chordariées.

Despite the clarity of the original description of *Corynophlaea* by Kützing (1843), where that genus is described as having a medulla "parenchyma continuum, compactum excellulis majoribus hyalinis vesicatis, laxe conjunctis, ellipticis constitutum"[4] as distinct from *Corynephora* C. Ag (= *Leathesia*) with a "medullare ex filis hyalinis majoribus laxis reticulatim conjunctis compositum"[4], the validity of the former genus remained a subject of debate until Kuckuck's (1929) study. Following J.Agardh's(1882) demonstration that *Corynophlaea baltica* was a small form of *Leathesia marina* (= *L. difformis* (L.) Aresch.), the validity of the other two European species (*C. umbellata* Kütz. and *C. flaccida*) was doubted by various authorities including Schiffner (1916) who treated the subject in some detail, concluding that *Leathesia* was the only genus. Very young specimens of *L. difformis* can show separate terete medullary filaments towards the edge of the thallus but the central filaments have cruciate cells. More recently Inagaki

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4. Kützing, F.T. (1843): p.331. "a compact continuum of parenchyma constituted of large hyaline cells bladderlike, loosely thrown together, and elliptical" . . . "a medulla of large hyaline filaments loosely thrown together as if in the form of a net".

(1958), in his treatment of the Japanese taxa, also recognized only *Leathesia*. He too dismissed the difference in medulla structure as sufficient to separate the genera, and in this he followed Setchell & Gardner (1925). *Corynophlaea* is still included in *Leathesia* by many authors.

A debate has continued about the limits of *Cylindrocarpus* and *Petrospongium* (See also Table V.iii, p. 136). As can be seen from Table 1a, Kjellman (1897) placed all taxa from *Myriactis* to *Petrospongium* (= *Cylindrocarpus* in Kjellman & Svedelius (1911)), together with *Mesogloia* and *Liebmannia*, in Section III (Mesogloieae) of the Chordariaceae, as those genera were distinguished from other sections by having a compact but filamentous medualla.

Table 1b shows the fluctuations in the limits of the families and the movements of various genera, up to Papenfuss (1951). As the lists are based on regional floras, certain genera do not occur in all lists. Only Oltmanns (1922) and Fritsch (1945) have attempted to review these algae on a world scale, since the revision of Kjellman (1897) by Kjellman & Svedelius (1911).

1.4.2 Recent systematic changes

Loiseaux' (1967a) revision of the family Myrionemaceae reduced the number of genera to five (*Myrionema*, *Hecatonema*, *Chilionema*, *Compsonema* and *Ulonema*), distributed between two tribes. This is a marked reduction of the family from the wider concepts of Hamel (1935, 1939) and Feldmann (1954), who included both ralfsioid and streblonemoid taxa, in separate tribes, in the family, or Papenfuss (1951), who included the ralfsioid taxa in the family. There is still some discussion about the connexion between some of these taxa and discoid life stages in other brown algae.

The emphasis placed by Hamel (1935) on the absence of hairs in

the Elachistaceae reduced the number of genera to four. Recent work by P.M. Pedersen (1978) has suggested a position in the Dictyosiphonales for *Leptonematella*, close to *Pogotrichum* (= *Litosiphon* pro parte), reducing the size of the family still further.

The Corynophlaeaceae have been more or less stable since Kjellman (1897), except for discussion of generic limits. One interesting proposal, by Hamel (1939), was the expansion of Elachistaceae to include the Corynophlaeaceae as one of two tribes. This has not received support. The genus *Strepsithalia*, erected by Sauvageau (1896), and included by him in the Myrionemaceae (Sauvageau 1897), has been included in the Corynophlaeaceae by various authors (Oltmanns 1904, 1922; Kuckuck 1929; Hamel 1935) often as a genus 'incertae sedis', although Papenfuss places it in the Myrionemaceae.

The genus *Giraudya* was historically included in the Elachistaceae, because of the possession of intercalary sporangial regions on the upper axes, supposedly similar to those on the long assimilators of *Halothrix*. Oltmanns (1922) was the first to query this, suggesting it was similar to "... an Jugendstadien von *Dictyosiphon* oder *Scytosiphon*."[5] Kylin (1933), on the basis of Sauvageau's (1927) culture studies, placed the monotypic genus as a forerunner to the Dictyosiphonales, while Hygen (1934) and Hamel (1935) included it in a new family, Giraudyaceae, near the Striariaceae.

With some modifications, because of more recent discoveries, the systematic scheme of Papenfuss (1951) still holds today. Table II shows the genera in the four families in chronological order of publication, and is intended to supplement Table Ia and b.

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5. Oltmanns, F. (1922): p.78 "...a juvenile stage of either *Dictyosiphon* or *Scytosiphon*."

TABLE Ia

W.H. Harvey 1846	J. Agardh 1848	Kützing 1843 1846, 1849	Thuret 1849	J. Agardh 1882	Hauck 1885	Kjellman 1897
Chordariaceae	Chordarieae (Tr.I. Mesogloiaceae)	Mesogloeaceae	Myrionemées	Chordariaceae		Elachistaceae
Myrionema	*Myrionema*	*Myrionema*	*Myrionema*	*Myrionema*		*Elachista*
Elachista (inc. Phycophila)	*Leathesia*	*Elachista*	*Elachista (inc. Phycophila)*	*Elachista (inc. Myriactis; Phycophila)*	*Elachista (inc. Myriactis)*	*Symphoricoccus*
Leathesia		*Myriactis*	*Myriactis*	*Corynophlaea*	*Leathesia (inc. Corynophlaea)*	*Halothrix*
		Phycophila	*Leathesia*	*Leathesia*	*Petrospongium*	*Leptonema*
		Corynophlaea				*Giraudya*
		Corynephora = Leathesia			Ectocarpaceae	Chordariaceae
		Petrospongium			*Myrionema*	Section I
					Giraudya	*Myrionema*
						Ulonema
						Compsonema
						Strepsithalia
						Section III
						Myriactis
						Corynophlaea
						Leathesia
						Microcoryne
						Petrospongium = Cylindrocarpus

TABLE Ib

Oltmanns 1904	Kylin 1907	Oltmanns 1922	Setchell and Gardner 1925	Kuckuck 1929	Hamel 1935	Fritsch 1945
	Myrionemaceae *Myrionema* *Ascocyclus* *Hecatonema* *Chilionema* *Leptonema* *Elachista* *Giraudya*	Myrionemaceae *Myrionema*	Myrionemaceae *Myrionema*	Myrionemaceae (without list of genera)	Myrionemaceae Tribe I *Myrionema* *Ulonema* *Hecatonema* *Chilionema* *Ascocyclus* *Clathrodiscus*	Myrionemataceae *Myrionema* *Chilionema* *Compsonema* *Hecatonema*
Elachista (inc.) *Symphoricoccus* *Halothrix* *Leptonema* *Giraudya*		Elachistaceae *Elachista* *Philippia* *Leptonema* *Halothrix* *Giraudya ?*	Elachistaceae *Elachista* *Gonodia* *(= Myriactis, Myriactula)* *(Cylindrocarpus Halothrix; Symphoricoccus; Leptonema)*	Elachistaceae *Elachista* *Symphoricoccus* *Philippia* *Leptonema* *Halothrix* *Giraudya*	Elachistaceae *Elachista* *Halothrix* *Leptonema*	Elachistaceae *Elachista* *Halothrix* *Leptonema* *Symphoricoccus* *? Giraudya*
Strepsithalia *Myriactis* *Leathesia* *Cylindrocarpus* *Petrospongium* Ectocarpaceae *Myrionema*	*Myriactis* *Leathesia*	Corynophlaeaceae *Strepsithalia* *Myriactis* *Corynophlaea (inc. Leathesia)* *Microcoryne* *Cylindrocarpus*	Leathesiaceae *Leathesia* *Petrospongium*	Corynophlaeaceae *Myriactis* *Strepsithalia* *Corynophlaea* *Leathesia* *Microcoryne* *Cylindrocarpus*	Corynophlaeaceae *Gonodia (= Myriactis)* *Corynophlaea* *Leathesia* *Microcoryne* *Cylindrocarpus (inc. Petrospongium* *? Strepsithalia* Giraudyaceae *Giraudya*	Leathesiaceae *Corynophlaea* *Cylindrocarpus* *Leathesia* *Myriactula* Ectocarpaceae *Ascocyclus* Mesogloeaceae *Strepsithalia*

Papenfuss 1951: - Chordariales
Myrionemaceae: *Myrionema, Chilionema, Compsonema, Ascocyclus, Hecatonema, Strepsithalia;* + Ralfsioids
Elachistaceae: *Elachista, Halothrix, Leptonema, Philippia*
Corynophlaeaceae: *Corynophlaea, Cylindrocarpus, Leathesia; Microcoryne, Myriactula, Petrospongium*
Giraudyaceae (Dictosiphonales): *Giraudya*

TABLE II

Date	Genus and Author	Type Species	Notes
1821	*Leathesia* Gray	*L. difformis* (L.) Aresch.	(*Corynephora* C.Ag. 1824)
1827	*Myrionema* Greville	*M. strangulans* Grev.	(*Ulonema* Foslie 1894; *Ascocyclus* Magnus 1874)
1832	*Elachista* Duby	*E. scrutulata* (Sm.) Duby	nomen conservandum contra *Opospermum* Rafinesque 1814; (*Phycophila* Kutz. 1843; *Symphoricoccus* Reinke 1889)
1843	*Corynophlaea* Kützing	*C. umbellata* Kütz.	
1851	*Giraudya* Derbes et Solier	*G. sphacalarioides* D. et S.	
1851	*Cylindrocarpus* Crouan et Crouan	*C. microscopicus* Crouan et Crouan	These two often combined
1858	*Petrospongium* Naegeli ex Kützing	*P. berkeleyi* (Grev.) Naegeli	
1888	*Microcoryne* Strömfelt	*M. ocellata* Strömf.	
1889	*Halothrix* Reinke	*H. lumbricalia* (Kütz.) Reinke	
1896	*Strepsithalia* Bornet ex Sauvageau	*S. curvata* Sauvageau	
1898	*Myriactula* Kuntze	*M. rivulareae* (Suhr) Feldm.	(*Gonodia* Nieuwland 1917; *Myriactis* Kütz. 1843)/

TABLE II Cont'd

Date	Genus and Author	Type Species	Notes
1899	*Compsonema* Kuckuck	*C. minutum* (C. Ag.) Kuckuck	
1970	*Portphillipia* Silva	*P. australis* (J.Ag.) Silva	(*Philippia* Kuck. ex Oltsm. 1922; *Philippiella* Silva 1959)
1974	*Herpodiscus* South	*H. durvilliae* South	incertae sedis
1897	*Hecatonema* Sauv.	*H. maculans* (Coll.) Sauv.	{ to Ectocarpales
1897	*Chilionema* Kjellman	*C. ocellatum* (Kützing) Kuckuck	

These two genera have previously been included in the Myrionemaceae, and synonomy exists with some species of *Myrionema*.

1.5 Culture work and life histories

1.5.1 Thuret to Kylin

It was early realized (Thuret 1849) that knowledge of life histories in the Phaeophyta was essential to the understanding of systematics in the Division. This necessarily required at least crude culturing of the various taxa. Many early culture attempts (e.g. Thuret (1849), for numerous algae including *Elachista scutulata* (Sm.) Duby, *Myriactis pulvinata* Kützing and *Leathesia difformis;* and Goebel (1878) for *Giraudya sphacelarioides*), achieved germination of zooids, but no complete life histories were obtained. Sauvageau (1915a,b, 1918) and Kylin (1916) were rather more successful with the Laminariales in seawater cultures, where ovum retention by the female gametophyte led directly to the formation of minute sporophytes. Similar results were obtained by the same two researchers for the Cyclosporae.

Kylin (1933) revised the systematics of the Phaeophyta, placing as much emphasis on comparison of life histories as on comparative morphology. The use of enriched seawater media, following the methods of Schiller and Schreiber (see Kylin 1933), for culture of brown algae already had become common. A few individual taxa from most groups within the division had been cultured to the point where a life history could be determined, and both the Fucales and Laminariales had been extensively cultured. Kylin described four types of life history, the *Fucus* Type, with direct regeneration of the sporophyte, and three types involving an alternation of sporophyte and gametophyte generations, the *Dicytota* Type (with isomorphic generations), the *Cutleria* Type (where the gametophyte is dominant); and the *Laminaria* Type (where the sporophyte is dominant). Based on these life history types, the new system for the division involved

three classes, the Isogeneratae (including the *Dictyota* and *Cutleria* Types), the Heterogeneratae (including the *Laminaria* Type) and the Cyclosporae (including the *Fucus* Type). While later discoveries have shown this model to be too simplified, it still remains as a milestone in the understanding of systematics for the division.

1.5.2 Recent advances in techniques

After 1945 there was a rapid expansion of interest in life histories and culturing of marine algae (see reviews edited by Feldmann (1972), and Wynne & Loiseaux (1976) for Phaeophyta). The development of artificial seawater media, and of better enrichment media, along with advances in the technology of growth facilities, has made it possible to study the parameters which affect the growth of the various life forms within the life history of an alga. Knaggs (1972) presented a timely criticism of methodology, with a warning on too ready comparison of results obtained under widely differing growth conditions. There also remains the problem of standardization of terminology.

The study of life histories necessitates investigation of nutrition and trophic responses. The importance of comparative work at various carefully chosen temperatures and day lengths, already foreseen by Kylin (1933, notes in preface), to stimulate stages in a life history has been very clearly demonstrated by Colijn & Hoek (1971) for *Sphacelaria*, and implied for numerous other taxa. Dring & Lüning (1975a, b) have started investigations with different wavelengths of light and their effects on morphogenesis in brown algae. Recent work has also been done on the requirements for and role of various halides (Hsiao 1969; Müller 1964; M. Pedersén 1969a; Woolery & Lewin 1973) and of plant hormones (M. Pedersén 1968, 1973; Iwasaki 1965) in the growth and development of brown algae.

Experiments with morphologically identical macrothalli of what appear to be the same taxon collected from different parts of the world have shown that there may be much plasticity in the life histories of these organisms, especially in the form of the microthallus. *Punctaria* and *Scytosiphon* are two genera in which species, considered the same from morphological observations, show different life histories when collected either in the Atlantic or Pacific (Clayton 1978; Clayton & Ducker 1970; Edelstein *et al.* 1965; Lund 1966; Nakamura 1965; Wynne 1969, 1972a).

Another intriguing recent discovery is that species within one genus, e.g. *Myrionema* (Loiseaux 1967c), *Elachista* (Hoek *et al.* 1972) and *Coilodesme* (Wynne 1972b), may possess macrothalli which show the same morphological suite of characters but very different life histories. For example, Wynne (1972b) found that one species of *Coilodesme* would form a sterile tuft stage and regeneration of the macrothallus proved impossible *in vitro* , while other species showed an alternation of macrothallus and microthallus. The implication from these two last mentioned points is that much that is found to occur in vitro may not be a close reflection of what happens *in vivo* .

1.5.3 Problems of sexuality

In the Phaeophyta, sexuality presents a number of problems. In theory the unilocular sporangia are the sites of meiosis and release flagellated meiospores, while the plurilocular organs (on haploid plants, often the microthalli) release flagellated gametes, and the plurilocular organs (on diploid plants, usually macrothalli) release neutral flagellated spores, after mitosis.

The detailed and exhaustive studies by Müller (1964, 1967, 1972, 1976a, b) of *Ectocarpus siliculosus* (Dillw.) Lyngb. have highlighted several variations from this pattern and also shown the importance of

isolation of strains in populations as well as from separate localities. Müller (1967, 1972) has shown that under certain growth conditions meiosis in unilocular sporangia may be suppressed, and that parthenogamy (parthenogenesis by the direct germination of (? haploid) zooids from plurilocular sporangia, without fusion) may be the rule, rather than the exception in some strains of *E. siliculosus*. Müller (1967, 1976b) has also demonstrated that a chemical attractant is produced by female gametes from *E. siliculosus*, and also (Müller 1976a) refutes the occurrence of relative sexuality previously claimed to occur in this taxon.

Sexuality, and consequent alternation of generations, appears to be a comparactively rare phenomenon among the Chordariales, Dictyosiphonales and Scytosiphonales. The work of several researchers, particularly Hoek & Flinterman (1968) and Colijn & Hoek (1971), indicates that reproductive readiness (the plant's physiological readiness to reproduce), in at least some taxa, is controlled by external factors such as day length and temperature.

Together with the problems of reproductive readiness there is the strange phenomenon of heteroblasty. This is the production within the same sporangium (either unilocular or plurilocular) of spores either the same size with different germination behaviour leading to morphologically dissimilar daughter plants, or of different sizes but also displaying the same divergence in behaviour. First recognized by Sauvageau (1924a) in species of *Castagnea*, it has been confused with heterospory and anisogamy, and the term used in several different ways. Loiseaux (1968a) discusses this phenomenon, at length, in the Myrionemaceae sensu lato. Caram (1972) gives a summary of current ideas on its significance in discussion of alternation of generations in Phaeophytan life histories. Both authors make a very clear distinction between "L'heteroblastie vraie" and "dimorphisme". Loiseaux (1968a: 241) defines *heteroblasty* as

"L'hétéroblastie est caractérisée par la formation de feux (ou plusieurs?) catégories de plantes, morphologiquement et physiologiquement differentes, issues de zoides de même provenance et n'ayant par subi de sort différent (copulations par exemples)"

and *dimorphism* as

"...les zoides qui sont à son origine, même s'ils sont légèrement spécialisés, sont de même type, et les plantes, même très différentes morphologiquement, son physiologiquement semblables, ayant les même organes reproducteurs, la même place et le même rôle dans le cycle."

1.5.4. Life history studies of the four families

The earliest attempt at culturing *Myrionema* (and *Hecatonema*) was by Sauvageau (1897), but consisted of little beyond germination of zooids. Sauvageau (1933a) again grew *Myrionema strangulans* but, because of the complexity of his results, which involved both discoid and filamentous forms, he stated "en somme je ne comprends par ce *Myrionema vulgare*".[6] Kylin (1934) also successfully grew sporelings from field plants of *M. strangulans*. His results indicated that both discoid and filamentous plantlets arose from zooids released by plurilocular sporangia, while larger infertile filamentous plantlets derived from zooids of unilocular sporangia. The most comprehensive comparative culturing of (European) taxa in the Myrionemaceae (sensu lato) has been done by Loiseaux (1964a, b; 1966; 1967a, c; 1968a, b). For *Myrionema*, she demonstrated two general forms of life history, one involving a sexual phase, as for *M. strangulans* and *M. feldmanii* Lois., and one involving two asexual phases, as for *M. orbiculare* J. Ag. and *M. magnusii* (Sauv.) Lois. (Loiseaux 1967c). Some species of *Myrionema* and *Compsonema* from Pacific North America have also been studied (Loiseaux 1970b). As with the European taxa,

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6. Sauvageau (1933a): p. 114 *M. vulgare* Thuret = *M. strangulans* Grev.

the results of the cultures led to a review of previous taxonomic concepts among the forms cultured.

Apart from Thuret's (1849) germination experiments with *Elachista scutulata*, the first cultures of members of the Elachistaceae were those of Kylin (1934, 1937). Kylin's (1937) results indicated that "apomictic" zooids from unilocular sporangia were responsible for the direct regeneration of the macrothallus in *E. fucicola*. The life history Kylin (1934) proposed for *E. stellaris* Aresch. involved the direct regeneration of the macrothallus by the zooids from plurilocular sporangia, while the plethysmothalli produced by zooids from unilocular sporangia acted as gametophytes, although he (1937) showed that these plants too could form erect assimilators similar to those of the macrothallus. More complicated life histories have been suggested by later workers (Blackler & Katpitia 1963; Hoek *et al.* 1972; Wanders *et al.* 1972). Here again the cycle is asexual and, in part, parthenogenetic Koeman & Cortel-Breeman (1976) demonstrated sexuality in *E. fucicola*, but also showed that external conditions, light and day length particularly, were involved in the induction or suppression of changes from the haploid to the diploid state.

Here again culturing has been demonstrated to be a major aid in unravelling the taxonomy of both species and genera. Jaasund (1960), from phenological studies, proposed that the presence of hair-like filaments in the *Elachista lubrica* variety of *E. fucicola* indicated that it should be treated as a species of *Myriactula*, although such structures were very rare and only found in juvenile stages of the plant. Edelstein *et al.* (1971), in reporting a direct, asexual life history for *E. lubrica* noted the absence of hairs in any life history stages in their cultures. Recently P.M. Pedersen (1979) has shown that longer than normal cells, with less compact cytoplasm, are found in some filaments in crowded cultures of the *E. lubrica* variety of *E. fucicola*. Wanders *et al.* (1972) showed that the life history of *Elachista* (formerly *Symphoricoccus*) *stellaris* was similar to that of *Elachista fuciola*, confirming the results of Sauvageau (1933b), so that the existence of a

monotypic genus for this partially endophytic species was no longer warranted.

Considering the numerous difficulties which members of the Corynophlaeaceae pose for taxonomists, this family has not received much attention at the life history level. As was noted above, Thuret (1849) germinated the zooids from plurilocular organs of *Myriactis pulvinata* (= *Myriactula rivulariae* (Suhr) Feldm.) and *Leathesia difformis*. The germlings formed branched filaments, but did not develop beyond a few cells. Sauvageau (1925a) described at least part of a life history for *Strepsithalia liagorae*, but although the second and third generation plants bore plurilocular organs, no unilocular organs were found in culture. Arasaki (1948) described the life history of *Petrospongium rugosum* (Okam.) S. & G., which involved an alternation of (? diploid) macrothallus and filamentous, not myrionemoid (? haploid) microthallus. In an investigation of the life history of *P. berkeleyi*, Caram (1957) found that 10-15% of zooids from unilocular sporangia underwent copulation and formed new macrothalli directly. She does not mention what happens to the other 85-90% of zooids. Her recommendation, for the inclusion of this species among the Isogeneratae, is perhaps premature. The possible occurrence of isomorphic alternation of generations in some taxa in the smaller Chordariales needs further investigation.

Various studies have been made of *Leathesia difformis* in culture (Sauvageau 1925b; Kylin 1933; Dangeard 1965a,1969; Cole & Lin 1968) but no two sets of results fully agree. Perhaps the most exhaustive study was that of Dangeard; his results involve both a "sexual" macrothallial/microthallial alternation of generations, with zooids derived from unilocular sporangia, and also a direct regeneration of the macrothallus by zooids from plurilocular sporangia, as well as the formation of plethysmothallial stages and various degrees of dimorphism.

He did not record the reappearance of the medullary and cortical structures as found in field specimens.

Goebel (1878) germinated zooids (unspecified) of *Giraudya sphacelarioides* and observed both fusion followed by germination and the settling of single zooids. Sauvageau (1927) isolated the three different forms of sporangia developed by this species and achieved germination and the production of either filamentous or discoid microthalli or both from the zooids of each of these organs. While some cultures produced erect processes, of which some were multicellular, the overall results were inconclusive, but sufficient to suggest a Dictyosiphonalean relationship for this genus (Kylin 1933, Hygen 1934).

1.6 Ultrastructural Research

1.6.1 Pioneer work

The use of the electron microscope as a valuable tool in probing the fine structure of brown algae was first demonstrated by Manton & Clark (1951a, b). The external morphology and flagella types and structure of *Fucus* spermatozoids (Manton & Clark 1951a), the zoospores of *Pylaiella* and *Laminaria* (Manton & Clark 1951b) and spermatozoids of *Dictyota* (Manton, Clark & Greenwood 1953) shed dramatic new light on the differences and similarities between the two classes of the Phaeophyta (Phaeophyceae and Cyclosporae). Wettstein (1954) and Leyon & Wettstein (1954) demonstrated the structure of the chromatophore (phaeoplast) of *Fucus vesiculosus* L. showing that the thylakoids were in bands, but the grana masses found in green plants were absent. Dawes, Scott & Bowler (1960, 1961) used the electron microscope for the investigation of the chemical contents of the walls of brown algae, prompted by the presence there of alginates and

sulphated polysaccharides.

1.6.2 Comparative morphology and the Bouck model

The comparative morphology of the brown algal cell has received sporadic attention. Bouck (1965) provided the first review. From studies of *Chorda filum* (L.) Stackh., *Fucus vesiculosus* and a *Giffordia* sp., he described and illustrated a generalized brown algal assimilatory cell. It possesses (1) a large *nucleus* having a prominent *nucleolus*, and associated, often numerous, *dictyosomes;* (2) large *vacuoles* with a single membrane *tonoplast*, and often densely staining contents; (3) an *endoplasmic reticulum* continuous with the *nuclear envelope* and *phaeoplast* envelope; (4) the *mitochondria* differ from those of higher plants by possessing *tubular* rather than villiform *cristae;* (5) the *phaeoplast* has a continuous *outer envelope* contiguous with the endoplasmic reticulum, a *peripheral thylakoid*, a *genophore ring* of nucleic acid material, and parallel bands of *three thylakoids*. This plastid type is described as algal Type IIIb by Bisalputra (1974). Pyrenoid morphology is variable, depending on the order. For all its generalizations, the Bouck model has so far stood the test of time. Further reviews by Dodge (1974) on whole cell features, Evans (1974) on pyrenoid structure and other organelles, and Bisalputra (1974) on plastid morphology, have expanded and clarified various points within Bouck's general model.

During the past two decades, ultrastructural research on the brown algae has taken three major lines:-

(i) the investigation of wall structure, wall chemistry and translocation mechanisms (especially on the larger taxa in the Laminariales and Fucales),

(ii) the relative positions and comparative morphology of the various organelles, with a view to their uses in systematics and phylogeny,

and (iii) the intriguing pyrenoids.

Little specific attention has been given to the walls of the pulvinate taxa under discussion here. Bailey & Bisalputra (1969) have investigated the structural aspects of the walls of two filamentous species (*Ectocarpus* and *Elachista*), demonstrating several differences in layout of fibres and so indicating a possible phylogenetic value in such investigations. The presence of pores in the wall of both *Leathesia* and *Eudesme*, allowing protoplasmic continuity between cells, has been demonstrated (Cole 1969, Cole & Lin 1968).

Apart from *Fucus vesiculosus*, which has received considerable attention from the earliest studies, and some of the larger Laminariales, only selected Phaeophyta have been extensively investigated at the subcellular level. One of the major reasons for this is the presence of the sulphated polysaccharides in the walls of the cells. This has made very difficult the selection of suitable rapid and thorough fixitives for vegetative material.

Of the Chordariales, only *Leathesia difformis* (Cole & Lin 1968; Cole *et al.* 1968), *Elachista fucicola* and *Myrionema orbiculare* (Loiseaux 1967a, 1973) and *Eudesme virescens* (Carm.) J. Ag. (Cole 1969), have been studied at the subcellular level. Toth (1976) also discussed the ontogeny and morphology of the unilocular sporangium of an *Elachista* species.

Loiseaux (1967a) showed that the phaeoplast of *Myrionema orbiculare* was irregular in structure with numerous thylakoids, but otherwise

like those of other brown algae. The pyrenoid was of the stalked "ectocarpoid" kind, and the intercellular walls possessed plasmodesmata. A very thorough treatment of the changes in organelles during zooidogenesis in *Elachista fucicola*, as well as *Hecatonema streblonemoides*, *Pylaiella littoralis* (L.) Kjellm. and *Giffordia granulosa*, is to be found in Loiseaux (1973). She demonstrates that the kind and form of the organelles in the unilocular sporangia of *E. fucicola* fit into the Bouck pattern. Cole & Lin's (1968) exhaustive study of the vegetative cells of *L. difformis* showed that they fit very closely to the Bouck model. The presence of pore fields and plasmodesmata has already been mentioned; "ectocarpoid" stalked pyrenoids are present; and there is also a very nice demonstration of phaeoplast division, in undifferentiated cells from cultured material.

CHAPTER II

MATERIALS AND METHODS

2.1 Field and herbarium collections

Fresh collections were transported in a drip-wet state, in clean plastic bags in a refrigerated container, usually polystyrene ice boxes, to the laboratories in Adelaide. Collections stored in this manner would remain viable for up to three days. Local collections, i.e. those made within a day's drive of Adelaide, were placed in seawater in trays in a 16°C constant temperature room, and would remain in good condition for examination on the following day.

When large or numerous collections were made at a considerable distance from Adelaide, they were bathed in 40% Formalin diluted in seawater (final strength between 4% and 10%), either in plastic bags or preserving jars. Specimens thus treated were used for comparative morphological studies.

Voucher specimens of all collections were made as herbarium sheets or mica mounts. Wet preserved specimens, in either 4% Formalin or 70% Alcohol with 5% Glycerine were kept for all species, but not all collections. Slides of specimens were placed in a reference collection.

2.2 Staining techniques

2.2.1 Morphological Stains

Staining of the cytoplasm of algal material was achieved by using 1% Aniline Blue. The mounting fluid for specimens was Karo (concentrated maize syrup). The following schedule was used:-

2 drops 1% Aniline Blue	2-10 minutes
1 drop IN Hydrochloric acid	
1-2 washes Distilled water	
2 drops 20% Karo (with 2% Phenol)	2 minutes (remove)
2 drops 50% Karo (with 2% Phenol)	2 minutes (remove, or stop process here if distortion of material apparent)
1 drop 80% Karo (with 2% Phenol)	add coverslip and weight and allow to dry

The first three steps can be circumvented for very small or delicate material, by direct staining with 20% Karo incorporating 1% Aniline Blue and 1N HCl.

Saf ranin in alcohol was also used as a wall stain, but results were disappointing due to the stain being taken up by mucilage, thus obscuring detail.

2.2.2 Cytological Stains

Acaetocarmine staining for nuclei and chromosomes was tried using (1) the method of Godward (1948), as in Cole (1969); or (2) the method of Russell (1962), modified in that the bleaching and fixing agent was 3:1 95% Ethanol:glacial Acetic Acid, and the mordant (a saturated solution of Iron Alum) was added separately, just prior to staining. Poor results were obtained with both methods.

2.3 Culture techniques

The culture medium used for all culture experiments was that attributed to Provasoli (James 1974; Starr 1971; Provasoli *et al.* 1957). This is an enriched seawater medium, involving the addition of excess soluble phosphates and nitrates to aged, heat sterilized seawater. This has the advantage over other enriched seawater media

of containing only specified additives. As all experiments were designed to be qualitative and not quantitive, the use of an artificial seawater medium, like ASP6F (Fries 1963), was not contemplated. The medium was used without the vitamin additives recommended as the cultures were not axenic and bacteria could thus provide the vitamins; however, additions of three plant hormones (Kinetin; a gibberelin (GA_3); and Indole-1-Acetic Acid) were made in certain experiments. The quantities chosen were those shown to cause responses in other algae (M. Pedersén 1972; Fries & Pettersen 1968; Iwasaki 1965; Mowat 1965; Jennings 1968.)

Culture medium

		Stock Concentration
$Na_2\ C_3\ H_5\ (OH)_2\ PO_4\ .11\ H_2O$	500mg	1.59mM
$NaNO_3$	3.5g	41mM
Tris	5g (Tris HCl 4.05g) (Tris base 0.95g)	41mM
$(NH_4)_2\ SO_4.FeSO_4.6H_2O$	176mg	0.448mM
Na_2 EDTA	165mg	0.443mM
Trace metals (see below)	250ml	in 1000ml distilled H_2O

Trace metals

H_3BO_3	285mg
$FeCl_3.6H_2O$	12.25mg
$MnSO_4.4H_2O$	41mg
$ZnSO_4.7H_2O$	5.5mg
$CoSO_4.7H_2O$	1.2mg
Na_2EDTA	250mg

add 20ml final Stock to make up 1000ml autoclave — sterilized seawater.

Unialgal cultures were initiated by the hanging drop technique for spore release and settling. This method usually afforded a purity of culture requiring no extra additions of anti-contaminatory substances, but the addition of two or three ml of germanium dioxide (500mg in 500ml dist. H_2O, equivalent to 2 to 3 ppm) was used routinely to avoid diatom contamination. The cultures were not axenic as removal of bacteria was not attempted. Bacterial contamination had no direct effects on the success of zooid settling, and, since bacteria provide a source of vitamins, may have alleviated the need to add vitamins to the medium to promote normal growth. There were no occasions when bacterial blooms occurred. A small protozoan ciliate occasionally appeared in the initial cultures, but was removed by washing, and did not appear to have any adverse effects on the algal sporlings.

All cultures were initiated from zooid suspensions collected in hanging drops of medium from fragments of parent material with mature sporangia. Attempts to excise single sporangia were unsuccessful. Especially in the case of species of *Elachista* and *Corynoplaea*, the sporangia could not be removed from the rest of the cortex without damage, and in *Strepsithalia* removal of fragments of the endophyte presented considerable problems. Therefore it was thought best to excise small fragments of the parent plant which contained a minimum of non-reproductive tissue. The excised fragments were given a series of three washes in sterilized medium, to minimize bacterial and other surface contaminants. They were then individually placed in hanging drop suspension on heat sterilized coverglasses attached by a drop of medium to the inside of the lid of 50 ml petri dishes. Each dish contained 10 ml of medium to provide a humid atmosphere, and prevent drying out of the drop. All glassware used was thoroughly washed, air dried and heat sterilized before use. The aged seawater and stock solutions of the medium were heat sterilized before mixing. All stages in preparation of

culture were performed under sterile conditions in an Oliphant Laminar Flow Cabinet (HLF 4/L, S./No. 125).

The petri dishes were transferred to a controlled temperature room at 16°C, with banks of "Groplus" fluorescent globes, giving an illumination of 300-600 lux at 20 cm, and set for long day illumination (14:$\overline{10}$ h). The suspensions were examined with a dissecting microscope (100X) at 12, 18 and 24 hours after culture initiation and thereafter at suitable intervals. After spore release and settlement, the parent fragments were removed and the coverglasses transferred to the medium in the bottom of the petri dishes, again under sterile conditions. Permanent slides were kept at this and subsequent examinations.

After establishment of the primary generation, the culture medium was renewed, under sterile conditions, at fortnightly intervals. When plants reached a size and population density where thinning and selection was required, the new subsamples of the original population were established in crystalizing dishes in 50-100 ml of medium. Where new generation plants were both attached to the coverglass and floating in the medium, these two forms were separated if morphologically distinct. Often floating plants later settled out and became attached to the base of the container. Subsequent generations were established by either selection of germlings in parent subsamples or by the hanging drop method of fertile specimens.

To obtain contrasting conditions of growth for cultures, subsamples from the primary generation were transferred to the appropriate controlled temperature room, or into growth cabinets (Warren: Sherer, 1500 cc capacity) which became available in late 1978, for such daylength and temperature experiments.

Labelling of cultures, on both the glassware and the labels of slides, was descriptive. A typical example consisted of a top row of two or three letters, a dash and a roman numeral, a second row with subsample number, temperature, day length, and added nutrients, and a third row (on slides only) giving date of sampling for slide mounting. For example, a culture of *Giraudya sphacelarioides* may

have been labelled

GA - III	*Giraudya* Aldinga - third series
3 16° LD + K	subsample 3, 16°C, long days, + Kinetin
(-21.xi.1978)	date of slide mounting

2.4 Ultrastructural techniques

The Phaeophyta have proved a difficult Division to work with for ultrastructural examination. While some careful experimentation with kinds of stains and length of time in staining must be done for any groups of organisms, the main sources of difficulty with the brown algae are inhibition of fixation by wall colloids, encountered with nearly all taxa, and insufficient penetration of resins for block making and consequent problems with sectioning.

The choice of fixative for the most rapid penetration and least plasmolysis of tissues to be examined varies with the material from which the tissues come. Several different fixatives were tried. To overcome problems with penetration of resin, it has been suggested (Woelkerling, pers. comm.) that the degree of penetration is enhanced and the time required for penetration to occur is considerably shortened if the procedure is done under vacuum.

The fixative tried first was that of Markey & Wilce (1975, 1976a, b), viz. a 25% aqueous solution of glutaraldehyde which is diluted to 20% by volume with millepore cleaned seawater, and the pH adjusted to 7.4. Several other preparations involving glutaraldehyde have been tried, including the addition of HEPES Good Buffer with the Markey & Wilce recipe, and the method of Calvert, Dawes & Borowitzka (1976). The use of paraformaldehyde, has also been tried. No fully satisfactory fixative has been

found for the plants studied here.

The fixative failed to prevent leaching from most organelles and of wall material. The fibres of the walls of *Elachista orbicularis*, *Leathesia intermedia* Chapm. and *Giraudya sphacelarioides* fragmented and separated. Similarly, while the general form of the phaeoplast was preserved, the endoplasmic reticulum was deformed or lost, and individual thylakoids had a fragmented and ropey appearance. Other membranes and membrane bound structures were deformed or lost.

So, after several attempts at successful fixation of specimens, the study of the ultrastructure of these algae was abandoned.

The general schedule of operation was as follows:-

Fixative, 2-24 hours

2% K MnO_4 or 2% OsO_4, 1 hour

Distilled H_2O, 3 hours (6 changes)

Ethanol or Acetone series 10% - 100% dry, 1 hour in each dilution

Spurrs Resin + Ethanol 1:1, 24 hours (TAAB + Acetone 1:1)

Spurrs Resin, 24 hours (TAAB)

Bake resin for 3 days

Sectioning - glass knives in an Ultramicrotome

Reynolds lead citrate/Uranyl Citrate (Reynolds 1963)* see p.35

Examination under a Seimans electron microscope.

2.5 Statistical studies

In this study, numerical analytical techniques for taxonomic problems were found to be of use in clearly distinguishing the two taxa in the genus *Giraudya*. From the examination of the 53 separate collections available at the time, a set of 17 morphological characters, which could be objectively observed to be present or absent on any sample, was put together, and a data sheet, indicating presence or absence, was made up from all specimens. These data were subjected to standard factor analysis using SSBS packets for use with the University of Adelaide's CIBER computer. Other taxa were not treated statistically either because there were too few specimens available for valid use (as with the *Myriactula* complex), or no requirement was found for computer treatment of statistics.

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* Length of time in Uranyl Acetate varied between 1½ and 5 mins. Lead citrate time for staining 1½ mins.

CHAPTER III

MYRIONEMACEAE* FOSLIE 1890

3.1 The family Myrionemaceae, morphology and taxonomic characters

The Myrionemaceae is a family of semi-macroscopic brown algae occurring as discs on their hosts, and are marine or estuarine epiphytes. The thallus consists of a monostromatic basal disc with free erect filaments, hairs and reproductive structures forming a cortex arising directly from the basal disc, without an intervening medulla. The habit of growth (the hairs are usually independent of the assimilators and are the first erect structures produced) and the dimorphic life-history demonstrated by members of the Myrionemaceae suggest close affinities with the simpler Chordariales, especially *Strepsithalia* Sauvageau and *Myriactula* Kuntze in the Corynophlaeaceae, rather than the Streblonemaceae (Ectocarpales).

Loiseaux (1967a) accepted three tribes in the family Myrionemaceae - Myrionemeae, Hecatonemeae and Ralfsieae - excluding *Streblonema* and related forms which she did not examine and retained in the Ectocarpales (Hamel 1939; Feldmann1954). In the tribe Myrionemeae she placed the genera *Myrionema* Greville, *Ulonema* Foslie and *Clathrodiscus* Hamel, although she questioned the validity of the later two, as had Jaasund (1951) for *Ulonema*. In the tribe Hecatonemeae she placed *Hecatonema* Sauvageau, *Chilionema* Sauvageau, *Compsonema* Kuckuck and *Protectocarpus* Kjellman. In Abbott & Hollenberg (1976), Loiseaux, Abbott and Hollenberg have the three

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* Although Thuret (1849 : p. 236), whom Foslie recognized as the author of the name, used the term "Myrionemées", he did not outline clearly the limits of the family, and included all pulvinate Chordariales.

genera *Myrionema*, *Hecatonema* and *Compsonema* in the Myrionemaceae, and the Ralfsieae as a separate family Ralfsiaceae. Nakamura (1972) has even suggested the creation of an order, Ralfsiales, although this step has not received widespread approval (but see Bold & Wynne 1978).

Feldmann (1954) placed the genera *Hecatonema* and *Chilionema* (both genera with a distromatic disc and indeterminate growth in erect filaments) in the Ectocarpaceae. Clayton (1974) also placed *Hecatonema* in the Ectocarpaceae but discussed the close affinites of *H. maculans* (Collins) Sauv. with the plethysmothalli and gametophyte stages of various Dictyosiphonales. Loiseaux (1967c) has demonstrated *Myrionema*-like life histories for several other species of *Hecatonema*. In this discussion of Australian taxa in the family Myrionemaceae, only those taxa which exhibit a monostromatic basal layer will be considered, leaving *Hecatonema* in the Ectocarpaceae. Therefore the family in Australia includes only the genus *Myrionema*, (including *Ulonema*, *Clathrodiscus* and *Ascocyclus* Magnus pro parte)

One of the major taxonomic problems with a family such as the Myrionemaceae is the small number of morphological characters available on which to base distinctions between taxa. Coupled with this is the variability shown by any one taxon when specimens are collected from several different hosts, with dissimilar external surfaces. A third problem arises from the morphological similarity between the microthalli of phylogenically distant taxa and some

forms of taxa in this group. As the culture of the taxa discussed below has not always been successful or possible, the taxonomic status of all four species is not final.

The retention of discussion of the taxon here called *Compsonema compactum* has been maintained in the light of its equivalence to *Myrionema compactum* Lindauer, even though its taxonomic status is very much in doubt.

3.2.1 *MYRIONEMA* Greville 1827:pl.300. J. Agardh 1882:53. Kylin 1947:36. Loiseaux 1964a:2383; 1964b:203; 1967a:326; 1967c:526; 1970:248. Sauvageau 1897 161; 1927:13. Setchell & Gardner 1925:454.

Ascocyclus Magnus 1874:73, pro parte

Clathrodiscus Hamel 1931:102

Phaeosphaerium Kjellman 1890:41

Phycocelis Strömfelt 1888:383

Ulonema Foslie 1894:132

Thallus a compact or spreading monostramatic disc, either adherent to the host surface or slightly raised in the centre, usually

under 5mm in diameter, epiphytic on various algae and seagrasses.

Basal layer of subdichotomously branching filaments which may be closely appressed to form a discrete disc, or may be free and spreading to form a diffuse plate. All cells of the disc may produce erect structures, the central cells first; some basal cells may produce rhizoids; expansion of the disc by meristematic marginal cells.

Assimilatory filaments erect, uniseriate, simple or bifurcate from the first cell above the base, and in some cases with lateral branches of one or two cells, height uniform (giving the thallus a domed appearance), usually of ten or fewer cells, growth determinate. Hairs with a basal collar, a one celled pedicel and a meristem above which the cells are cylindrical, several times longer than broad, and with a slight concentration of pigment in the centre of the cell. Ascocysts produced directly from the disc or on a one celled pedicel and filled with tannin-like storage products or perhaps abortive unilocular sporangia, are present in some species.

Unilocular sporangia ovoid or clavate, opening by rupture, either borne directly on a disc cell or laterally on the basal cell of an assimilatory filament.

Plurilocular sporangia filiform, uniseriate or with oblique divisions giving a partially biseriate appearance, with 8-24 loculi, opening by a terminal pore, borne directly on the disc cell, or with a pedicel, or terminally on modified assimilatory filaments.

Type species:- *Myrionema strangulans* Greville

A genus of 19 or 20 species found throughout the world,

but commonest in cooler waters. *Myrionema* differs from *Compsonema* by showing determinate growth in the assimilatory filaments and by having filiform uni- or biseriate plurilocular sporangia. The general life history as outlined by Loiseaux (1967c) consists of a discoid phase and a loose filamentous stage, but an alternation of generations and the presence of sexuality varies with species. True heteroblasty and/or dimorphism may be encountered in members of this genus.

3.2.2 Key to the genus *Myrionema* in southern Australia

1. Each cell of basal disc supporting a single erect filament or organ. 2

1. Each cell of basal disc supporting usually two (occasionally one) erect filaments or organs. 3

2. Erect assimilatory filaments numerous, of 4-6 (-10) cells, terminal cell inflated; ascocysts (very rare or) absent; hairs narrow, cells 10-12 µm in diameter, unilocular sporangia lateral on basal cell of erect filament; plurilocular sporangia unknown in Australian specimens.

1. *Myrionema strangulans* Grev.

2. Erect assimilatory filaments infrequent, of 3-5 cells, terminal cell not inflated; ascocysts common, narrow, terete, as long to twice as long as plurilocular sporangia; hairs broad, cells 15-20 µm in diameter; unilocular sporangia rare, sessile; plurilocular sporangia long, with sixteen or more loculi.

2. *Myrionema latipilosum* sp. nov.

3. Erect assimilatory filaments narrow, short, patent, of 3-5 cells; hairs with a single basal cell; unilocular sporangia clavate; plurilocular sporangia formed on a modified, branching, erect filament, each sporangium of 4-8 loculi.

3. *Myrionema ramulans* sp. nov.

3. Erect assimilatory filaments broad, long, flexible, of 8-20 cells; hairs with a two to three-celled pedicel; unilocular sporangia elongate ovoid; plurilocular sporangia unknown.

4. *Myrionema myriodesmae* sp. nov.

There is a further taxon, usually credited to this genus as *M. incommodum* Skottsberg. A recent collection was made of *Adenocystis*, from Safety Cove, Tasmania (ADU, A50536) among which one or two plants showed irregular dark patches. The epiphyte which caused these patches agreed closely with the description of *M. incommodum* Skottsberg. However, the general habit of the plant, and the weaving nature of the basal layer, which has rhizoidal filaments, support the removal of this taxon to a genus in the Streblonemaceae.

3.2.3 Species descriptions

1. *Myrionema strangulans* Greville 1827:pl.300. DeToni & Forti 1923:78. Guiler 1952:78. Hamel 1931:88. Harvey 1851:pl.208. Kjellman 1890:40. Loiseaux 1967c:547. Lindauer, Chapman & Aiken 1961:105. Womersley 1967:229.

M. leclancheri Harvey 1846:pl.41A; 1860:193. Lucas 1909:18; 1929a:13.

M. punctiforme Harvey in Hooker 1863:391. Harvey 1846:pl.41B.

M. vulgare Thuret 1864:82. Hauck 1885:320. Sauvageau 1897:185.

Figure 2,A; Plate I, A, B; Pl. 19,A, B.

Thallus a more or less regular disc, 0.5-2mm in diameter, with short erect filaments, epiphytic on various algae, brown (Fig.2, A2-3, Pl. 1A).

Basal layer monostromatic, composed of subdichotomous, closely appressed filaments radiating from a central point, adnate to the host surface. Cells 10-20 µm long, 5-10 µm across, 4-7 µm high, with pigmented cytoplasm, each cell producing an erect structure, forming a shallow, even dome from margin to centre.

Erect assimilatory filaments 100-130 µm long, of 5-8 (-10) cells, the basal cell short and contracted above, next 3-8 cells narrow, cylindrical, 15-25 µm long, about 5 µm in diameter, and the terminal cell inflated and ovoid, often containing storage substances, 15-25 µm long, 6-10 µm in diameter (Fig.2A1). The cell contents include a discoid nucleus, several discoid phaeoplasts with one or two pyrenoids in each, and considerable vacuole. Hairs with a basal collar, a pedicel as wide as the cells of assimilatory filaments, a short meristem of four to eight cells and cylindrical cells with a small, central, densely-staining mass of cytoplasm, L/B 3-5, 10-12 µm in diameter (Fig.2A1).

Unilocular sporangia borne singly or in pairs, laterally on the short basal cell of assimilatory filaments, ovoid, 50-80 µm long, 20-30 µm in diameter, opening by rupture, wall persistent (Pl. 1B).

Plurilocular sporangia borne on a short one-celled pedicel in the same manner as the assimilatory filaments, filiform, uniseriate with occasional oblique walls, 8-12 loculi, opening by a terminal pore, up to the height of erect filaments. (All Australian material examined bore only unilocular sporangia.)

Type locality:- Appin, Scotland.

Type:- E.

Distribution:- Kangaroo Island, and from Adelaide, eastwards in South Australia; also Victoria and Tasmania. Widely distributed throughout the world.

Host range:- (in Australia) *Ulva lactuca*, *Enteromorpha* sp. aff. *E. compressa*. Present in southern Australian waters from August to February, with a shorter season in warmer waters; from the uppermost eulittoral to 9m deep.

Representative specimens examined:-+

SOUTH AUSTRALIA: Robe. (*Womersley*, 20.xii.1953; ADU, A19128; 6.xi.1965; ADU, A29639; *Skinner*, 30.x.1976; ADU, A47501*; 13.xi.1978; ADU, A50220; 10.ii.1979; ADU, A50267). Wallaby I. American R. inlet, Kangaroo I. (*Womersley*, 28.viii.1950; ADU, A15285). Encounter Bay. (*Skinner*, 26.x.1976; ADU, A47498*; 28.ix.1977; ADU, A48259*, and on *E.* aff. *compressa* A48260; 12.x.1977 (on *E.* aff. *compressa*); ADU, 48571; 21.viii.1978; ADU, A49513* and (on *E.* aff. *compressa*) A49514). Nora Creina. (*Skinner*, 30.x.1976; ADU, A47502*). Hallet's Cove, Adelaide. (*Fox*, 19.x.1977; ADU, A48589). Lady Bay, Normanville on *Enteromorpha* sp. aff. *E. compressa*. (*Skinner*, 12.x.1977; ADU, A48633). Beachport. (*Skinner*, 14.xi.1978; ADU, A50219).

VICTORIA: Crawfish Rock, Western Port Bay. (*Watson*, 15.ix.1968; ADU, A32741; *Watson*, 30.xi.1968 (at 9m depth); ADU, A33590; *Womersley*, 29.viii.1971; ADU, A39441). Point Lonsdale. (*Ducker*, 7.ii.1969; MELU, 4288; 4.ii.1965; MELU, 2011; *Skinner*, 4.i.1978;

+ All specimens on *Ulva lactuca* unless otherwise stated.

ADU, A49064). Portland. (*Kraft*, 30.xii.1976; MELU, K6308). London Bridge. (*Turner*, 9.i.1966; MELU, 2461). Mallacoota Inlet. (*Ducker, and King*, 15.xi.1970; MELU, 20654). Point Wilson. (*King*, 2.ii.1970; MELU, 4853). St Leonards. (*King*, 16.x.1969; MELU, 4739). Summerland, Phillip I. (*Ducker*, 10.ii.1963; MELU, 325). *TASMANIA:* Bombay Rock, Tamar Estuary. (*Womersley*, 27.i.1949; ADU, A10373). Port Arthur. (*Cribb*, 8.iii.1950; ADU, A16026). Swan I. (*King*, 3.xii.1969; MELU, 20162). Maatsuijker I. (*King*, 8.xii.1969; MELU, 20172). Hunter I. (*King*, 15.xii.1969; MELU, 20340). Deal I., Kent Group. (*King*, 21.xi.1969). Blackman's Bay. (*Skinner*, 20.ii.1978; ADU, A49158). Safety Cove, Port Arthur. (*Skinner*, 21.ii.1978; ADU, A49159). Georgetown. (*Skinner*, 23.ii.1978; ADU, A49160). Woodbridge. (*Skinner*, 24.ii.1978; ADU, A49161). Gordon. (*Skinner*, 24.ii.1978; ADU, A49162). Specimen numbers with an asterisk indicate those used for cultures.

Culture studies:-

Figure 18 , A; Plate 11.

Loiseaux 1967c, fig. II, gives a summary of the life history which she obtained for *Myrionema strangulans* collected on the French Atlantic coast; both plurilocular and unilocular sporangia are found together on the one plant. It involves an alternation of generations as well as considerable dimorphism in the vegetative cycle. To obtain pseudodiscoid plants (A') there are two pathways: (1) zygote formation from zooids from unilocular sporangia, or (2) heteroblasty among the zooids of plurilocular sporangia, the amoeboid zoospores forming either new true discs or pseudodiscs.

The formation of zygotes from zooids of unilocular sporangia

is an interesting phenomenon, found occasionally among the Ectocarpales and Chordariales. In theory the zooids from unilocular sporangia are meiospores, and should act to form the gametophyte of the mother plant, germinating singly to do so.

Results:-

Although five attempts were made to culture the race of *Myrionema strangulans* from southern Australia, the three early cultures, with material from Encounter Bay (A47498), Robe (A47501) and Nora Creina (A47502), did not proceed far beyond germination. Culture ME-II (from A48259, Encounter Bay, South Australia) was cultured in Provasoli's enriched seawater at 16°C, under 14:$\overline{10}$ h. Later, a subsample was transferred to 20°C, 14:$\overline{10}$ h. Culture ME-III (from A49513, Encounter Bay, South Australia) was grown in Provasoli's ES with Kinetin under 4°C, 24:$\overline{0}$ h; 16°C, 8:$\overline{16}$ h or 14:$\overline{10}$ h; 20°C, 8:$\overline{16}$ h, or 14:$\overline{10}$ h. After 3 months in culture, plants from the 16°C 14:$\overline{10}$ h were subcultured into a series of treatments involving all four day lengths and eight treatments involving the three plant hormones, Kinetin, Indole Acetic Acid and Gibberellic Acid No. 3.

Culture ME-II showed tubular germination from zooids of unilocular sporangia. The new plantlets formed a protrate radiating filamentous mass, which later became compacted into a dark cushion. After 32 days at 16°C, 14:$\overline{10}$ h or 50 days at 20°C, 14:$\overline{10}$ h some plants bore long intercalary multiseriate plurilocular sporangia (Pl. 11.G). These released zooids which settled to reproduce similar filamentous plants.

Culture ME-III was established from zooids, of two different sizes, from unilocular sporangia, at 16°C, 14:$\overline{10}$ h. Of the twelve original subsamples, one showed a high concentration of amoeboid

germlings, three others a mixture of amoeboid and tubular germlings (with 50% tubular germlings), while seven of the remaining eight sub-samples showed mainly tubular germlings (Table 3, 1.a). Amoeboid germination involves the settling of zooids, which germinate in a lobed fashion, on all sides, rather than in the form of a tube from one end of a zooid. No fusion of zooids has been observed, and thus it seems probable that heteroblasty occurs, at least in some cases, in the southern Australian race of *M. strangulans*.

After ten days, subsamples were removed and subdivided, for establishment at the various temperature and day length regimes described above. Both filamentous and pseudodiscoid plantlets (Pl. 11 F & B) appeared in subsamples at 16°C, 8:$\overline{16}$h and 20°C 8:$\overline{16}$ h while in other subsamples - where only tubular germination was observed - only filamentous plants grew. Unilocular sporangia occurred on some plantlets only, in 16°C, 8:$\overline{16}$ h and 20°C, 8:$\overline{16}$ h and 14:$\overline{10}$ h after 30, 23 and 30 days respectively, while plurilocular sporangia occurred in only 20°C, 14:$\overline{10}$ h samples after 23 days. Neither 4°C, 24:$\overline{0}$ h nor 16°C, 14:$\overline{10}$h subsamples ever showed reproductive structures of any kind, nor did they produce second generation plantlets. Second generation plantlets in the other three subsamples were of both filamentous and pseudodiscoid kinds, with forms of plantlets rarely showing hairs (Pl. 11).

After three months of growth and subsampling, the experiment was terminated, except for subsamples (now in the fourth generation) grown at 16°C, 8:$\overline{16}$ h. These were used as the basis for an experiment to find the effects of various hormones on the plants, now mostly pseudodiscoid, with unilocular sporangia, but lacking hairs or any

TABLE 3.1.a

ME-III (16°, 14:10 for germination)

	1	2	3	4	5	6	7	8	9	10	11	12
Amoeboid germination	+ 10%	+ 50%	+ 20%	+ 20%	+ ?	+ 50%	-	+ ?	+ 10%	-	+ 50%	+ 70%
Tubular germination	+	+	+	+	+	+	-	+	+	+	+	+
Date sampled	24. viii	25. viii	29. viii	2.ix	removed to separate treatments, 4.ix.1978						23. viii	23. viii

TABLE 3.1.b

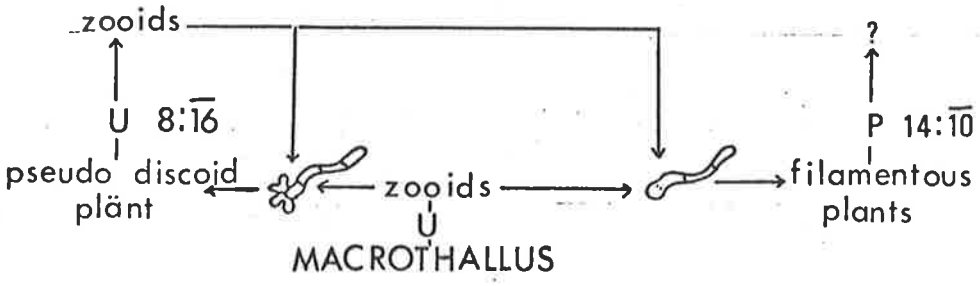
Results of culture of *M. strangulans*

	ME-II (1977) 16°, 14.10 h	ME-III (1978) 16°, 14:10 h	16°, 8:16 h	20°, 14:10 h	20°, 8:16 h	4°, 24:0 h
Amoeboid germination without fusion		+? (< 5%)	+ (50%)	+? (< 5%)	+? (10%)	
tubular germination	+	+	+	+	+	+
heteroblasty			+		+?	
pseudodiscoid plants		+ distinguishable after 22 days	+	+	+	
filamentous plants	+	+	+	+	+	+
intercalary plurilocular sporangia	+ 32 days	-	-	+ 23 days on filamentous plants	-	-
unilocular sporangia	-	-	+ 30 days on pseudo-discoid plants	+ 30 days on pseudo-discoid plants	+ 23 days on pseudo-discoid plants	-

20° 14:10 h + 50 days

organized pattern of growth. The levels of hormones were chosen from those reported to be optimal for other algae. Kinetin was administered at 20 µM (Pedersén, M. 1973); Indole acetic acid at 5×10^{-4} M (Mishra & Kefford 1969), and Gibberellin (as GA_3) at 1.7 µM. (Jennings 1968). The test was designed to be qualitative, and the number of samples per treatment was reduced to the minimum - four, one at each day length and temperature setting. The experiment was run for one month. The inoculum appeared to reproduce by fragmentation. Some samples, when treated with IAA, either alone or in combination with other hormones, regained hairs for a short while, and did produce unilocular sporangia and ranked filaments. No recognizable macrothallial plants were obtained, and neither of the other hormones showed marked effects on the cultures.

The partial life history diagram below is obviously incomplete; however, it summarizes the results obtained.



Textfigure 3.1 Life history diagram for southern Australian race of *Myrionema strangulans*.

Discussion

In contrast to the results of Loiseaux (1967c), no regeneration of the macrothallus was obtained in culture.

Plants of *Myrionema strangulans* collected in Australia produce only unilocular sporangia. The zooids released from these unilocular sporangia have not been observed to fuse and so form zygotes. As southern Australian plants have never been recorded with plurilocular sporangia, these plants cannot have the same life history as those from France.

It is noticeable that *Myrionema strangulans* is often highly fecund when collected, and the very numerous tiny plants associated with large, fertile plants on the blades of *Ulva lactuca* are discoid. It is clearly possible to observe two or three size generations of discoid plants, the largest plants bearing mature unilocular sporangia. From such field collections, it would appear that at least early in the growing season regeneration of the macrothallus is direct and from zooids from unilocular sporangia.

No crossing of subsamples of motile zooids was attempted, but as this is readily available to zooids in the field, it is tempting to postulate that fusion of zooids from different plants may be involved in the successful production of new discoid plants, since Loiseaux (1967c) has demonstrated this phenomenon in culture with gametes of the French race. The other real possibility is that the formation of discoid plants may be a direct result of a response to the surface morphology (or perhaps chemistry) of *Ulva* and *Enteromorpha*.

Table 3, 1.b gives a summary of the results obtained in cultures of the southern Australian race of *Myrionema strangulans*.

The asexual cycle, where the zooids from unilocular sporangia germinate in the amoeboid form and proceed to a pseudodiscoid plant which bears unilocular sporangia, reflects, in part, what is observed in the field. The development of a truely discoid thallus form may be controlled by the environment of the host, in this race. The rate of production of unilocular sporangia may be a response to temperature, comparing the 16° and 20° short day treatments. But, comparing the two high temperature treatments, the response also shows some connexion to day length. This result requires further investigation.

The production of filamentous plants, following tubular germination, leads to the development of intercalary plurilocular sporangia. Plurilocular sporangia were only formed by plants grown under long days, in both ME-II and ME-III. Why the 16° treatment in ME-III did not produce plurilocular sporangia is not known. The products of the zooids of these sporangia appeared to be similar to the products of the unilocular sporangia, in ME-III. This phenomenon, not recorded in field collections, may be part of a now superceded sexual cycle.

The only hormone treatment to show any promise was IAA. Although unilocular sporangia were induced, and hairs, usually rapidly lost, were retained, no clear-cut results were obtained.

The southern Australian race does show heteroblasty as does the French race.

As with Sauvageau (1897, 1933) and Kylin (1934), the present author's results are inconclusive.

2. *Myrionema latipilosum* sp. nov.

Diagnosis:- Thallus usque ad *M. magnusii* sed pilis latibus, cum cellulis 15-20 µm diametro, atque sporangiis **plurilocularibus longis** filiformibus cum sedecim ad viginti loculis; ascocysts filiformes teretes ad bis longe sporangiis.

Figure 2, B; Plate 1, C-F.

Thallus a slightly domed regular disc up to 1mm in diameter, brown, epiphytic on *Zostera* sp.(Pl. 1C).

Basal layer of subdichotomous, closely appressed filaments radiating from a central group of (4) cells, adnate to the host epidermis towards the margins only, resulting in the slightly domed appearance of the disc. Cells 15-20 µm long, 6-10 µm wide, 4-6 µm high, pigmented, truncated rhomboid to irregular in shape; each cell capable of producing an erect structure.

Erect assimilatory filaments infrequent, short, 55-65 µm high, of 3-5 cyclindrical cells, 10-12 µm long, 4-7 µm broad; terminal cell rounded, of same diameter as lower cells. Hairs with a basal collar, pedicel as wide as disc cell, 10-12 µm long, 3-4 meristematic cells, and above cyclindrical cells, with a central region of densely staining cytoplasm only, L/B 3-10; 15-20 µm in diameter. *Ascocysts* thickwalled, 2-3 times taller than assimilatory filaments, terete and terminally rounded,10-15 µm wide, contents hyaline, arising directly from disc cell (Fig. 2B1,4).

Unilocular sporangia (abortive?) ovoid, borne directly on a disc cell, opening by rupture, wall persistent, 55-65 µm long, 20-30 µm broad (Fig. 2B1, Pl. 1F).

Plurilocular sporangia filiform, with 16-20 loculi, uniseriate to biseriate (by oblique divisions of the loculi), increasing rapidly in length just prior to spore release, opening by a terminal pore, 85-120 µm long, 10-15 µm wide, arising from the disc cell. New sporangia develop within the persistent wall of empty sporangia (Fig. 2B5, Pl. 1E).

Type locality:- Onkaparinga River, S. Aust.

Holotype:- ADU, A48142 (*Thomas*, 28.iv.1977).

Distribution:- Only known in southern Australia from the Onkaparinga estuary, S. Aust. (*Thomas*, i.vii.1977; ADU, A48143).

Host range:- *Zostera* sp.

In its only known locality, this is an estuarine species.

Myrionema latipilosum is one of the *M. balticum* (Reinke) Foslie group of the genus. Feldmann (1937) provides the clearest descriptions of the French taxa in this group, with clear illustrations and a discussion of distribution of taxa and points of confusion between them. It differs from all other members in the broadness of the cells of the hairs, and in having long, filiform plurilocular sporangia, rather than the shorter plurilocular sporangia of *M. magnusii*, *M. orbicularis* and *M. balticum*. All four taxa have few assimilatory filaments and numerous ascocysts In the other three taxa these are often ovoid-ellipsoid, in *M. latipilosum* they are narrow, terete and more or less rigid. The only similar plants recorded in southern Australia are the "Ascocyclus" microthallial stage of *Giraudya*.

In the field, *M. latipilosum* is difficult to recognize. The *Zostera* in the Onkaparinga estuary is common, and often luxuriant, in the tidal region. But the blades are colonized by a profusion of diatoms, with resultant fouling of the blades with detritus. Under the more favourable conditions of tank culture, in still water, the *Myrionema* came into its own, and competed favourably with the epiphytic diatoms. Thus, the specimens which we have of this species come from the tank plants of the *Zostera*.

Culture studies:-

The life history proposed by Loiseaux (194b, 1967c) for the two taxa *Myrionema orbicularis* and *M. magnusii*, which most closely resemble *M. latipilosum*, is wholly diploid. The unilocular sporangia of *M. magnusii* failed to release spores (Loiseaux 1967c). The zooids from the plurilocular sporangia, of both taxa, germinate to produce the next generation of plants. The life history involves three different zooid size groups. Production of discoid (A) or pseudo-discoid (A') plants followed amoeboid germination of zooids, and filamentous plants (C, or plethysmothallial plants) followed tubular germination. The three categories of plants produced plurilocular sporangia. While those from the discoid or pseudo-discoid plants were uniseriate and repeated all parts of the cycle, those from the filamentous C plants were multiseriate and their zooids only regenerated C plants. The whole cycle was diploid.

Results:-

Figure 18, B; Plate 12.

The parent plants for unialgal culture were obtained from those plants growing on blades of *Zostera* sp. in tanks, at 12°C, 14:$\overline{10}$ h; the *Zostera* had been transplanted from the Onkaparinga Estuary.

Culture ZT-I 1-10 16°C, 14:$\overline{10}$ h and 1-10 12°C, 14:$\overline{10}$ h were set up on 1st July, 1977, at 10 a.m. The parent plants showed a predominance of plurilocular sporangia. In the 16°C, 14:$\overline{10}$ h cultures, the zooids from the plurilocular sporangia had begun to settle. They displayed negative phototropism and were either amoeboid or spherical in form. Only one of the ten subsamples at 12°C released spores which formed new plants.

The following day, the amoeboid spores had reached the two-celled stage, but few of the spherical spores had formed a tube. On the fourth day discoid plantlets could be distinguished from pseudodiscoid ones, which were common, but very few filamentous plants were found. After one week, single hairs were present on all three forms of plantlets, and by the eleventh day erect filaments, including ascocysts, other than the now numerous hairs were visible. By the fourteenth day floating plants of all forms were found (Pl. 12B,C,D).

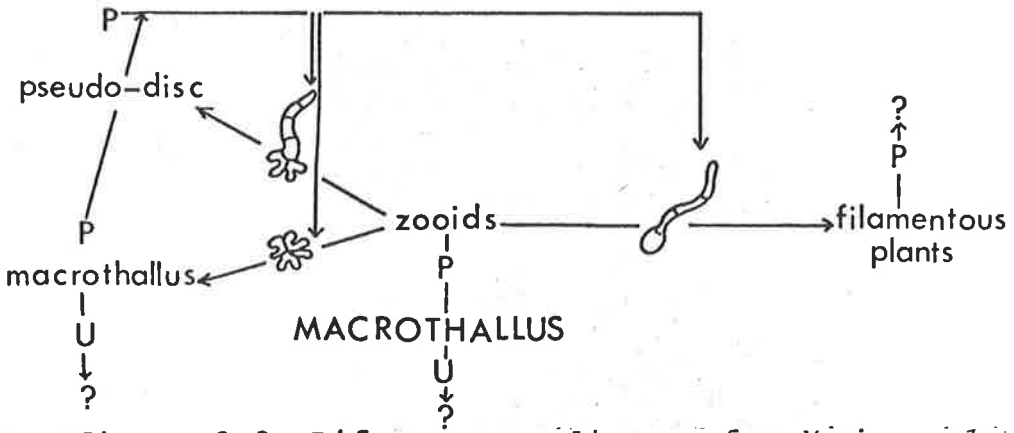
After twenty-one days all three plant forms were fully fertile, with normal filiform uniseriate to biseriate plurilocular sporangia. On one discoid plant young unilocular sporangia were visible. The plantlets, especially of the pseudodiscoid form, showed a tendency to form stolon-like filaments and new discoid attachments. New germlings of both amoeboid and tubular forms were visible (Pl. 12A).

Separation of discoid and pseudodiscoid plants (the filamentous plants were very rare and were not selected) resulted in cultures which contained both forms in the next generation. Further selection showed the same result, but with the predominance of discoid forms, especially when attached, in all four subsamples.

The cultures were maintained for eleven weeks, by which time older stocks showed the presence of numerous ascocysts and, particularly on the discoid plants, healthy looking unilocular sporangia. The unilocular sporangia, however, appeared to expand rapidly towards maturity, reach gross proportions and so abort (Pl. 12I).

This species shows a direct life history (discoid and pseudodiscoid plants) involving zooids from plurilocular sporangia, with a subsidiary filamentous form, and has a generation time of three

weeks at 16°C, 14:$\overline{10}$ h.



Textfigure 3.2 Life history diagram for *Myrionema latipilosum*

In ZT-I 4 & 9 16°C, 14:$\overline{10}$ h an interesting contaminant occurred. The initial prothallus was filamentous, had globular cells towards the centre of the plant, and was altogether larger than either the A-A' or C plants of *Myrionema latipilosum*. New terete erect axes arose from this prothallus, and, while some of these grew rapidly into a flattened thallus, somewhat like *Punctaria*, others became rapidly fertile with patches of sporangia round the erect axis. ZT-I 9 16°C, 14:$\overline{10}$ h isolates went through two generations without producing any *M. latipilosum* like plants.

Summary:-

The life history as described here, of *Myrionema latipilosum*, most closely corresponds to that of *M. magnusii* (Loiseaux 1967c).

Only the A and A' phases, (used as described for *Myrionema orbicularis* and *M. magnusii* by Loiseaux 1967c) have been demonstrated to be fertile, and part of the cycle of *M. latipilosum*. As with *M. Magnusii* (Loiseaux 1967c), while *M. latipilosum* developed unilocular sporangia

on both field and cultured plants, these unilocular sporangia did not appear to release spores. The C phase of the cycle is reduced in *M. latipilosum*. This may indicate that a process of reduction has occurred in the lifehistories. The haploid phase initiated by the production of meiospores in unilocular sporangia, may have become obsolete, and been paralleled by the C phase in *M. orbicularis* and *M. magnusii*. In *M. latipilosum* the C phase has been reduced further, to a vegetative tuft which produced uniseriate plurilocular sporangia, the products of which are unknown, while the A/A' phases complete the asexual reproduction of the next generation. This is possibly a reflection of the specialization of habitat of *M. latipilosum*.

3. *Myrionema ramulans* sp. nov.

Diagnosis:- Thallus maculiformis, 0.5 - 5mm in diametro; fila erecta teretes, saepe ramosa; pili cum cellulis 10-12 µm late. Sporangiis unilocullariis clavatibus pediculatibus; sporangiis plurilocullariis in sporangiophore ramose, cum 4-8 loculis.

Figure 2, C; Plate 2, A-C

Thallus a more or less regular disc, 0.5 - 5mm across, with short, sometimes bifurcate erect filaments, epiphytic, brown.

Basal layer of subdichotomous, appressed, radiating filaments; cells 7-10 µm long, 5-7 µm wide, and up to 5 µm high, pigmented, each cell giving rise to one, or sometimes two, erect processes. *Erect assimilatory filaments* of 5-8 (-10) cells, to 50 µm high; cells cyclindrical, L/Bc.2,5-7 µm in diameter, terminal cell rounded (Fig. 2C2, Pl. 2C). Branching of assimilatory filaments occurs among the upper cells. Hairs with a pedicel and 4-6 celled meristem; upper cells cyclindrical, L/B 2-8, 10-12 µm in diameter.

Unilocular sporangia narrow clavate, L/B 3-4, 7-10 µm in diameter, on a one-celled pedicel (Fig. 2C5).

Plurilocular sporangia filiform, uniseriate, rarely with oblique cross walls in the loculi, 6-8 loculae per arm, 25-35 µm long, on a one or two celled pedicel or as sub- to terminal laterals on erect bi- or trifurcate filaments (Pl. 2B).

Type locality:- Queenscliff, Victoria (*Skinner*, 4.i.1978)

Holotype:- ADU, A49058.

Host range:- *Sargassum* spp.; *Caulocystis* sp.; *Cystophora* spp.

Distribution:- Only known from the following localities:

South Australia:- Lady Bay, Normanville, on *Sargassum* sp. (*Skinner*, 14.ix.1977; ADU, A48246).

Victoria:- The type and Point Lonsdale, on *Sargassum* sp. (*Skinner*, 4.i.1978; ADU, A49065); on *Caulocystis* (*Skinner*, 4.i.1978; ADU, A49066).

Tasmania:- Eastern Beach, Low Head, on *Cystophora retroflexa*. (*Skinner*, 23.ii.1978; ADU, A49163).

This taxon is similar to *Myrionema furcatum* Jaasund, and also *M. globosum* (Rke) Foslie. Like *M. furcatum*, this taxon shows long basal cells which support one or frequently two filaments, and sporangiophores bearing the plurilocular sporangia. Jaasund (1951) describes the plurilocular sporangia of *M. furcatum* as possessing numerous loculi. *M. ramulans* has plurilocular sporangia with between four and eight loculi. The unilocular sporangia of *M. ramulans* are distinctly clavate, while those of *M. furcatum* are elongate ovoid.

4. *Myrionema myriodesmae* sp. nov.

Diagnosis:- Thallus maculiformis incompositus, 0.5 - 3mm in diametro; fila erecta flexibiles teretes, cum 8-20 cellulis; pili cum pediculis 2-3 cellularum, atque cellulis 10-15 µm in diametro; sporangii unilocularii elongato-ovoides laterale ad basem fili; sporangiis plurilocularis ignotis.

Figure 2, D; Plate 2, D-E.

Thallus an irregular, spreading patch, 0.5-3mm across, with long, flaccid erect filaments, epiphytic on *Myriodesma calophyllum* J.Ag., dark brown (Pl. 2D).

Basal layer of irregular branched filaments following the contours between the cells in the outermost layer of the host; cells 10-25 µm long, 10-15 µm broad, pigmented.

Erect assimilatory filaments flaccid, of 10-15 (-20) cells; cells cyclindrical with a few discoid phaeoplasts, L/B 2-4, 10-15 µm in diameter, arising sometimes two together from cells of the basal layer, not in sequence over the disc; longer filaments interspersed with shorter ones (Fig. 2DI). *Hairs* with a 2-3 celled pedicel, a many celled meristem to the same height as the assimilatory filaments, upper cells cyclindrical, L/B 5-10, 10-15 µm in diameter, with pigmented cytoplasm without phaeoplasts concentrated in the centre of the cell (Pl. 2E).

Unilocular sporangia developing often in pairs laterally from basal cell of erect filaments on a short pedicel therefrom, elongate-ovoid, opening by rupture, 40-60 µm long, 20 µm at maximum width (Fig. 2D3). *Plurilocular sporangia* unknown.

Type locality:- Stanley Beach, Kangaroo Island, South Australia. (*Womersley*, 7.ii.1956).

Holotype:- ADU, A20111.

Distribution:- Kangaroo I.

Host range:- *Myriodesma calophyllum* J.Ag.

Representative specimens examined:- Type material, and Seal Beach, Kangaroo I. (*Womersley*, 21.i.1956, ADU; A28591).

The specific epithet was chosen from the generic name of the common host. This species differs markedly from other *Myrionema* species, except *M. siliquosum* Sauvageau and some Japanese species, by having long assimilatory filaments. The position of the unilocular sporangium is similar to that found in *M. strangulans*. The form of the hairs, with their several-celled pedicels, of this taxon distinguishes it from all other members of the genus.

3.3.1 Note:- The following taxon is included because the one specimen collected in southern Australia agrees with the description of *Myrionema compactum* Lindauer in Lindauer (1949) and Lindauer *et al.* (1961). The taxon's inclusion in the genus *Compsonema* is disputable on two grounds (i) the phaeoplasts, although large, are lens-shaped, and (ii) the basal layer is compact rather than diffuse, as is more usual in that genus. Two points which suggest that it should be placed in *Compsonema* (at least until the *Hecatonema/Compsonema/Chilionema* complex is reviewed in the light of research completed since Kuckuck & Kornmann 1953), are (i) the erect filaments are more like those of *Myrionema* than *Ectocarpus* (which those of *Hecatonema* and *Chilionema* are comparable with), and (ii) the basal layer is predominantly single layered, not double layered as in the other two genera.

3.3.1 *COMPSONEMA* Kuckuck 1899:92; 1953:340. Abbott & Hollenberg 1976:160. Loiseaux 1967b:345.

Thallus a disc or spreading monostromatic layer, 0.5-10mm across, with erect filaments of indeterminate growth, epiphytic or lithophytic.

Basal layer monostromatic or in places becoming distromatic by expansion of the cells at the base of erect filaments; filaments subdichotomous, compacted or spreading, cells irregularly isodiametric, becoming longer than broad. *Erect assimilatory filaments* of indeterminate growth, uniseriate, occasionally producing lateral branches (in some species). Hairs forming either directly from the basal plate cells or as laterals on erect filaments, meristem usually of numerous cells. Ascocysts occasionally present.

Unilocular sporangia either arising directly from the basal plate cells (either sessile or on a short pedicel) or laterally or intercalary on erect filaments.

Plurilocular sporangia on a pedicel of one to five or more cells or terminal on lateral branches of erect filaments, multiseriate, opening by a terminal pore.

Type species:- *C. minutum* (C. Ag.) Kuckuck 1953:341, fig. 13 (= *C. gracile* Kuckuck 1899:92, fig. 6, 6-9).

One species in the area.

3.3.2 *Compsonema compactum* (Lindauer) comb. nov., species incertae sedis.

Myrionema compactum Lindauer 1949:343, fig. 3a-4.

Lindauer, Chapman & Aiken 1961:206, fig. 35.

Figure 2, E ; Plate 2, F-H.

Thallus a compact collar or patch, 3-5mm wide, epiphytic on *Hormosira banksii*, grey brown.

Basal layer of closely appressed subdichotomous filaments; cells especially in compacted areas of basal layer, isodiametric, 12-15 µm across. Stoloniferous marginal processes (Fig. 2E2, Pl. 2H) similar, irregularly branched, with poorly pigmented cells. *Erect assimilatory filaments* short, 55-70 µm long of 4-8 (-12) cells, L/B c.1, 10-15 µm in diameter. Hairs with basal cell and short meristem; non-pigmented cells cyclindrical, L/B 3-5, 10-20 µm in diameter. Ascocysts numerous, ellipsoid, c. 30 µm long (Fig. 2E3).

Unilocular sporangia sessile or more rarely shortly pedicellate, pyriform, c. 50 µm long, c. 20 µm in diameter, not present in Australian material.

Plurilocular sporangia multiseriate, ectocarpoid, on a 1-5 celled pedicel, opening by a terminal pore, 35-60 µm long (Fig.2E3, Pl. 2G).

Type:- Lindauer 11306, formalinized material. Herb. Auckland University.

Type locality:- Long Beach, Russel, Bay of Islands, New Zealand.

Distribution:- Type locality and Encounter Bay, S. Aust. (*Skinner*, 7.xii.1976; ADU, A47831).

Host range:- *Hormosira banksii*.

This species seems nearest to *C. serpens* S. & G. in form, but is more compact than other species.

The genus *Compsonema* Kuckuck is separated from *Hecatonema* Sauvageau and *Chilionema* Sauvageau by Kornmann in Kuckuck (1953) on two points. The first of these is the nature of the phaeoplasts, which in *Compsonema* are single, platelike and sometimes reticulate, while those of the latter two genera are numerous, small and lens-shaped (Kuckuck & Kornmann 1953, page 318). The second distinction is that in *Compsonema* the basal layer and the marginal processes from it are one cell thick, while the basal plates of *Hecatonema* and *Chilionema* are usually distromatic. It is often difficult to make this separation between a monostromatic or distromatic basal plate, especially where the cells immediately above the basal cell expand to meet one another along their lateral faces and thus conform with the basal cell. The presence of processes at the margins of the basal layer make a distinction between these three genera, but whether it is sufficient to be used as a generic distinction is a matter for debate. The taxon given above as *Compsonema compactum* has marginal processes; it is

thus placed in that genus rather than *Hecatonema*, with which it could be easily confused.

3.4 Summary

The genus *Myrionema* may be divided into four sections; Section I. *Myrionema strangulans*, *M. feldmannii* Lois. and their allies, with numerous clavate erect filaments, and active unilocular sporangia; Section II. *Myrionema balticum* and its allies, with few filiform erect filaments, abortive unilocular sporangia, and numerous, conspicuous ascocysts. These two sections conform with those given by Loiseaux (1967c). Section III. *Myrionema globosum*, *M. furcatum* and their allies, with numerous short erect filaments and branched sporangiophores bearing plurilocular sporangia. Section IV. *Myrionema siliquosum* and its allies, with long filiform erect filaments.

Each of these sections is represented by one species in southern Australia. *Myrionema strangulans* is in Section I; *M. latipilosum* in Section II; *M. ramulans* in Section III; and *M. myriodesmae* in Section IV. While the life history found for the southern Australian race of *M. strangulans* does not conform closely with that of species in Section I as described by Loiseaux (1967c), the life history of *M. latipilosum* is very similar to that of other species in Section II. Nothing is known of the life histories of species in the other two sections.

Compsonema compactum, which in respect to its form and shape of erect filaments and plurilocular sporangia shows similarities to some forms of *Hecatonema maculans* (Coll.) Sauv., shows plate-like phaeoplasts, stoloniferous marginal processes and a primarily monostromatic basal layer. The taxonomic status of this organism is still in doubt.

CHAPTER IV

ELACHISTACEAE KJELLMAN 1890

4.1 The family Elachistaceae includes three genera and about 30 species, and is usually placed in the order Chordariales. The absence of any hair-like structures, and the presence of cortical assimilatory filaments ("paraphyses") in combination with long, indeterminate assimilatory filaments clearly separates this family from all other brown algae. *Myriogloia* Kuckuck in the Chordariaceae, while lacking hairs, also has only one kind of assimilatory filament. The pattern of construction (Fig. 1.D) in the Elachisteaceae is similar to that of *Corynophlaea* and *Leathesia*, being truly pulvinate with a medullary system which radiates from a basal layer and supports a cortex of both assimilatory filaments and reproductive structures and from which project the long assimilatory filaments. The cells of assimilatory filaments of all three genera contain a large central nucleus and numerous parietal discoid phaeoplasts often with prominent pyrenoids projecting from them. They are all epiphytes.

The genera included in the family are *Halothrix* Reinke; *Elachista* Duby (including *Symphoricoccus* Reinke); and *Portphillipia* Silva. The inclusion of a fourth genus, *Herpodiscus* South (1974), requires further investigation, particularly into its peculiar life cycle. These algae occur in cool temperate and polar waters in both northern and southern hemispheres.

Portphillipia australis (J. Agardh) Silva has been recorded from Victoria and Tasmania (Womersley 1967). The present study will show that there are also two species of *Elachista* and at least one

species of *Halothrix* to be found in southern Australian waters.

4.1.1 Key to the genera of the Elachistaceae in southern Australian waters

1. Medulla of pyriform to terete cells arising from a compact basal plate, external to host tissue; cortical assimilatory filaments linear. 2

1. Medulla of very long cylindrical cells arising from a rhizoidal base shallowly penetrating the outer tissues of the host; cortical assimilatory filaments recurved. *Portphillipia* Silva

2. Plurilocular sporangia uniseriate, filiform, borne in corymbose groups in cortex; cells of long assimilatory filaments L/B 2 or greater. *Elachista* Duby

2. Plurilocular sporangia developing in intercalary sori on assimilatory filaments; cells of long assimilatory filaments L/B 1-1½. *Halothrix* Reinke

4.2 *ELACHISTA* Duby 1832:972 nom. cons. J. Agardh 1848:7; 1882:9. Chapman 1961:16. Hamel 1935:117. Harvey 1846:59. Kjellman 1897:220. Kuckuck 1929:21. Lindauer, Chapman & Aiken 1961:214. Rosenvinge 1935:19. Sauvageau 1936:139. Skottsberg 1907:53; 1953:537. Svedelius 1911:162. Takamatsu 1938a:145. Yamada 1927:11.

Opospermum Rafinesque 1814:48. Kuntze 1891:908.

Areschougia Meneghini 1843:293.

Phycophila Kützing 1843:330, pro magna parte.

Symphoricoccus Reinke 1889:17. Kuckuck 1929:32. Kjellman 1897:219. Wanders *et al.* 1972.

Thallus epiphytic, pulvinate, hemispherical or spreading, up to 2 cm high, brown to dark brown. Thalli usually agregated in considerable numbers on host.

Basal cells isodiametric, small, often with short, rhizoid-like pegs as extensions of the lower cell wall, forming a plate on the host surface. *Medullary filaments* of non-pigmented, pyriform, cylindrical or subglobose cells arising from the basal cells, branching subdichotomously. *Cortical assimilatory filaments* (paraphyses) develop terminally on medullary filaments either in association with or separated from long assimilatory filaments, but always associated with the medullary filaments which bear the reproductive organs. Filaments clavate, arcuate or linear; cells 5-20, cylindrical to inflated cylindrical, with fewer phaeoplasts than cells of long assimilators; terminal cell truncated and rounded; growth determinate. The meristematic zone of the thallus occurs at the junction of the cortex and the medulla, and growth is radial and most active towards the margins of the thallus adjacent to the host; the long assimilatory filaments have a separate meristem at the base of the pigmented cells of the individual filaments. *Long assimilatory filaments* arising either individually from cells of the basal plate, with individual medullary filaments, or on leading axes of branching medullary filaments; uniseriate, with a meristem of short cylindrical cells above the terminal medullary cell in either form, and short to long ($L/B > 2$), cylindrical, pigmented cells with thick walls in the remainder of the filaments; growth indeterminate.

Unilocular sporangia, lying in the cortex on a short pedicel on terminal medullary cells or base of assimilatory filaments, ovoid, pyriform or

truncated cylindrical, with a terminal pore mechanism, and, at maturity, a coating of mucilage separating the zooids from the wall.

Plurilocular sporangia uniseriate, filiform, with 8-48 loculi, either on specialized, corymbose lateral branches from the medulla (or medullary cells of long assimilatory filaments) or as lateral intercalary projections from long assimilatory filaments, or both.

Type species:[1] *Elachista scutulata* (Sm.) Duby

A genus of at least a dozen species found on a wide variety of hosts; known from both sides of the north Atlantic and the Mediterranean, Japan, New Zealand, the Antarctic and sub Antarctic, South America and the Pacific coast of North America; two species in Australia. Sexuality has never been clearly demonstrated in the life cycle, which, at least in some species, appears to be direct.

Elachista (Symphoricoccus) stellaris Areschoug, which shows rhizoidal development from the medulla, and so is partially endophytic, can develop intercalary sori (on assimilatory filaments), which may include both unilocular and plurilocular sporangia, (Kuckuck 1929; Wanders *et al.* 1972). However, its life history is sufficiently similar to *E. fucicola* to warrant inclusion in this genus (Sauvageau 1933; Hoek *et al.* 1972). The genus is divisable into three sections:- Section I, where the medulla has only one form of filament, the branched form, and most species show both unilocular and plurilocular sporangia, including *E. scutulata, E. fucicola,* and related species; Section II, where the medulla has two forms of filaments, the branching ones and the specialized ones for the support of the long assimilatory filaments, and usually only plurilocular sporangia, including *E. intermedia, E. orbicularis* and related species including several

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1. The type is sometimes given as *E. fucicola* since *Opospermum nigrum* of Rafinesque 1814 is said to refer to this species, however, the International Code (1978) supports *E. scutulata.*

Japanese taxa, some of which are presently included in *Gonodia*; and Section III, for *E. stellaris*, with its partially endophytic habit and intercalary sporangia on assimilatory filaments.

The generic limits of *Elachista* and *Gonodia* are not clearly defined in publications by Japanese researchers. As has been noted below (p.99), Takamatsu (1938a) published several taxa in *Elachista* with phaeophytan hairs. Nieuwland (1917) intended *Gonodia* to replace *Myriactis*, based on *M. pulvinata* which was separated from *Elachista* by Kützing because of its partly endophytic habit and the presence of hairs. Several taxa, including *Gonodia orbicularis* Ohta, recently published by Noda (Noda 1964, 1969, 1974; Noda & Kitani 1971) & Ohta (1973) have been described as epiphytes and as lacking phaeophytan hairs. The Japanese taxa referred to *Elachista*, *Gonodia* and *Myriactula* are in need of taxonomic and nomenclatural revision, to remove this confusion.

4.2.1 Key to species of *Elachista* in southern Australian waters

1. Medullary cells narrow pyriform or cylindrical; long assimilatory filaments arise on individual unbranched medullary filaments from basal cuboid cells . . . . . *E. orbicularis* (Ohta) comb. nov.

1. Medullary cells ovoid-pyriform to subglobose; long assimilatory filaments arise on terminal cell of branched medullary filaments. . . . . *E. secundata* sp. nov.

4.2.2 *Elachista orbicularis* (Ohta) comb. nov.

Gonodia orbicularis Ohta 1973:21, fig. 11. Noda, 1975: 101, fig. 12.

Figure 3; Plate 3, A, B, Pl. 19, C.

Thallus pulvinate, hemispherical, but sometimes spreading as a line of small plants when juvenile, 0.5 - 4.0mm high, black-brown, epiphytic on *Ecklonia radiata*, where numerous thalli may cover both

margins and lamina of laterals (Fig. 3.1, Pl. 19C).

Basal layer of short cells, 2-4 µm broad and 1-2 µm high, adhering to the surface of the host without penetration but with short (to 1 µm) peglike projections from the basal cells. The basal layer is compact in the central region of the thallus, becoming diffuse towards the margins, where the cells in the medullary filaments are fewer.

Medullary filaments of two forms; (1) essentially unbranched filaments of large, thick walled cells (sometimes with rhizoids from bottom cell, and very occasional lateral cells) leading to long assimilatory filaments, individual cells terete, 5-15 µm in diameter, L/B 3-5, non-pigmented, 5-10 cells/filament; and (2) subdichotomously branched filaments, with thinner walled cells, bearing the cortical assimilatory filaments and sporangia, individual cells pyriform to cylindrical, L/B 3-10, 2-6 µm in diameter (Fig. 3.2, 3).

Cortical assimilatory filaments linear to slightly curved or clavate with 4-6 narrow cylindrical lower cells, L/B 6-10, 2-3 µm in diameter and with 3-4 inflated cylindrical upper cells, the terminal cell rounded; cells L/B 2-6, 3-6 µm in diameter, with few discoid phaeoplasts, borne on cells of branched medullary filaments (Fig. 3.2).

Long assimilatory filaments arising on unbranched medullary filaments; cells cylindrical, L/B 1½-2½, 15-25 µm in diameter, lower 8-12 cells forming a hypermedullary meristem of short cells, L/B about 1. The assimilatory cells contain a central nucleus with long, forking cytoplasmic strands crossing the vacuolar space to the parietal cytoplasmic region containing numerous discoid phaeoplasts with distinct pyrenoids projecting from many of them (Fig. 3.3, 6a & b, Pl.3,B).

Unilocular sporangia unknown.

Plurilocular sporangia filiform, uniseriate with 16-24 (-48) loculi, with a terminal pore, developing successively on upper corymbose medullary filaments in cortex, zooids maturing from top loculi down; sporangial wall persistent, splitting lengthwise on one face, and a new sporangium may develop from the same base; occasional interlocular walls oblique (Fig. 3.2).

Type locality:- Tappi, Aomori Pref., Japan (*Ohta*, 1.i.1970)

Type specimen:- S.N. (Ohta 133).

Distribution:- Japan; in Australia, Encounter Bay to Port Stanvac, St Vincent's Gulf, S. Aust. (This species is present on its host throughout the year.)

Host range:- (in Australia) *Ecklonia radiata* (C.Ag.) J. Ag.

Representative specimens examined:- Type and Sado Is., Japan, on *Undaria* sp. (*Kitami*, 29.iii.1973, ADU, A49378).

Australian collections, all specimens on *Ecklonia radiata:* Port Noarlunga, S. Aust., 5m deep (*Thomas*, 16.xii.1975; ADU, A46752). Encounter Bay, S. Aust., drift (*Skinner*, 14.ix.1976; ADU, A47270*). Seaford, S. Aust. (*Skinner*, 14.ix.1976; ADU, A47273*). Port Noarlunga, S. Aust. (*Skinner*, 28.v.1976; ADU, A47215; 7.xii.1976; ADU, A47829*). Port Noarlunga, S. Aust. (*Skinner*, 10.i.1977; ADU, A47847*). Aldinga reef, S. Aust. (*Skinner*, 4.iv.1977; ADU, A47981; 5.vii.1977; ADU, A48124; 16.viii.1977; ADU, A48225; 14.x.1977; ADU, A48577). Aldinga reef, S. Aust. (*Skinner*, 22.iii.1978; ADU, A49196; 10.iv.1978; ADU, A49252*; 15.ix.1978; ADU, A49561; 31.x.1978; ADU, A49776*). Whitton Bluff, Port Noarlunga 0-3m deep (*Engler*, 25.xi.1978; ADU, A50226). Encounter Bay, S. Aust. (*D.J. Skinner*, 25.i.1979; ADU, A50236).

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* Those collections marked with an asterisk have been used for cultures.

Clark and *Engler* (6m deep), 19.iii.1979; ADU, A50315).

There is a group of four or five taxa which show two kinds of medullary filaments, and should be included in Section II of the genus *Elachista*. They include *E. intermedia* Crouan (see Kuckuck 1929), from the Mediterranean; the present species and *E. vellosa* Takamatsu; *E. nigra* Takamatsu; and *Gonodia fusiformis* Noda, the last three all endemic to Japan. While the other species show the formation of some laterals from those medullary filaments which support the long assimilatory filaments, *E. orbicularis* has very occasional laterals, from the lowermost cells only. *Elachista intermedia* differs from the other taxa by having shorter plurilocular sporangia with many fewer loculi.

The differences between Australian and Japanese specimens of *Elachista orbicularis* are slight, and consist of variations in the limits of size of the cortical filaments and of the plurilocular sporangia,and the dimensions of the cells of long assimilatory filaments. In Japanese specimens the cortical assimilatory filaments are 300-400 µm long and 15-25 µm wide, the plurilocular sporangia are 150-200 µm long and about 10 µm wide, and the cells of long assimilatory filaments are 24-36 µm long and 20-25 µm wide.

Culture studies:-

Figure 18,C;Plate13.

As discussed above (Chapter I.5.4, p.22) cultures of *Elachista stellaris*, *E. fucicola* and *E. scutulata* have shown either direct, or indirect by way of a self regenerating protonemoid stage, asexual life histories for diploid plants. There is some dispute about the 2n chromosome number for *E. fucicola* (Blackler & Katpitia 1963; Koeman & Cortell-Breman 1976), but the general concensus is that the macrothallus is

diploid and self regenerating by zooids from either unilocular or plurilocular sporangia. Where haploid plants, or plants with half the chromosome number of the parent plant, have been observed, somatic diploidization has been used to account for the subsequent regeneration of macrothalli on such protonemas (Wanders *et al.* 1972; Koeman & Cortell Breman 1976).

Results:-

Six cultures of *Elachista orbicularis* from southern Australian waters were established. One culture from material collected at Encounter Bay in September 1976, EY-I (A47270) also contained spores of an ectocarpoid which grew together with the *Elachista*. Cultures of material from Seaford SE-I (A47273), also in September 1976, and from Port Noarlunga EN-II; EN-III (A47820; A47874) in December 1976 and January 1977, were all unialgal and were grown in Provasoli's Enriched Seawater at 12°, 16°, and 20°C under 14:$\overline{10}$ h. Two further cultures, from material from Aldinga reef (A49252; A49776), were set up in April and November of 1978 respectively. Culture EA-IV (A49252) was grown in Provasoli's ES with added Kinetin at 16°C, 14:$\overline{10}$ h; while EA-V (A49776) was grown in either Provasoli's ES without hormones or with added Kinetin, Indole Acetic Acid and Gibberellic acid No. 3 (see Chapter II), at 16° and 20° under either 8:$\overline{16}$ h or 14:$\overline{10}$ h.[2]

All cultures were obtained by the release of zooids from plurilocular sporangia from macrothalli. The zooids are pear-shaped, 5.4 - 5.8 µm long and 4.8 - 5.2 µm at the widest point, and have two lateral flagella, of which the lower one is about one third the length of the upper one. An eyespot is present, and retained in the 1-celled stage after settling. No fusion of these negatively phototrophic zooids was observed at any time. Germination was tubular; the new plantlet was filamentous and began to form lateral branches

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2. The reason for the different, not reversed day lengths here was that the facilities were shared, and sufficiently distinct long day responses were obtainable under 14:$\overline{10}$ h with other taxa.

after seven to ten days. By the 24th day a basal system had developed from which healthy long assimilatory filaments quickly developed, and by that time new filiform plurilocular sporangia, similar to those of the parent macrothallus, had also appeared near the bases of new erect filaments (Pl. 13.A). Isolation of these sporangia resulted in a similar pattern of regeneration, again without any fusion of zooids. Short cortical assimilators tended to dominate the new plants after the first three weeks of growth, while the production of long assimilators was boosted by each refreshment of the medium (every 14 days). In EN-III, which culture was run for longer than four months, only the oldest of the plants showed any medulla-like cells in the disorganized filamentous basal system; no other cultures showed any medulla formation.

A secondary regenerative process displayed by the cultured plants involved the long assimilatory filaments (Pl. 13.C,D). A secondary meristem would be formed at some distance from the primary meristem. Lateral branching from this meristem resulted in the formation of a basal system from which arose further plurilocular sporangia and cortical filaments. Following the decay of the assimilatory cells immediately below the secondary meristem, the now independent plant would grow further to produce new long assimilatory filaments. Similar behaviour has been described in both field and cultured plants of *E. stellaris* (Wanders *et al.* 1972).

Cultures SE-I, EN-II and EN-III demonstrated that while this plant will grow well at 12°C and 16°C - the general range of water temperatures in Gulf St Vincent during the cooler part of the year - the most rapid growth of young plantlets was obtained at 20°C 14:$\overline{10}$ h, conditions which prevail during late spring and early

summer. The direct influence of temperature, however, is short lived. The 16^{o} plants grew best under the culture conditions, while 20^{o} plants rapidly depleted the medium, with a resultant slowing of growth. Insufficient data precluded any further comparison of field and culture plants.

Cultures EA-IV & V demonstrated both the effects of day length and the addition of hormones. In all cases, the restricted availability of culture space reduced the number of subsamples, preventing quantification of results. Although any one subsample contained a large number of plants, few comparisons within treatments were possible, so that the results are qualitative and sometimes contradictory; at best the conclusions can only be tentative.

Day length influenced growth rate, differentiation and fecundity. Plants grown under short days were, in general, slower growing, and took longer to bear cortical assimilatory filaments and bore fewer plurilocular sporangia than those grown under long days. The final products, after a month, were similar.

The addition of Kinetin (20 μM) to culture EA-IV enhanced, rather than stimulated, the differentiation of erect processes, bringing about more rapid development of the prostrate system and the appearance of the long assimilatory filaments - which occurred before the seventh day.

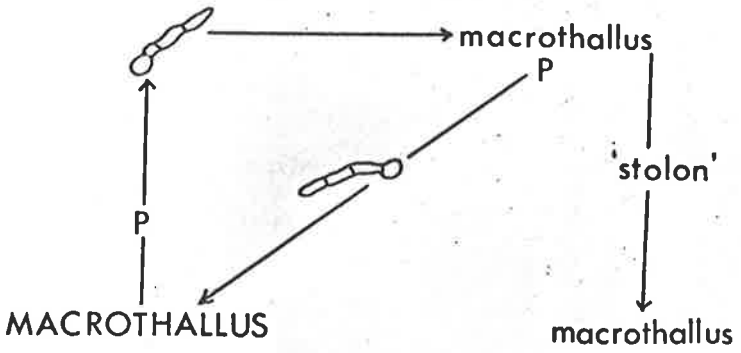
When the three hormones were used together, there were no specific changes, but a general enhancement of growth, differentiation and fecundity. There were marginally more stolon-like processes formed by those cultures treated with hormones.

To further check the behaviour of the zooids, two additional cultures of *Elachista orbicularis* were established from material from Aldinga reef (ADU, A50154) and Port Stanvac (ADU, A50155), S. Aust. Cultures were labelled EPS.VII and EA.VIII. They were initiated on 1.V.1980, from plurilocular sporangia in hanging drop suspension. The zooids from both samples settled individually and had maturing macrothalli by the 3.VI.1980. Subsamples from EA.VIII and EPS.VII with plurilocular sporangia were then placed together in hanging drop suspension. By 5.VI.1980 free swimming zooids were present in all five subsamples, and no clumping or pairing behaviour was visible. On 9.VI.1980 the subsamples were again examined, and no paired zooids were found, all settled zooids had done so individually and had reached the two celled germtube stage. The life history of *E. orbicularis* in southern Australia has so far proved to be asexual.

Summary:-

Therefore the apparent life cycle for *Elachista orbicularis* involves

the direct asexual regeneration of the macrothallus by germination of zooids from the plurilocular sporangia. The generational time for this species is three to four weeks. A secondary vegetative regeneration mechanism is provided by the stolon-like behaviour of the long assimilators.



Textfigure 4.1 **Life history diagram for** *Elachista orbicularis*

4.2.3 *Elachista secundata* sp. nov.

Diagnosis:- Thallus pulvinate, 0.5-5mm alte; fila medullae conferta, cum cellulis aut pyriformibus inferne aut subglobosis superne; fila assimilata corticata aut stricta aut leviter arcuata, filiforma cum 15-20 cellulis; fila assimilata longissima cum cellulis teretibus, L/B 1½-2½, 15-20 µm diametro; sporangia unilocularia pyriforma; sporangia plurilocularia uniseriata, filiforma in sporangiophoribus corymbosis aut ex medullo superne aut secundate ex filis longissimis.

Figure 4; Plate 3, C, D, Pl. 20, A.

Thallus pulvinate, hemispherical, 0.5-5mm high, very dark brown, epiphytic on the margins and lamina of the leaflike lower laterals of *Sargassum* species (Fig. 4.1).

Basal layer of irregular isodiametric cells, 8-15 µm in diameter, each bearing one medullary cell. *Medullary filaments* closely packed, subdichotomous, cells pyriform below grading to subglobose above, non-

pigmented, L/B 2½-4, 20-45 µm in diameter. *Cortical assimilatory filaments* straight or slightly curved, filiform, with 15-25 pigmented, cylindrical cells, L/B 1, 10-12 µm in diameter, borne terminally on branches of medullary filaments along with reproductive structures. *Long assimilatory filaments* arising from terminal medullary cells and extending in length two or three times beyond the rest of the thallus. Meristematic zone indefinite; assimilatory cells cylindrical, L/B 1½-2½, 15-20 µm in diameter, with numerous discoid phaeoplasts.

Unilocular sporangia: On MELU 21207 there are pyriform unilocular sporangia, L/B 2-3, 23-28 µm in diameter, among the plurilocular sporangia (Fig. 4.4). These unilocular sporangia have a pore and plug mechanism. Stalked spherical organs, among the plurilocular sporangia initials, have been observed in MELU 20520. Undisputable zooid masses were not observed in such organs (Fig. 4.5, Pl. 3.D).

Plurilocular sporangia (borne collectively on corymbose branches on medullary filaments either separately or immediately below and lateral to the meristematic region of long assimilatory filaments where the corymbose sporangiophores are arranged secundly) filiform, uniseriate, with occasional oblique locular walls; 24-36 loculi, opening by a terminal pore, outer wall persistent (Fig. 4.2,3,7).

Holotype:- MELU 20520 (*Clayton*, 21.ix.1970).

Type locality:- Ocean Beach, Sorrento, Victoria.

Distribution:- Type locality, Queenscliff and Point Nepean, Victoria.

Host range:- *Sargassum* spp.

Representative specimens examined:- Type and Queenscliff, Vic. (*Clayton*, 6.ix.1969; ADU, A50331); Sorrento, Vic. (*Clayton*, 4.ix.1971;

MELU 21207); Point Nepean, Vic. (*Clayton*, 4.v.1969, ADU, A50332).

The specific epithet, "secundata", is chosen from the position of sporangiophores/secund, which was to long assimilatory filaments - a feature which distinguishes this species from all others in the genus(Fig. 4.7). The form of the medulla suggests an association of this species with *E. scutulata* and *E. fucicola*, in Section I of the genus, as proposed above.

Clayton (pers. comm.) has had some success in culturing *Elachista secundata*. She set up four cultures from MELU 21207, numbered 181-184 in her records. 181-183 consisted of fragment cultures, with both unilocular and plurilocular sporangia present. These cultures did not proceed beyond the fragment stage. Culture 184 involved "6 separate isolates of unilocular sporangia from the same plants. They were cultured at 15°C and L:D 12:$\overline{12}$ h. After two weeks in culture the 184 isolates had grown into small plants bearing uniseriate plurilocular sporangia on narrow prostrate filaments and they were beginning to form broader erect filaments. ... The later ones show considerable development of erect parts, and plurilocular sporangia . There is no record of unilocular sporangia developing, ..." These results, while incomplete, reflect the pattern obtained for other species in Section I of the genus.

4.3 *HALOTHRIX* Reinke 1889:49. Hamel 1935:126. Kuckuck 1929:26. Rosenvinge 1935:37. Takamatsu 1938b:181. Yamada 1928:513. Yendo 1909:123.

Thallus pulvinate, hemispherical, loosely compacted, up to 2 cm high, brown, epiphytic on seagrasses. Individual plants may be densely clustered, giving the appearance of one plant.

Basal layer a central disc of isodiametric cells with, at the margins, a rhizoidal system from small isodiametric cells in the lowermost medulla. *Medullary filaments* of pyriform or subglobose non-pigmented cells, with branching confined mainly to upper cells. *Cortical assimilatory filaments* ("paraphyses") clavate, arcuate or straight, of a few inflated cylindrical cells, formed immediately below the meristematic zone of the long assimilatory filaments, on lateral medullary cells. *Long assimilatory filaments* tapering basally, extending in length many times beyond the rest of the thallus, with short cells, L/B about 1, with numerous scattered phaeoplasts.

Unilocular sporangia arising, with the "paraphyses", from upper medullary cells, ovoid, cylindrical or urceolate, with a terminal pore and plug, and at maturity a wide band of mucilage between wall and spore mass.

Plurilocular sporangia in sori on anticlinally divided groups of cells in upper parts of long assimilatory filaments.

Type species:- *H. lumbricalis* (Kutz.) Reinke

A genus of five described species, *H. lumbricalis*[3] from the north Atlantic and Baltic, and four species from Japan, and one new species from southern Australia. The principal difference between this genus and *Elachista* is the specialized plurilocular sori on the surface of the long assimilatory filaments in *Halothrix*. While *E. stellaris* forms epicellular sori, they do not involve the prior subdivision of the whole mother cell as in *Halothrix*.

4.3.1 *Halothrix ephemeralis* sp. nov.

Figure 5; Plate 3, E, F, Pl. 20, B.

Diagnosis:- Thallus usque ad *Halothrix ambigua*, sed filis assimilatis

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3. There are two specimens, MELU, 21072, and 21143, from localities in Victoria, which are labelled *H. lumbricalis*, but the plants are very small, not very fertile and not identifiable beyond genus with any real certainty.

corticatis strictis filiformibusque nec arcuatis cum cellulis inflatis, atque sporangiis unilocularis pyriformibus, sporangiis plurilocularis intercalaribus ab cellulis fili longissimi.

Thallus pulvinate, loosely compacted, 5-15mm high, brown, epiphytic on *Heterozostera tasmanica* leaf blades, often so numerous as to cover the greater part of the blade (Fig. 5.1, Pl. 20.B).

Basal plate of small isodiametric cells 10-15 µm in diameter, adnate to host surface. *Medullary filaments* with 3 or 4 lower pyriform cells L/B 2½-3, 20-25 µm in diameter, infrequently branching, and 2 to 4 upper subglobose cells, $L/B_{c.}$1, 20-30 µm in diameter, branching subdichotomously. *Cortical assimilatory filaments* straight, filiform, of 8-15 slightly inflated cylindrical cells, L/B 1-1½, 10-15 µm in diameter, lightly pigmented (Fig. 5.3). *Long assimilatory filaments* of short narrow cells L/B ½ to 1, 30-50 µm in diameter, with numerous small discoid phaeoplasts; meristem tapering basally, cells short but broad; whole filament many times longer than rest of thallus.

Unilocular sporangia pyriform, with a terminal domed plug and pore, 100-150 µm long and 30-50 µm in diameter, usually paired on lateral medullary branches arising immediately below the meristem of a long assimilatory filament, together with cortical assimilatory filaments, maturing sequentially (Fig. 5.5, Pl. 3.E).

Plurilocular sporangia in intercalary sori borne on 2 to 6 modified cells of long assimilatory filaments; often present on plants before unilocular sporangia develop (Fig. 5.4, Pl. 3.F).

Type locality:- Aldinga reef, S. Aust.

Holotype:- ADU, A32664. (*Womersley*, 29.vii.1968)

Distribution:- Only known from type locality.

Host range:- *Heterozostera tasmanica.*

Representative specimens examined:- Aldinga reef, S. Australia. (*Skinner*, 14.ix.1977; ADU, A48249 and A48250; *Skinner*, 15.ix.1978; ADU, A49553 and A49554).

Comparative specimens examined:- *H. ambigua*, Muroran, Hokkaido, Japan (*Kurogi*, 8.v.1978; ADU, A49376).

The macrothallial stage has a very short season, hence the specific ephithet. It is present, often in very large numbers, on *H. tasmanica* in the intertidal pools of the lower eulittoral of the reef, only during August and September, for a period of less than six weeks. This species differs from *H. ambigua* Yamada (Fig. 5.2) by possessing straight, not curved, slightly medianly inflated cortical filaments, and a pyriform, not ovoid, unilocular sporangium. The differences between this species and *H. lumbricalis* are the possession of unilocular sporangia, the absence of inflated cells towards the top of the cortical filaments, and in the possession of a discrete basal layer rather than a rhizoidal system as in *H. lumbricalis* which also does not develop a very extensive medulla.

Cultures:-

Plate 14, A, B.

P.M. Pedersen (1979) obtained a direct asexual life cycle for *Halothrix lumbricalis*. The presence of hairlike filamentswas explained as an effect of the culture conditions, otherwise the life history agrees closely with results for most other members of the family.

Culture HA-I (from A48249, Aldinga reef, 14.ix.1977) was established from zooids released by unilocular sporangia, at 16°C, 14:$\overline{10}$ h in Provasoli's Enriched Seawater. Release and settling of zooids proceeded for nine days. The zooids showed no marked phototrophism, did not fuse and germinated by a tube. Many branched, prostrate, filamentous plants developed after two to three weeks.

The filamentous plants formed compact tufts, which multiplied by fragmentation and produced no distinguishable organs. After two months short, four celled, plurilocular sporangia could be found on some tufts. They appeared to be little more than modified filament ends. These sporangia released spores which recycled the tufts. Although the culture was maintained for four months, no regeneration of the macrothallus was found.

Specimens collected in 1978 failed to release spores.

4.4 *PORTPHILLIPIA* Silva (1970):944.

Philippia Kuckuck ex Oltmanns 1922:34, fig. 327. Kuckuck 1929:19, fig. 8 (non *Philippia* Klotzsch 1835:354). *Philippiella* Silva 1959:63. Lindauer, Chapman & Aiken 1961:215, fig. 42. Womersley 1967:229. (non *Philippiella* Spegazzini 1897:566).

Thallus pulvinate, globose, compact, dark ochre, epiphytic on *Xiphophora* spp.

Basal region of short rhizoidal filaments penetrating the host surface layers for a short distance. *Medullary filaments* long, narrow, irregularly branched with cylindrical, non-pigmented cells. The medullary filaments produce downward growing narrow filaments ('Klammerorgane' = clampirons, of Kuckuck (1929)) which may act as buttresses for the flexible medullary filaments. *Cortical assimilatory filaments* recurved, with narrow, pigmented cells, arising on short laterals with swollen cells, among the upper medullary cells. *Long assimilatory filaments* of short cylindrical cells, with dense pigmented cytoplasm, arising from a medullary filament at the level of the cortex with a meristem above the terminal medullary cell.

Unilocular sporangia elongate-globose with a terminal plug and pore mechanism, borne among the cortical assimilatory filaments often on a one-celled pedicel, slightly asymmetrical at the base. *Plurilocular sporangia* unknown.

Type species:- *Portphillipia australis* (J. Ag.) Silva.

One species known, from south-eastern Australia and New Zealand.

4.4.1 *Portphillipia australis* (J. Agardh) Silva 1970:944.

Elachista australis J. Agardh 1882: 13. De Toni 1895:440. Guiler 1952:78. Lucas 1909:19; 1913:58. 1929a:14.

Philippia australis Kuckuck ex Oltmanns 1922:34, fig. 327. Kuckuck 1929:19, fig. 8.

Philippiella australis Silva 1959:63. Lindauer, Chapman & Aiken 1961:216, fig. 42. Womersley 1967:229.

Figure 6; Plate 3, G, H. Pl. 20, C.

Thallus 0.5-1.5m high, epiphytic on upper ramuli of *Xiphophora* species (Fig. 6.1).

Medullary cells L/B 5-8, 7-15 µm in diameter. "Klammerorgane" usually of 5 or more cells, unbranched; cells L/B 5-7, 5 µm in diameter. *Cortical assimilatory filaments* of 25-30 cylindrical cells, L/B 3-5, 7-10 µm in diameter. *Long assimilatory filaments* with cylindrical cells L/B 1-2, 10-15 µm in diameter, extending beyond the thallus in length more than twice. *Unilocular sporangia* 45-60 µm long, 20-30 µm in diameter.

Type locality:- Port Phillip Heads, Victoria (Harvey, Alg. Aust. Exsicc. No. 101 as *Leathesia* sp. nov. ?)

Type:- Herb. Agardh, LD (45972).

Distribution:- southern and western coast of Victoria, Tasmania; also New Zealand.

Host range:- *Xiphophora chondrophylla*, and, in New Zealand, also *X. gladiata*.

Representative specimens examined:- Port Phillip Heads, Victoria (*Harvey*, A.A.Exsicc. 101.E; ADU, A18551); Apollo Bay, Victoria, (*Womersley*, 10.xii.1969; ADU, A34,809); Point Lonsdale, Victoria, (*Skinner*, 4.i.1978; ADU, A49067).

4.5 Summary

The family Elachistaceae in southern Australia consists of four taxa, *Elachista orbicularis*, *Elachista secundata*, *Halothrix ephemeralis* and *Portphillipia australis* with the possible addition of a further species of *Halothrix*, if the report of *H. lumbricalis* from Victoria is confirmed.

Elachista orbicularis, which also occurs in Japan and may possibly have been imported here, shows affinities with *E. intermedia* and other endemic Japanese species and, having two kinds of medullary filaments and long, narrow plurilocular sporangia, belongs with those taxa in Section II of the genus. The life history of this species shows close parallels with other members of the genus.

Elachista secundata, which is endemic, shows affinites with *E. fucicola* and *E. scutulata* and belongs in Section I of the genus. The partly completed life history of this species suggests that its behaviour corresponds closely with other members of the genus.

Halothrix ephemeralis is most nearly related to *H. ambigua* from Japan. Some explanation must be found for the consistently short lived appearance of the macrothallus. Rapid and successful release of zooids from both forms of sporangium needs to be obtained, and day length and temperature responses of the resultant sporelings may unravel the mystery.

Portphillipia australis remains the most exceptional, and widespread,

Australian member of this family. It displays the important criteria of two forms of assimilatory filaments and the absence of hairs which characterize the family, but its internal construction and more mucilagenous context show close parallels with the Corynophlaeaceae. Unfortunately *Portphillipia* did not respond to culture.

CHAPTER V

CORYNOPHLAEACEAE OLTMANNS 1922, KUCKUCK 1929

(Syn:- Leathesiaceae Setchell & Gardner 1925;
Elachistaceae sensu Hamel 1939)

5.1 General Introduction

The family Corynophlaeaceae is a small family of seven genera and some 30 to 40 species in the Chordariales. These algae have been found in most temperate and cooler waters throughout the world (*Myriactula arabica* (Kützing) Feldmann has been found in tropical or subtropical waters in the Arabian Sea and Indian Ocean (Jaasund 1969)).

There are two general kinds of habit and structure shown by the members of the family. Partly endophytic, pulvinate thalli with the medullary filaments reduced to only a few cells are shown by the genera *Strepsithalia* Bornet in Sauvageau and *Myriactula* Kuntze, in the tribe Myriactuleae. In the tribe Corynophlaeideae, epiphytic or epilithic cushion-like or crustose thalli with many celled, much branched medullary filaments are shown by the genera *Corynophlaea* Kützing, *Leathesia* Gray, *Cylindrocarpus* Crouan & Crouan, *Petrospongium* Naegeli and *Microcoryne* Strömfelt. All taxa have the typically chordarialian characters of a thallus enclosed in mucilage; non-pigmented hairs with a short basal meristem, arising from upper medullary cells; and uniseriate assimilatory filaments forming an open cortex within which are carried the reproductive organs.

In southern Australia there are three species of *Strepsithalia*, *S. aemula* sp. nov., *S. liagorae* Sauv., and *S. clavata* sp. nov.; two species of *Myriactula*, *M. rivulariae* (Suhr in Areschoug) Feldmann, and

M. haydenii (Gatty) Levring; three species of *Corynophlaea*, *C. cystophorae* J. Agardh, *C. cristata* sp. nov. and *C. filiformis* sp. nov.; two species of *Leathesia*, *L. difformis* (L.) Areschoug and *L. intermedia* Chapman; and one species of *Petrospongium*, *P. rugosum* (Okamura) Setchell & Gardner.

The family Corynophlaeaceae differs from the two most closely allied families of the Chordariales (Elachistaceae and Chordariaceae) on morphological characters rather than ones based on developmental morphology or sexual reproduction (see Fig. I, A-D). The Elachistaceae do not have the whole thallus enclosed in mucilage and so the filaments of the cortex are separated and free, nor do they produce phaeophytan hairs. The thallus anatomy of the members of the Chordariaceae, with much appressed medullary filaments, and the hairs and cortical assimilatory filaments held at right angles to the direction of growth of the medullary filaments, is in sharp contrast to the directly upward development of the cortex and hairs in the thallus of members of the Corynophlaeaceae, where the medulla also is open and radiating.

5.2 Key to the genera of the Corynophlaeaceae in southern Australian waters

1. Thallus pulvinate, partly endophytic, with medullary filaments restricted to a few cells. Tribe I Myriactuleae 2

1. Thallus globose and compact, or coarsely aplanate, epiphytic or epilithic, with medullary filaments of numerous cells.

Tribe II Corynophlaeideae . . . 3

2. External thallus covering an extensive area of the host surface; plurilocular sporangia formed singly or in pairs lateral to the

cortical assimilatory filaments.

(1) *Strepsithalia* Bornet in Sauvageau

2. External thallus in discrete patches; plurilocular sporangia formed sequentially in groups of three or more, terminally on medullary cells, laterally to the base of cortical filaments.

(2) *Myriactula* Kuntze

3. Medullary filaments loosely compacted with at least some lacunae between cells; cortical filaments undivided 4

3. Medullary filaments closely compacted without lacunae between cells; cortical filaments bifurcate at about half their length.

(5) *Petrospongium* Naegeli

4. Medullary cells pyriform or terete, not forming anastomoses with adjacent cells; cortical assimilatory filaments of four to more than fifty cells, terminal cell not distinctly swollen.

(3) *Corynophlaea* Kützing

4. Medullary cells subglobose, cruciform or stellate, forming anastomoses with adjacent cells; cortical assimilatory filaments of three to fifteen cells, terminal cell markedly inflated. (4) *Leathesia* Gray

5.3 Tribe I Myriactuleae nov. trib.

Thallus, ex parte endophytico, cum filis corticibus sporangiisque ex cortice hospitis emergentibus, medullo rhizoidibusque inter cellulas hospitis penetrantibus.

Type genus:- *Myriactula* Kuntze

The members of this tribe all have a partly endophytic thallus with an extensive rhizoidal system penetrating among the cortical and medullary cells of the host. The rhizoidal system, aiding in the

proliferation of the organism within the one host plant, has a stoloniferous character. The medulla may be almost completely replaced by the rhizoidal system, as in species of *Strepsithalia*. In this case the cortex arises from one or two lightly pigmented cells coming from the rhizoidal system, the cortical filaments being of irregular lengths. A medulla organized into short, frequently branched filaments of ten or fewer cells is shown by many *Myriactula* species. Here the cortex of assimilatory filaments, of uniform length, forms a corona above the medulla. The rhizoidal system in both genera extends from one thallus to develop further adjacent thalli.

Two genera are included:- *Strepsithalia* Bornet in Sauvageau; *Myriactula* Kuntze (including *Gonodia* Nieuwland)

5.3.1 *STREPSITHALIA* Bornet in Sauvageau 1896:53, figs 1-8. Sauvageau 1897:21; 1925a:1464. Batters 1902:28. Hamel 1935:149, fig. 34; 1939:XXVI. Kjellman & Svedelius 1911:164. Miranda 1928:457. Newton 1931:151. Oltmanns 1904:379; 1922:29.

Thallus partly endophytic, pulvinate and spreading, usually 0.1-0.2mm high.

Rhizoidal system filamentous, frequently branching, penetrating into the medullary tissue of the host and forming secondary thalli at a distance from the original thallus. *Medulla* of a few cells only, cells cylindrical or irregularly subglobose, lightly pigmented, giving rise to external structures of the thallus. *Cortical assimilatory filaments* short, of 5-10 (-12) cells, usually with the upper few cells inflated and the lower cells cylindrical. Hairs formed on medullary cells, with a short meristem and cylindrical, non-pigmented cells above.

Unilocular sporangia elongate-globose or clavate on a short pedicel from the basal cell of an assimilatory filament, opening by rupture.

Plurilocular sporangia short, uniseriate, with occasional oblique crosswalls and about 8 loculi.

Type species:- *S. curvata* Sauvageau

A genus of six species, from Britain (*S. buffhamiana* Batters), France (*S. curvata* Sauv. and *S. liagorae* Sauv.) and Spain (*S. liebmanniae* Miranda, which also occurs in France), with three species in southern Australia, *S. liagorae*, *S. aemula* sp. nov. and *S. clavata* sp. nov. It seems likely, however, that the genus is represented on other temperate coasts of the world.

There has been much discussion as to the correct systematic position for this genus. Sauvageau (1896) placed it in the Myrionemaceae because of the lack of medullary development. Oltmanns (1904) suggested that the genus was possibly a reduced form of *Castagnea*, but in the same group as *Leathesia*, while later (1922) regarding it as an endophytic form of *Cylindrocarpus*. Kuckuck (1929) listed it in his Corynophlaeaceae. Hamel (1935) placed it after the Corynophlaeaceae as a *genus incertae sedis*, noting that it showed links with the Myrionemaceae and the *Streblonema*-like Ectocarpaceae, as well as with *Myriactula*. Later Hamel (1939) placed the genus *Strepsithalia* in the tribe Streblonemeae of the Myrionemaceae. Fritsch (1954) discussed *Strepsithalia* as a proto-*Aegira*, and placed it in the Chordariaceae.

The similarities with the Streblonemaceae of Feldmann (1954) are superficial. *Streblonema* and related genera have diffuse growth in both the endophytic system (which is more restricted within the host cortical tissue than is the case with *Strepsithalia*) and in the erect emergent

filaments, as well as frequently possessing multi-seriate plurilocular sporangia. The affinities of *Strepsithalia* with *Myriactula* appear strongest, for it shows the same ramifying basal system and has a tendency towards a pulvinate external habit. With its lack of real medullary development, it may be regarded as a proto-*Myriactula*, with strong links with the Ectocarpaceae and Myrionemaceae, thus suggesting that the Corynophlaeaceae may have developed directly from an ectocarpoid-like ancestor rather than via an *Elachista*-like ancestral form - the two families being independent and parallel in development.

The distribution of specimens of *S. curvata* by Bornet under the name "*Herponema ambiguum* Thuret" and the obscurity of these algae in field collections, as well as confusion of *S. buffhamiana* Batters with *Streblonema sphaericum* (cf Newton 1931:figs 76 and 94, which are transposed) may all have contributed to the apparent disjoint distribution of these algae.

Key to the species of *Strepsithalia* in southern Australia.

1. Cortical filaments straight, filiform, terminal cell not inflated; endophytic in Helminthocladiaceae. 2

1. Cortical filaments curved, clavate, terminal cell (and one or two below) inflated, ovoid; partly endophytic in *Caulocystis* sp.
3. *S. clavata* sp.nov.

2. Cortical filaments short (40-60 µm); unilocular sporangia as long or longer than cortical filaments, subglobose.
1. *S. aemula* sp. nov.

2. Cortical filaments long (75-130 µm); unilocular sporangia much shorter than cortical filaments, elongate ovoid.
2. *S. liagorae* Sauvageau

1. *Strepsithalia aemula* sp. nov.

Diagnosis:-

Thallus partim in endophytico partim in filis myrionemoidibus extrariis; fila cortices 40-60 µm longe; sporangia unilocula subglobosa aut elongato-ovoidia, 55-65 µm longe; sporangia plurilocula in sporangiophoribus, uniseriatia, filiforma, cum 8-16 loculis.

Figure 7, A; Plate 4, A.

Thallus partly endophytic with an external myrionemoid portion 1-2mm across, less than 1mm high, hardly exceeding the host surface, mucoid, growing from and among the cortical branches of the host (*Helminthocladia australis*), brown.

Basal system of irregularly branched filaments, with short recurved side branches, of terete cells, L/B 1-2, 6-8 µm broad, with larger isomorphic cells at branching points; rhizoidal filaments similar, with less well pigmented cells, penetrating into the host medulla. Cortical filaments and/or hairs arising singly or, more rarely, in pairs from basal cells, or in short erect branches of five or more filaments on the one cell, sometimes secondarily branched.

Cortical filaments uniseriate, straight, short, 40-55 (-60) µm long, with little or no taper, terminal cell rounded; 5-7 cells per filament, L/B 1-1½, 6-8 µm broad, each with one or two laminar, parietal phaeoplasts (Fig. 7.A5). *Hairs* with a pedicel of one cell, a meristem of short cells (sometimes up to 20) and poorly pigmented cylindrical cells above, L/B 3-10, 7-10 µm broad (Fig. 7.A.1,4).

Unilocular sporangia terminal or subterminal on a modified cortical filament, subglobose to elongate-ovoid, 55-65 µm long, 40-45 µm

broad, with a thin walled terminal cap (Fig. 7.A2, Pl. 4.A).

Plurilocular sporangia borne on a corymbose sporangiophore subtending a hair, uniseriate, filiform, 15-20 µm long with 8-16 loculi, opening by a terminal pore, outer wall persistent, within which new sporangia may form.

Type locality:- Sou' West River, Kangaroo Island, S. Aust.

Holotype:- ADU, A49564 *(Bailey*, 8.i.1966).

Distribution:- only known from type specimen.

Host range:- *Helminthocladia australis*.

Differs from the type species (*S. curvata*) in having short cortical filaments which the unilocular sporangia exceed in length, hence the specific epithet. *S. aemula* differs from *S. liebmanniae* Miranda (Miranda 1928), which also shows short cortical filaments, by having much longer plurilocular sporangia, and in having a host in the Helminthocladiaceae not the Chordariaceae. The three larger species, (*S. buffhamiana*, *S. liagorae* and *S. clavata*) have longer, distinctive cortical filaments and a more *Myriactula*-like habit.

2. *Strepsithalia liagorae* Sauvageau 1896:59, figs 5-8; 1897:21; 1925:1464. Hamel 1935:149, fig. 341; 1939:xxvii.

Figure 7, B; Plate 4, B.

Thallus pulvinate, appearing as brownish tufts or bands in areas where calcification of the host is incomplete (possibly due to the presence of the epiphyte), extending 100-150 µm from host surface(Pl. 4.B).

Rhizoidal system of extensive, ramifying filaments of irregular cylindrical or subglobose pigmented cells penetrating the whole tissue of the host and acting as a stolon for proliferation of the thallus. *Medulla* of subdichotomous filaments of pigmented cells giving rise to

a fan of assimilatory emergent filaments, hairs and unilocular sporangia. *Assimilatory filaments* straight, of 5-10 (-12) cells and overall length 70-130 µm; cells cylindrical, L/B 2-3, diameter 4-5 µm, the upper 3 or 4 cells slightly inflated. Hairs rare, very long, with nonpigmented cells up to 150 µm long and 6-8 µm wide, exceeding the rest of the thallus by up to 8 times their length (Fig. 7.B.1).

Unilocular sporangia elongate ovoid, 20-40 µm long, L/B about 3, opening by a terminal rupture; sporangial wall persistent (Fig. 7.B.3).

Plurilocular sporangia known from French specimens only (Sauvageau 1896).

Type locality:- Guethary, France. (Thuret et Bornet, 8.ix.1854).

Type:- Herb. Thuret, PC.

Distribution:- Mediterranean coast of France. In Australia from Point Sinclair, South Australia to Apollo Bay, Victoria, on rough-water coasts.

Host range:- in Australia, *Liagora harveyiana* and *L. wilsoniana*, in summer.

Representative specimens examined:- Apollo Bay, Victoria, on *L. harveyiana* (*Skinner*, 24.ii.1977; ADU, A47959*); Nora Creina, S. Aust., on *L. harveyiana* (*Skinner*, 11.ii.1979; ADU, A50268); Pennington Bay, Kangaroo I., S. Aust., on *L. wilsoniana* (*Womersley*, 22.i.1947; ADU, A49567), on *L. harveyiana* (*Womersley*, 22.i.1948; ADU, A49566); Point Sinclair, S. Aust., on *L. harveyiana* (*Womersley*, 8.ii.1954; ADU, A49565).

Cultures:-

Sauvageau (1925a) cultured *S. liagorae*, obtaining new irregular filamentous plants from zooids from both plurilocular and unilocular sporangia. The germination of zooids was without fusion, direct and

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* specimen used for culture.

tubular in both cases (the zooids of the plurilocular sporangia being a little larger than those from unilocular sporangia), and irregular filamentous plants, which remained sterile for up to four months, resulted. Secondary plants were derived from plurilocular sporangia on the cultured plants and developed in a similar manner. No unilocular sporangia were obtained on cultured plants. Sauvageau compared this behaviour with that of *Mesogloia* (Sauvageau 1923), and suggested in both cases that this is their method of overwintering.

Results:-

Plate 14, C-E.

One set of cultures of *Strepsithalia liagorae* (Apollo Bay, Vic.; ADU, A47959) was obtained from unilocular sporangia, and grown at 16°C, 14:$\overline{10}$ h. Zooids settled individually and germination was tubular. There were problems with contaminants, including an ectocarpoid and a green alga.

After eight days, two forms of plantlet were distinguishable, as well as the green contaminant, a narrow-celled filamentous plantlet (which later proved to be ectocarpoid) and a filamentous plant with a central disc from which developed laterals with partly biseriate filaments with subglobose cells, and hair filaments.

These later plants developed a tuft-like habit, with lateral branches from the tuft, which showed a similar form to the parent plant. Plurilocular sporangia, uniseriate or biseriate, developed on these plants by the thirtieth day. Some erect filaments from the tufted plants were infrequently branched and developed moniliform chains of cells not unlike the cortical filaments of *Corynophlaea cystophorae*. These plants went through several generations before the culture was terminated.

Summary:-

The results from this set of cultures are insufficient to draw any clear conclusions about the life history of the southern Australian race of *Strepsithalia liagorae*. The delay of only one month before the appearance of plurilocular sporangia, rather than the four months in Sauvageau's (1925a) results, may be due more to the advance in technology of culturing than any real biological difference. Further cultures of Australian material are needed before valid comparison with Sauvageau's results can be made.

3. *Strepsithalia clavata* sp. nov.

Thallus partim ex pulvinario partim in endophytico in ultimis ramulis hospitis; medulla rhizoidesque inter cellulas cortices hospitis; fila corticata clavata, cum cellulis ultioribus inflatis atque cellula terminale pyriforme; sporangia uniloculata clavata, pluriloculata unseriatia filiforma, in sporangiophoribus.

Figure 7, C; Plate 4, C-E.

Thallus partly endophytic, partly emergent and then pulvinate, forming a spreading coat on upper ramuli of fucoid host; mucoid, 0.1-0.2mm high, dark brown (Pl. 4,D).

Rhizoidal system filamentous, branching, penetrating between the epidermal and cortical cells of the host and along the walls of conceptacles, cells L/B 2-3, to 10 µm in diameter. *Medullary cells* formed between the emergent processes of the thallus and the rhizoidal system among the epidermal and outermost cortical host cells, irregular or subglobose, 10-25 µm in diameter.

Cortical assimilatory filaments borne on medullary cells, clavate, 125-175 µm long, determinate, of 4-7 (-10) cells; lower two or three cells terete, L/B 2½-5, 5-10 µm in diameter, upper cells inflated, L/B 1-1½, 10-15 µm in diameter, terminal cell pyriform, L/B c. 1½, 12-15 µm in diameter; phaeoplasts discoid. *Hairs* arising from the medullary cells, infrequent, with a short basal cell, a meristem of 4-6 pigmented cells and terete, non-pigmented cells above, L/B 5-15, 10-15 µm wide.

Unilocular sporangia borne on short corymbose sporangiophores with the cortical filaments, clavate, L/B 3-4, to 100 µm long, opening by a terminal pore, wall persistent; new sporangia may form within the empty sporangium.

Plurilocular sporangia borne on short corymbose sporangiophores among the cortical filaments, uniseriate, L/B 8-10, 90-125 µm long with occasional oblique walls, 8-16 loculi, opening by a terminal pore, wall persistent; new sporangia may form within empty sporangia (Fig.7C2). A second kind of plurilocular structure (Fig.7C3), uniseriate but branched, with a small number of loculi may form on the upper two or three cells of cortical filaments.

Type locality:- Venus Bay, South Australia

Holotype:- ADU, A48890 (*Skinner*, 1.xii.1977)

Distribution:- from Streaky Bay, S. Aust. to Victoria and northern and eastern Tasmania, at least as far south as Blackman's Bay.

Host range:- *Caulocystis* spp., *Sargassum* sp.
Not uncommon in spring and summer in deep eulittoral pools and upper sublittoral.

Representative specimens examined:- * South Australia and type:- Little I ., Blanche Port, Streaky Bay (*Skinner & Gardiner*, 30.xi.1977; ADU, A48881); Normanville *Skinner*, 14.ix.1977; ADU, A48242; 10.xi.1977; ADU, A48826); Encounter Bay (*Skinner*, 23.xi.1977; ADU, A48860); Cape

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* Host is *Caulocystis* sp., unless otherwise stated.

Lannes, Robe (*Skinner*, 11.ii.1979; ADU, A50269).

Victoria:- Queenscliff (*Skinner*, 4.i.1978; ADU, A49059); Point Lonsdale, on *Sargassum* sp. (*Skinner*, 4.i.1978; ADU, A49082); Point Lonsdale (*Skinner*, 17.i.1979; ADU, A50235).

Tasmania:- Low Head (*Skinner*, 23.ii.1978; ADU, A49168); Blackman's Bay (*Skinner*, 20.ii.1978; ADU, A49166 and A49167).

Strepsithalia clavata differs from other species of *Strepsithalia* in the shape of the assimilatory filaments and in the production of sporangiophores for unilocular sporangia. With its more regular medulla, it stands closer to *Myriactula* in form than any other known species of *Strepsithalia*. *S. buffhamiana* has moniliform chains of inflated cells in its cortical filaments and is perhaps closest in morphology to *S. clavata*. The specific epithet was chosen to describe the club-shaped assimilatory filaments.

5.3.2 *MYRIACTULA* Kuntze 1898:415. Feldman 1937:272; 1943:222. Hamel 1939:xxxii. Levring 1937:56. Kylin 1947:47.

Myriactis Kützing 1843:330; 1849:539. Batters 1902:36. Kjellman 1897:228. Kuckuck 1929:35. Newton 1931:142. Sauvageau 1936:151. Thuret 1850:257. Non *Myriactis* Lessing 1831:127 (Compositae).

Phycophila Kützing 1843:331; 1849:541 pro parte.

Elachista sensu J. Agardh 1882:9.

Gonodia Nieuwland 1917:30. Setchell & Gardner 1925:505. Hamel 1935:131. Rosenvinge 1935:28. Skottsberg 1921:21

Thallus partly endophytic, pulvinate above, usually in discrete patches, less than 2mm high.

Rhizoidal system an irregularly branched stoloniferous filament,

penetrating among both the cortical and medullary tissues of the host. *Medulla* of lightly pigmented or non-pigmented isodiametric cells in subdichotomous filaments produced at points of emergence of the rhizoidal system. *Assimilatory filaments* of 10 to 30 or more cells, arising terminally from medullary cells. Hairs with a basal meristem and cylindrical non-pigmented cells above, usually narrower than assimilatory filaments.

Unilocular sporangia terminally rounded and ovoid to cylindrical, opening by a pore, borne on uppermost medullary cells.

Plurilocular sporangia either borne in groups at the base of assimilators and on uppermost medullary cells, or singly on upper cells of assimilatory filaments, uniseriate (with or without oblique crosswalls), filiform and opening terminally.

Type species:- *M. rivulariae* (Suhr in Areschoug) J. Feldmann.

A genus of about fifteen species in temperate and cooler waters throughout the world. Two species in southern Australian waters, *M. rivulariae* and *M. haydenii* (Gatty) Levring.

Kützing (1843) described the genus *Myriactis*, containing only one species, *M. pulvinata* (= *Myriactula rivulariae* (Suhr) Feldm.). He separated it from *Corynophlaea* on the basis of its simpler development, lacking long medullary cells or a distinct basal layer, but with a more penetrating rhizoidal system. The similarity of the arrangement of the assimilatory cortex, with occasional hairs, conformed with the rest of the Chordariaceae (except *Elachista*).

Kützing (1843, 1849) also erected the genus *Phycophila*, to contain all species of *Elachista* sensu Areschoug, and *Areschougia* Meneghini which had been erected to separate *E. stellaris* from *Elachista* on account of

its partly endophytic habit. Many of the large number of taxa placed in this new genus have been shown to be forms of *Elachista fucicola* (see Rosenvinge 1935) and the rest species or subspecies of *Myriactula* or *Elachista*. *Elachista* Duby was retained by Kützing (1849) with one species, *E. scutulata*.

J.G. Agardh (1882) referred all taxa of the three genera to *Elachista*, using the other two Kützing names for sections. He queried the recognition of several genera by other authors and their reasoning for doing so. Kjellman (1897) only accepted one species, *Myriactis pulvinata*, and thought the systematic position of the genus was doubtful. He included *Phycophila* Kützing in *Elachista* Duby. Kuntze (1898) renamed the genus *Myriactis* as *Myriactula* since the former had been used previously (Lessing, 1831) for a genus in the Compositae. Batters (1902) placed all partly endophytic forms in *Myriactis* Kützing and the rest in *Elachista* Duby. Skottsberg (1921) persisted with *Myriactis* and discussed at length the difficulty he had in placing some of his subantarctic species, which showed both long assimilators and hairs, but, on the advice of Kuckuck, placed them in *Elachista*.

Kuckuck (1929) placed all taxa with long assimilators in *Elachista* and all forms with only long hairs in *Myriactis*. Newton (1931), who also used the name *Myriactis*, made no comment on the confusion between the two genera.

Nieuwland (1917) proposed the name *Gonodia* to replace the still usually used *Myriactis*, but made no comment on the limits of this genus, and by overlooking Kuntze, seems to have added to the confusion. Skottsberg (1921) noted the name change of Nieuwland in a footnote. Setchell & Gardner (1924, 1925) and various Japanese authors followed

Nieuwland, as did Hamel (1935) and Rosenvinge (1935).

Hamel (1935) originally placed all forms with hairs in *Gonodia*, later (1939) transferring them to *Myriactula*. Levring (1937) referred the Norwegian species to *Myriactula* and reaffirmed the validity of the Kuntze name, while Sauvageau (1936), having stated that the possession of hairs and one form of assimilatory filaments separated the genus from *Elachista* (with two forms of assimilatory filaments), would not accept the Kuntze name because many of his other revisions of 1898 had been shown to be invalid or confusing. Nor would he accept *Gonodia* Nieuwland, and maintained that there was no confusion caused by the retention of the two different *Myriactis* genera (as the genus in the Compositae is confined to East Asia) and suggested conservation of the genus. In this practice he stated that he was following Thuret (1850) who had known of the existence of both genera under the same name. Rosenvinge (1935) also stated that no species of *Elachista* could have hairs.

Takamatsu (1938a) described three species of *Elachista* with hairs, "paraphyses" and long assimilators. By doing this he appears to be inconsistent, as he gives as references publications wherein such taxa have either been doubtfully included in the genus (e.g. *E. rosarioides* of Skottsberg (1921)) or excluded from the genus and placed in *Gonodia* (Rosenvinge 1935). Takamatsu (1938c) described *G. clavata* with all three structures and considered that it differs from *Elachista* species in having very short cells in the assimilatory filaments. This same character is seen in the three species of *Elachista* in Takamatsu (1938a).

Feldmann (1937, 1943) used the name *Myriactula*, and (1943) gave

a checklist of the species he accepted as members of the genus, bringing the nomenclature up to date. He included Skottsberg's species and also *Corynophlaea cystophorae* (as *Myriactula cystophorae* as Kuckuck (1929) had done because of its rhizoidal basal system). Kylin (1947) accepted *Myriactula* Kuntze and used Rosenvinge's distinction.

It would appear that there are several important distinctions between the two genera *Elachista* and *Myriactula*. *Myriactula* has phaeophytan hairs (even if they only appear in the juvenile stages, e.g. *M. lubrica* (Ruprecht) Jaasund (Jaasund 1960)), the medulla does not have ranks of colourless cells in filaments, and the taxa have a well developed ramifying rhizoidal system penetrating the medullary tissues of the host. *Elachista* has no phaeophytan hairs but two types of assimilators, the long assimilatory filaments with a distinct basal meristem, and the cortical assimilators (or "paraphyses") among which the reproductive structures develop, a medulla of branched filaments of colourless cells in ordered ranks, and a basal layer of cuboid cells which are adnate to the surface of the host organism.

Key to the species and varieties of the genus *Myriactula* in southern Australia.

1. Assimilatory filaments moniliform chains of inflated cells; cells of assimilatory filaments narrow, to 15 µm wide.

   2. *M. haydenii* (Gatty) Levring

1. Assimilatory filaments terete, or with inflated cells confined to just above the meristematic zone; cells of assimilatory filaments broader than above, to 25 µm wide.

   1. *M. rivulariae* (Suhr in Aresch.) Feldmann

   2

2. Assimilatory filaments uniformly terete, cells uniform

throughout filaments, but variable in width from filament to filament. 1.iii *M. rivulariae* var. *arabica* (Kütz.) comb. nov.

2. Assimilatory filaments terete but tapering, cells immediately above meristem inflated; filaments of similar form and width throughout thallus. 3

3. Inflated cells one or two; medullary system well developed. 1.i *M. rivulariae* var. *rivulariae*

3. Inflated cells 2-6; medullary system reduced to rhizoidal system only. 1.ii *M. rivulariae* var. *chordae* (Aresch.) Rosenvinge

1. *Myriactula rivulariae* (Suhr in Areschoug) J. Feldmann 1937:274, fig. 46; 1943:223. Hamel 1939:xxxii.

Elachista rivulariae Suhr in Areschoug 1842:225.

Myriactis pulvinate Kützing 1843:330; 1849:539. Kjellman 1897:228. Kuckuck 1929:39, figs 40-41. Newton 1931:142.

Myriactula pulvinata (Kütz.) Kuntze 1898:415. Levring 1937:57. Rosenvinge & Lund 1943:7.

Gonodia pulvinata (Kütz.) Nieuwland 1917:30. Rosenvinge 1935:28, figs 27, 28.

Gonodia rivulariae (Suhr) Hamel 1935:135, fig. 31, 1-2.

Figure 8, A, B, C, Fig. 9, A; Plate 5, A-D.

Thallus pulvinate, partly endophytic, less than 1mm high, dark brown, emergent mostly in depressions of host surfaces, on a variety of hosts.

Rhizoidal system confined mainly to the host tissues below the emergent part of the thallus, filamentous and irregularly branched. *Medulla* of non-pigmented, irregular, subglobose (below) to pyriform (above) cells, L/B 2-3, 20-30 µm broad, in short subdichotomous filaments which bear the cortical structures.

Assimilatory filaments terete, filiform to tapering, straight or slightly curved, 250-450 µm long; cells cylindrical to inflated cylindrical, with numerous discoid phaeoplasts. *Hairs* with a basal cell, 3-6 meristematic cells, and cylindrical non-pigmented cells above, L/B 2-8, 7-12 µm wide: hairs may exceed the rest of the emergent thallus by two to three times.

Unilocular sporangia ovoid to cylindrical, terminally rounded, opening by a terminal pore, L/B 3/4, 30-35 µm wide, arising on a terminal medullary cell or laterally from the base of an assimilatory filament, on a one celled pedicel or sessile.

Plurilocular sporangia of two forms. Primary plurilocular sporangia filiform, uniseriate, 75-90 µm long with 8-16 loculi, borne in twos and threes on short, branched terminal sporangiophores from medullary cells, at the base of assimilatory filaments. Secondary plurilocular sporangia uni- or biseriate, irregularly branched, with a variable number of loculi, 25-30 µm long, borne on a pedicel laterally from upper cells of assimilatory filaments.

Type locality:- Europe ?

Type specimen:- Lost

a. variety *rivulariae*

Thallus emergent from crypts and conceptacles in thallus of Fucalean host. *Assimilatory filaments* of 10-20 cells, with two or three basal cells, increasing in diameter upwards, followed by two or three inflated cylindrical cells (to 15 µm in diameter), then five to ten cells above, tapering in diameter, terminal cell rounded. Hairs rare. Only unilocular sporangia observed on Australian material (Fig. 8.B).

Distribution:- (in Australia) Stanley Beach, Kangaroo I., S. Aust., on *Myriodesma integrifolia* (*Womersley*, 29.i.1957; ADU, A20836).

b. variety *chordae* (Areschoug) Rosenvinge 1935:31, figs 29-35, as *forma*.

Myriactula chordae (Aresch.) Levring 1937:57.

Thallus more diffuse than the type, emergent from among cortical filaments of host. Medulla reduced to large junction cells in the diffuse rhizoidal system. *Assimilatory filaments* tapering, terete, with two to six cells above meristem markedly inflated, L/B c.1, to 25 µm in diameter, upper cells terete L/B 1-1½, 10-15 µm in diameter. Hairs infrequent. Only unilocular sporangia seen on Australian material (Fig. 8.C).

Distribution:- (in Australia) Aldinga reef, S. Aust., on *Leathesia difformis* (*Skinner*, 31.x.1978; ADU, A49777*)

c. variety *arabica* (Kütz.) comb. nov.

Myriactula arabica (Kütz.) Feldm. 1937:276; 1943:223.

Thallus shallowly endophytic, the basal layer seldom penetrating beyond the cortex of the host tissue. Assimilatory filaments filiform, with a few lower cells inflated in some specimens, cells cylindrical, more numerous than in the type. Both unilocular and plurilocular sporangia on Australian specimens (Fig. 8.A1, 9.A1,A2).

Distribution:- Troubridge Light, S. Aust., 10m deep, on *Sargassum* sp. (*Shepherd*, 4.ii.1969; ADU, A33619); Normanville, S. Aust., on *Sargassum* sp. (*Skinner*, 14.ix.1977; ADU, A48241); Normanville, S. Aust., on *Hydroclathrus clathratus* (*Skinner*, 10.ix.1977; ADU, A48827*); Point Wittlebee, S. Aust., on *Asperococcus bullosus* (*Skinner & Gardiner*, 29.xi.1977; ADU, A48879); Point Lonsdale, Vic. on *Sargassum* sp. (*Skinner*, 4.i.1978; ADU, A49068).

There have been numerous attempts to rationalize the taxonomy of the various morphological forms which make up the genus *Myriactula*. Almost nothing is known about the life history of these algae, with

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* Specimens used for cultures.

the exception of *M. lubrica*, which is an aberrant form, the mature plant resembling closely *Elachista*.

The solution proposed by J. Agardh (1882) has already been discussed above. The most extreme proposal was that of Feldmann (1943), where numerous "species" were accepted, the major criterion for distinguishing them being difference in hosts, each taxon being assumed to be host specific. While many of these species may indeed be valid, very careful genetic and biochemical testing would be required to justify the proposal as a universal criterion. Most other proposals have been based on comparative morphology, and limited but not exclusive host ranges have been given for species. Kuckuck (1929) included notes on a small number of species, but included *Corynophlaea cystophorae*, because the basal system of that plant disrupts the host tissue.

Rosenvinge (1935) presented a thorough treatment of the morphological variation in specimens of *Gonodia pulvinata (= M. rivulariae)* from Denmark. He made the point that much similarity is to be found between *Myriactula rivulariae sensu stricto*, growing in the cryptostomata of Fucales, and *Myriactula chordae sensu* Levring, which invades the cortex and upper medullary systems of a wide range of "filamentous" algae. As a result he accepted one species, *Gonodia pulvinata* (Kütz.) Nieuwland, with two forms, forma *pulvinata*, for plants on Fucales, and forma *chordae* (Areschoug), for plants on other algae. Levring (1937) accepted two distinct species, *Myriactula pulvinata* (Kütz.) Kuntze and *M. chordae* (Aresch.) Levring.

"Ich ziehe jeden-falls gegenwärtig vor, sie als eine selbständige Art aufzufassen, weil es night sicher bewiesen ist, dass sie eine Form gerade von *Myriactula pulvinata* ist."[1]

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1. Levring, T. (1937):p.58. "I contend, anyway for the moment, that it (*M. chordae*) should be interpreted as a valid taxon, since it has not been clearly demonstrated that (this taxon) comes directly from *Myriactula pulvinata*."

Myriactula arabica (Kütz.) Feldm. has been treated by most authors as a separate taxon, because the assimilatory filaments are longer than those of either of the other two taxa, and show no taper. The secondary epi-filamentous plurilocular sporangia, which are exhibited by both *M. rivulariae* and *M. arabica*, have been the source of dispute about their exact nature and the validity of the separation of these taxa.

Kuckuck (1929) described and illustrated specimens from Tangier, which he placed in *Myriactis arabica* but which Børgesen (1934) contended were not typical of that taxon. Kuckuck's secondary plurilocular sporangia involved a whole cell of the assimilatory filament. Feldmann (1937) discussed the presence and nature of epi-filamentous plurilocular sporangia in all three taxa. He concluded that the differences between those borne by *M. rivulariae* and *M. rivulariae* var. *chordae* (*sensu* Rosenvinge 1935) which, like those of *Elachista stellaris* Aresch., were derived from the cells of the filaments "exclusivement lateraux"[2], and those of *M. arabica*, which "... résultent de la transformation de la cellule même..."[3], lay in the manner in which they arose. Feldmann's (1935, fig. 46, B & C) illustrations are similar to those of Børgesen (1934, fig. 5) and Jaasund (1969, fig. 7B) for *M. arabica*.

The treatment given here, where specimens agreeing with each of the three "species" have been found, is to regard each morphological type as a form of a very variable single species. Although the total number of specimens is small (only seven specimens have been available) it has been found difficult to distinguish clearly between the three forms. The degree of inflation of the lower and middle cells of assimilatory filaments may vary even within one plant; and the range of hosts, especially for forma *arabica*, suggests that any subdivision

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2. & 3. Feldmann, J. (1937):p. 276.

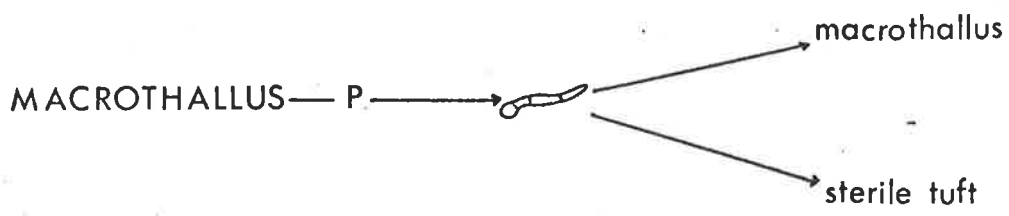
of this taxon on the basis of host specificity requires careful assessment.

Culture studies:-

Thuret (1849) demonstrated germination of zooids from this taxon to be tubular, and the initial plantlet to be filamentous and prostrate.

Results:-

Two cultures were set up from Australian material, ML-I (*Myriactula rivulariae* var. *arabica;* ADU, A48827) with plurilocular sporangia, and MA-II (*M. rivulariae* var. *chordae;* ADU, A49777) with unilocular sporangia. ML-I was formed from zooids which settled directly, germinated by a tube and after six weeks showed a mixture of sterile streblonemoid tufts and new plantlets similar to the parent in form which bore plurilocular sporangia. MA-II also showed direct germination of the zooids, which formed two kinds of irregularly branched filamentous plants, one a sterile streblonemoid tuft, the other a compactly organized pulvinate plant which formed intercalary plurilocular sporangia. No secondary plants were obtained and the culture was terminated after two months, due to contamination by minute dinoflagellates. It is not possible to draw conclusions from MA-II, but ML-I suggests that a direct, asexual phase is involved in the life history of *Myriactula rivulariae* var. *arabica*.



Textfigure V.i. Life cycle history diagram for *Myriactula rivulariae* var. *arabica*.

2. *Myriactula haydenii* (Gatty) Levring 1937:57 (as *M. haydeni* (Harvey) Levring). Jaasund 1965:65. Blackler 1961:-

Elachista haydenii Gatty 1863:-

Myriactis haydenii (Harvey) Batters 1902:36. Kuckuck 1929:37, figs 35-36. Newton 1931:143. De Toni 1889:418.

Figure 9, B; Plate 5, F, G.

Thallus pulvinate and spreading above, partly endophytic, less than 1mm high, brown (Pl. 5.F).

Rhizoidal system much ramified, penetrating between the medullary cells of the host, with stoloniferous filaments among the cortical cells of the host. *Medullary filaments* of only a few lightly pigmented cells, of various shapes fitting between the cortical cells of the host. *Assimilatory filaments* up to 500 µm long, of moniliform chains of 18-25 cells, thick walled and heavily pigmented, L/B 1-1½, 10-15 µm wide, arising from terminal cells of the medulla. *Hairs* numerous and narrow, arising from similar medullary cells, with two or three basal cells, a medulla of 4-6 cells and narrow, cylindrical, non-pigmented cells above, L/B 8-10, 8-10 µm wide; filaments may be two or three times longer than the rest of the emergent thallus.

Unilocular sporangia unknown.

Plurilocular sporangia arising as groups of two or three on terminal cells of medulla, filiform, 50-100 µm long, with 16-24 loculi, with a terminal opening. Secondary plurilocular sporangia short, with fewer than 10 loculi, developing on cells of assimilatory filaments, infrequent.

Type locality:- Scotland ?

Type:- St Andrews.(Herb. Gatty).

Distribution:- Great Britain. In southern Australia, Wanna, Port Lincoln, S. Aust., on *Scytosiphon* sp. (*Womersley*, 21.viii.1967; ADU, A31873); Cape Jervis, S. Aust. on *Colpomenia* sp. (*Skinner*, 25.viii.1976; ADU, A47621); Point Lonsdale, Vic. on *Scytosiphon* sp. (*Skinner*, 4.i.1978; ADU, A49083).

Host range:- Members of the Scytosiphonaceae.

This species has been considered as conspecific with *M. moniliformis* (Foslie) J. Feldmann by Levring (1937) and also Kylin (1947). However some evidence to the contrary was produced by Sauvageau (1936).

The similarity between *Myriactula haydenii*, distinguished by having longer, more delicate assimilatory filaments and a more extensive rhizoidal system, and *M. rivulariae* also requires more detailed examination than the few specimens at hand will allow.

5.4 Tribe II Corynophlaeideae nov. trib.

Thallus aut epiphyticus aut epilithicus, medullo externe ex superficie hospitis, base aut extera aut dirumpente superficies hospitis pro minore parte.

Type genus:- *Corynophlaea* Kützing.

The taxa which are included in this tribe are those which, with the exception of some forms of *Corynophlaea cystophorae* J. Ag., are wholely epiphytic or epilithic, with a clearly differentiated basal layer. The medulla consists of numerous filaments of non-pigmented cells, which may be variously branched, the terminal cells of these branches supporting the cortex. The assimilators of the cortex show determinate growth, producing an even surface to the thallus and a clearly delimited cortical layer, beyond which only the hairs protrude.

The meristematic zone lies at the junction of the cortex and the medulla; growth is radial and most active at the margins of the thallus nearest the host surface. The general shape of the plant is hemispherical or aplanate and convoluted, although Rosenvinge & Lund (1943), describe much branched plants of *Microcoryne ocellata* Strömfelt with cylindrical axes.

Five genera are included:-

Corynophlaea Kützing (1843)

Leathesia Gray (1821)

Microcoryne Strömfelt (1888)

Cylindrocarpus Crouan & Crouan (1851) and

Petrospongium Naegeli ex Kützing (1858)

5.4.1 *CORYNOPHLAEA* Kützing 1843:331; 1849:543. J. Agardh 1882:21. Hamel 1935:141; 1939:xxxvi. Kuckuck 1929:40. Lindauer, Chapman & Aiken 1961:218. Womersley 1967:230.

Leathesia sensu Hauck 1885:334. Inagaki 1958:100, pro parte.

Kylin 1907:83. Schiffner 1916:159. Setchell & Gardner 1925:510.

Thallus pulvinate, hemispherical to irregular, gelatinous, wholly epiphytic, or with slight disruptive penetration of the host cortex; yellow brown to dark brown.

Basal layer of short cubical cells adnate to the host surface, forming an open, filamentous plate, sometimes with a small amount of shallow rhizoidal development.

The *medulla* consists of variously branched filaments of non-pigmented cylindrical or pyriform cells, closely appressed, but not forming anastomoses. While a subcortex is absent, the uppermost cells of medullary filaments are often smaller and subglobose.

Cortical assimilatory filaments uniseriate and curved, determinate, forming the cortex. Lower cells of cortical filaments terete and having a few phaeoplasts, upper cells usually inflated or terete, often the inflation projected towards the upper side of the curve of the filament with larger or more numerous phaeoplasts. *Hairs* with a basal cell, a short pigmented meristem and long, narrow non-pigmented cylindrical cells above.

Unilocular sporangia pyriform or ovoid, with a terminal plug and pore, borne laterally at the base of assimilatory filaments.

Plurilocular sporangia either (1) uniseriate, filiform, opening by a terminal pore, in groups on short, branched sporangiophores on uppermost medullary cells; or (2) multiseriate, curved, ectocarpoid, on upper cells of assimilatory filaments.

Type species:- *Corynophlaea umbellata* (C. Ag.) Kützing.

A genus of five recognized species, four in the North Atlantic

and Mediterranean, and one species from Australia and New Zealand. Some taxa from Japan, described by Inagaki (1958) as members of the genus *Leathesia*, may possibly also belong to *Corynophlaea*. Two new species from southern Australia are described below.

The confusion between *Corynophlaea* Kützing and *Leathesia* S.F. Gray appears to stem from Kützing's (1843) original description of *Corynophlaea*, with the first species listed being *C. baltica* which, as J. Agardh (1882) stated, is conspecific with *Leathesia marina (= L. difformis)*. The often cited argument for joining the two genera is that they are at most separated on the degree of compactness of the medulla, which has been shown to vary with the age of the thallus. Kützing (1849) did use this distinction: *Corynophlaea* was described as "Phycoma (minutum) subglobosum, solidum, ..."[4] and *Leathesia* as "Phycoma olivaceum cavum, vesicatum molle..."[5]. He also (1843) carefully emphasized the anatomical differences in the medullary tissues of each genus. For *Corynophlaea* "medullare: parenchyma continuum, compactum, excellulis majoribus hyalinis, vesicatis, laxe conjunctis, ellipticis constituum,"[6] while for *Corynophora* C. Agardh (= *Leathesia* Gray) "medullare ex filis hyalinis majoribus laxis, reticulatim conjunctis compositum."[7] The differences between the two genera (Table V.ii), while not great, are consistent throughout each genus, and adequate to warrant their separation. Some species, e.g. *C. flaccida* (which has an anomalously small number of cells (4) in the

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4. Kützing, F. (1849):p.543, "A small subglobose solid thallus ..."
5. Kützing, F. (1849):p.543, "Olive green thallus (which is) hollow, a soft bladder."
6. Kützing, F. (1843):p.331. "medulla:- a continuum of parenchyma, compact, built out of elliptical, vesicate, largely hyaline cells loosely thrown together."
7. Kützing, F. (1843):p.331. "with the medulla composed of hyaline filaments, largely lax, thrown together as if in a net."

assimilators) and *L. primaria* (which has long filiform assimilators and long, narrow lower medullary cells which branch only above the second cell) show that the two genera are closely related.

TABLE V.ii

Comparison of *Corynophlaea* and *Leathesia*

Long medullary cells laterally appressed and terminally branching; filaments mostly uniseriate below, upper cells branching sub-dichotomously. No clearly defined subcortex.	Long often cruciate medullary cells anastomosing with adjacent cells; branching subdichotomous throughout; subcortex or subglobose cells distinct from lower medullary cells.
Assimilatory filaments long, usually curved, and of 4 to more than 50 cells; terminal cell not more inflated than cells below it.	Assimilators straight, 3-10 (-15) cells, ending in a pronouncedly inflated terminal cell.

Key to the genus *Corynophlaea* in southern Australia.

1. Assimilatory cells cylindrical throughout the filament.

(3) *Corynophlaea filiformis* sp. nov.

1. Assimilatory cells subglobose or laterally expanded, at least in upper parts of the filament. 2

2. Plurilocular sporangia borne on sporangiophores in the cortex; branching of medullary filaments subdichotomous.

(1) *Corynophlaea cystophorae* J. Ag.

2. Plurilocular sporangia borne singly on upper cells of assimilatory filaments; branching of medullary filaments from nodes, polychotomous. (2) *Corynophlaea cristata* sp. nov.

(1) *Corynophlaea cystophorae* J. Agardh 1882:22, Pl.1, fig. 1.

De Toni 1895:421. Lindauer, Chapman & Aiken 1961:218, fig. 43.

Lucas 1909:18; 1936:102. Womersley 1950:154; 1967:230.

Corynophlaea umbellata sensu Kützing 1849, for Australian specimens.

Leathesia umbellata sensu J. Agardh 1848:51. Harvey 1863:xiii.

Myriactis cystophorae Kuckuck 1929:40, fig. 42.

Myriactula cystophorae Feldmann 1943:223.

Corynophlaea cystophorae var. *longifila* Reinbold 1899:289.

Corynophlaea longifila Lindauer, Chapman & Aiken 1961:218, fig. 43.

Figure 10; Plate 6, D-F, Pl. 21, A.

Thallus hemispherical to globose, mucose, firm, 2-4 (-6)mm high, brown, epiphytic on various *Cystophora* species (where it occurs on the ramuli often with several plants on the one ramulus) as well as on several other algae (Fig. 10.3).

Basal layer of isodiametric cells in closely appressed radiating filaments amongst the surface cells of fucalean hosts or forming a diffuse plate on other hosts.

Medullary filaments with several large pyriform cells in the lower part grading to smaller subglobose cells above, branching subdichotomous; cells L/B 1-3, 12-25 µm in diameter (Fig. 10.8).

Assimilatory filaments borne in threes or fours on terminal medullary cells, curved, from 0.1-2.5mm long, with 8 to more than 60 cells, the lower half to two thirds of a filament with cylindrical cells, L/B 3-5, 8-15 µm in diameter, and the upper filament with inflated, subspherical cells, L/B 1-1½, 10-15 (-20) µm broad, which may be further inflated to a deltoid shape, with all projections on the upper surface of the curve of the filament. *Hairs* with a basal cell on the terminal medullary cell, a short pigmented meristem of 6-8 cells and cylindrical cells without phaeoplasts above, L/B 3-10, 10-15 µm in diameter; filament may exceed the thallus by two to three times its length, not common.

Unilocular sporangia cylindrical, basally attenuated, with a rounded terminal pore and plug mechanism, L/B 1½-3, 20-25 µm in diameter, borne laterally at the base of assimilators (Fig. 10.1, Pl. 6.E,F).

Plurilocular sporangia filiform, uniseriate, with 16-36 loculi, 30-50 µm long, opening by a terminal pore, outer wall persistent, borne on terminal medullary cell among assimilators on corymbose sporangiophore (Fig. 10.2) Some specimens show both unilocular and plurilocular sporangia on the same thallus.

Type locality:- Port Phillip Heads, Victoria (Harvey).

Type:- Herb. Agardh, LD (46193). (Harvey, Alg. Aust. Exsic. No. 102).

Distribution:- Fremantle, W. Aust. to Tathra, N.S.W., and around Tasmania. Also New Zealand.

Host range:- species of *Cystophora, Caulocystis, Sargassum, Xiphophora, Dictyota, Zonaria, Osmundaria, Metagoniolithon* (see Appendix III for complete list of specimens and table of frequency).

Representative specimens examined:- (for a more complete list see appendices).

W. Aust.:- Rottnest I, on *Cystophora brownii* (*Gordon*, 10.xi.1968; ADU, A33330).

S. Aust.:- Point Westall, on *C. moniliformis* (*Skinner*, 30.xi.1977; ADU, A48888); Venus Bay, on *C. brownii* (*Skinner*, 1.xii.1977; ADU, A48894); Fishery Bay, on *C. brownii* (*Skinner*, 4.xii.1977; ADU, A48909); Reevsby I., Yorke Pen., on *Metagoniolithon* sp., 3.5m deep, (*Baldock*, 13.xii.1977; ADU, A48923); Balgowan reef, Yorke Pen., on *Osmundaria prolifera* (*Kald*, 17.xii.1967; ADU, A32188); Sou' West R., Kangaroo I., on *C. intermedia* (*Womersley*, 17.1.1965; ADU, A28907); Aldinga reef, on *C. polycystidea* (*Skinner*, 14.x.1977; ADU, A48580; 11.xi.1977; ADU, A48830*); Encounter Bay, on *C. polycystidea* (*Skinner*, 28.ix.1977; ADU, A48263*).

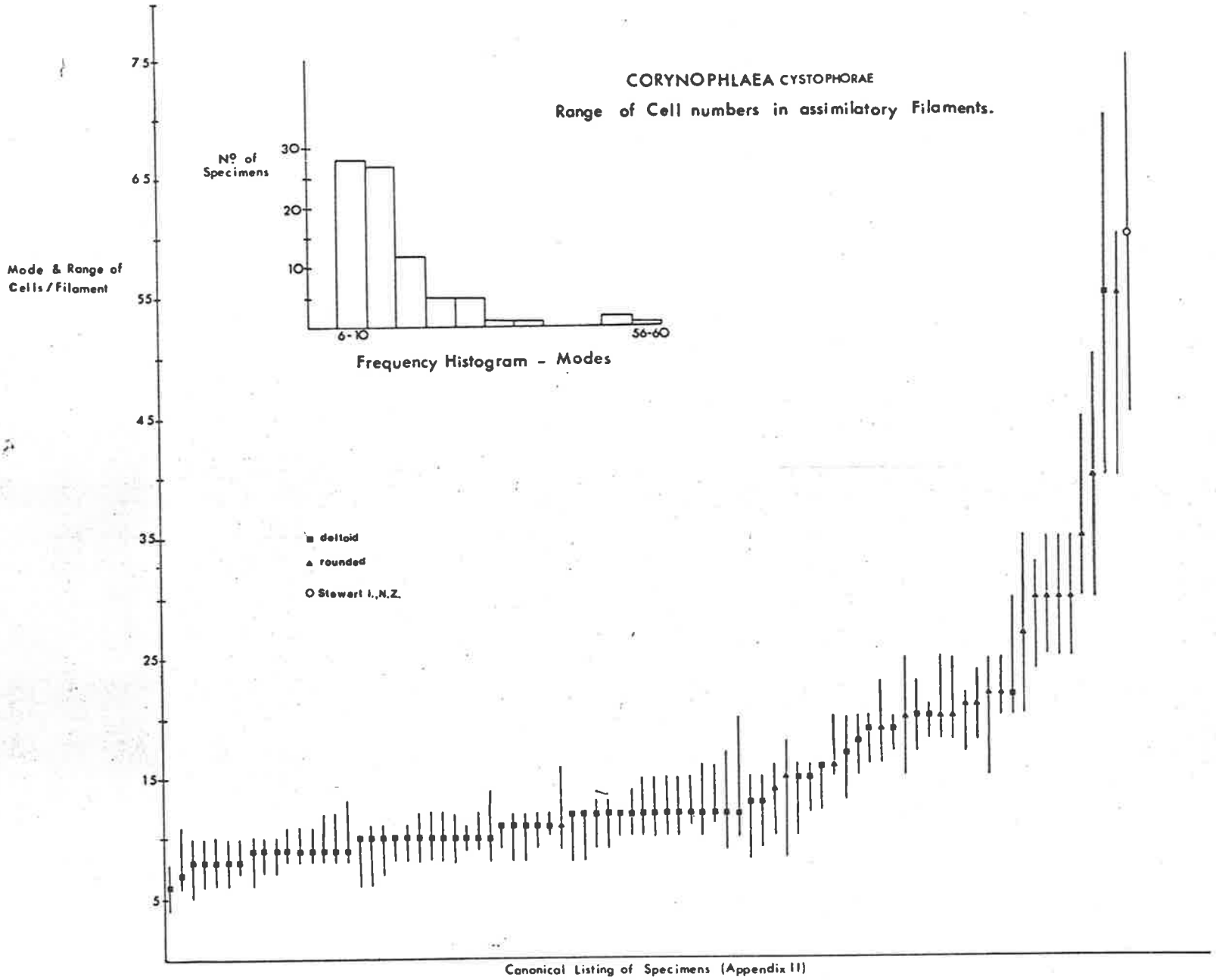
Vic.:- Marengo, on *C. torulosa* (*Skinner*, 22.i.1977; ADU, A47858*); Skene's Ck., on *Zonaria* sp.(*Skinner*, 24.ii.1977; ADU, A47963); Point Roadknight, on *C. subfarcinata* (*Skinner*, 6.i.1978; ADU, A49076); Point Lonsdale, on *C. torulosa* (*Skinner*, 4.i.1978; ADU, A49069); Queenscliff, on *Sargassum* sp. (*Skinner*, 4.i.1978; ADU, A49076).
Tas.:- Bicheno, on *C. moniliformis* (*Olsen*, 29.xii.1963; ADU, A27070); Gordon, on *C. moniliformis* (*Skinner*, 24.ii.1978; ADU, A49173).
N.S.W.:- Tathra, on *C. retroflexa* (*Cribb*, 5.x.1950; ADU, A21051).

Older assimilatory filaments have been observed on occasions to become secondarily meristematic and support new assimilatory filaments and purilocular sporangia.

Care must be taken in interpreting the description and drawing of the type material by J. Agardh (1882). Although Agardh only cites Harvey's Alg. Aust. Exsic. No. 102, there may be more than one specimen involved, as no recent specimens have been found with epicellular plurilocular sporangia and which agree in all other respects with *Corynophlaea cystophorae*. J. Agardh's (1882) figure 1d ("trichosporangium in faceview") is the source of confusion as the structure is not attached to any other part of the plant, nor are there any locular walls to be seen. If the "idem" has the usual meaning then Agardh assumed that his structure was an immature ("submaturum") plurilocular sporangium. Lindauer *et al.* (1961) have followed Agardh, even to redrawing his figure, placing Agardh's 1d terminally on a series of colourless cells, without trying to re-interpret the structure. This may indicate that specimens bearing plurilocular sporangia have not been collected in New Zealand. Kuckuck (1929) is justified in proposing, from Agardh's (1882) description and figures, two alternatives,

i.e. the plurilocular sporangia of *C. cystophorae* are modified assimilatory cells as he understood to be the case with *Myriactis arabica*, or are similar to those formed by species of *Eudesme* and *Castagnea*. The species newly described below (*C. cristata*) does show epicellular plurilocular sporangia like those of the latter two genera, but has an internal structure similar to *C. hamelii* Feldm., not *C. umbellata* or *C. cystophorae*.

Lindauer *et al.* (1961, pp. 218-220) recognize two species, *Corynophlaea cystophorae* which has "paraphases up to 30 cells, cells cylindrical". and *C. longifila* (Reinb.) Lindr. *et al.* with "paraphyses 27-50 cells, with horizontal, deltoid extensions to apical cells." In Australian material the occurrence of horizontal deltoid projections is not confined to forms with many celled assimilators, but may occur on even those with very few cells, e.g. specimens from Bicheno, Tasmania, (ADU, A30129) with 4-8 cells in the assimilatory filaments, have the upper four cells with such projections, while those from Marengo, Victoria, (ADU, A47858), which has 25-35 cells in the assimilators, and from Balgowan reef, Yorke Peninsula, South Australia (ADU, A32188), with 20-35 cells in the assimilators, both have moniliform chains of subspherical cells in the upper part of the filament. Rounded cells are most frequently encountered in specimens which have larger numbers of cells per filament, and are almost absent from filaments with only a few cells in southern Australian material. The most common number of cells in assimilators lies between 6 and 15, and specimens with greater than fifty cells per assimilatory filament are very rare (see Appendix II). Textfigure V.ii. shows that a continuum exists between the specimens with small numbers of cells in assimilators and those with large numbers of such cells.



Text figure V.II.

The other two points given by Lindauer *et al.* (1961) as distinguishing *C. longifila* from *C. cystophorae* are the larger size of the mature unilocular sporangia and "straight rather than arcuate tips of the paraphyses."[8] In Australian material the size of the unilocular sporangium varies with the size of the whole thallus rather than the assimilators alone. The relative curvature of the cortical assimilatory filaments appears to vary even within the same thallus. Unfortunately Reinbold's type specimen of var. *longifila* was not available for study.

The host range of *C. cystophorae* is not confined to *Cystophora* spp., although the commonest host in South Australia is *C. moniliformis*, and *C. torulosa* is an important host in Victoria. Appendix III assesses the host range of *C. cystophorae*, from the ADU collection.

Culture studies:-

No reports occur in the literature of cultures of species of *Corynophlaea*.

Results:-

Plate 14, F-H.

Three cultures of *Corynophlaea cystophorae* were established: CM-I (Marengo, Victoria; ADU, A47858) and CE-II (Encounter Bay, South Australia; ADU, A48263) from zooids released from unilocular sporangia, and CA-III (Aldinga reef, South Australia; ADU, A48830) from zooids released from plurilocular sporangia.

Culture CM-I was set up at 16°C, 14:$\overline{10}$ h and 20°C, 14:$\overline{10}$ h, in Provasoli's Enriched Seawater medium. Germination was most successful at 20°C, and the negatively phototrophic zooids produced a tubular germtube after settling singly. The prothallus, which developed rapidly, was irregular and filamentous, and, although erect filaments were quickly produced, hairs were not present until after fourteen days

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8. Lindauer, Chapman & Aiken (1961): p. 219.

of culture. By the twenty-second day uniseriate plurilocular sporangia were visible. These were formed singly lateral to the cells of the filaments in the prothallial tufts. The prothallial tufts were self regenerating and went through several generations before the cultures were terminated. The cultures at 16°C did not develop beyond the initial filamentous prothallial stage.

Culture CE-II was set up at 16°C, 14:$\overline{10}$ h in Provasoli's Enriched Seawater medium. Germination was tubular, without fusion of zooids, and irregular prothallial tufts developed. However, after one month, and before any reproductive structures appeared, mechanical failure caused the loss of these cultures.

Culture CA-III was established at 16°C, 14:$\overline{10}$ h in Provasoli's Enriched Seawater. The zooids settled without fusion and germinated by a tube. After five days of culture, two distinct forms of prothalli were recognizable. A diffuse filamentous prothallial form similar to that obtained in the cultures from unilocular sporangia, was present. As well, a more compact prothallus, still filamentous, but reminiscent of the pseudodiscoid prothalli of some species of *Murionema*, also occurred. This second form of prothallus grew vigorously and produced compact plantlets but at no stage regenerated a true macrothallus. Neither of these prothallial types were fertile when culturing was terminated, after six weeks.

Textfigure V.iii. Life history diagram for *Corynophlaea cystophorae*

Summary:-

The results were inconclusive. Further cultures of plants with either unilocular sporangia, or plurilocular sporangia or both are required, and should include experimentation with day length and the effects of Kinetin. Some investigation should also possibly be made of crossing of released zooids, because of the possibility of an "ectocarpoid" life history, similar to that obtained by Müller (1972).

(2) *Corynophlaea cristata* sp. nov.

Diagnosis:-

Thallus amplus aut subglobosus aut informis, mucosusque; fila medullae ex geniculis polybracchiata cum teretibus cellulis longis; fila corticata uniseriatia arcuataque cum cellulis altioribus aut subglobosis aut deltoidibus; sporangiis unilocularibus ignotis; sporangia plurilocularia multiseriata cristatis in soris quasi in jubo ex altioribus cellulis filorum corticium.

Figure 11,B; Plate 6, B, C, Pl. 21, B.

Thallus comparatively large, to 10mm across, subglobose to irregular in form, mucose, gelatinous and flaccid, light brown, epiphytic on ramuli of *Cystophora* spp (Fig. 11.B.2).

Basal layer a diffuse filamentous plate adnate to host, of small isodiametric cells. *Medulla* of long cylindrical cells L/B 2-5, 10-25 µm in diameter, in filaments, with two to three cells between nodes at which two to three branches lateral to the main axis may be cut off; terminal cells not markedly smaller than cells below (Fig. 11.B.4, Pl. 6.B).

Assimilatory filaments uniseriate, unbranched, curved, about 800 µm long; lower cells cylindrical, L/B 1-1½, upper cells subglobose

or with deltoid lateral inflation, on upper side of the curve of the filament, L/B 1-1½,10-20 µm wide, with two or three large discoid parietal phaeoplasts. *Hairs* with a basal cell, a meristem of 4-6 cells and terete cells above, L/B 4-10, 10-15 µm wide.

Unilocular sporangia unknown.

Plurilocular sporangia multiseriate, sub-conical, clavate, with numerous loculi, 25-40 µm long, opening by a terminal pore, epicellular on upper assimilatory filaments in crest-like sori(Fig. 11.B.1, Pl. 6.C).

Type locality:- Point Westall, S. Aust.

Holotype:- ADU, A48886 (*Skinner*, 30.xi.1977)

Distribution:- only known from collections below; South Australia.

Host range:- *Cystophora brownii*, *Cystophora botryocystis*.

Representative specimens examined:- Point Westall. S. Aust., on *C. brownii* (*Skinner*, 30.xi.1977; ADU, A48886); Partney I., S. Aust., on *C. botryocystis*, 10-12m deep (*Baldock*, 13.xii.1977; ADU, A48925); Reevsby I., S. Aust., on *C. brownii*, 0-3.5m deep (*Baldock*, 13.xii.1977; ADU, A48924); Aldinga reef, S. Aust., on *C. brownii* (*Skinner*, 26.x.1977; ADU, A48630).

This species shows a medullary structure similar to *Corynophlaea hamelii* Feldmann, but differing markedly from *C. umbellata* and *C. cystophorae*. The clusters of epicellular multiseriate sporangia on assimilatory filaments makes this species distinct from all others in the genus.

(3) *Corynophlaea filiformis* sp. nov.

Diagnosis:-

Thallus pulvinarius hemisphaericus atque mucosus, 0.5-1.5mm alte;

medulla cellulis subglobosis inferne, atque cellulis in filibus subdichotomis teretibus superne; fila corticata cum cellulis teretibus, L/B 1-3; sporangiis unilocularibus ignotis; sporangiae pluriloculares principales uniseriates in sporangiophoribus corymbosis, secundariae in cellulis fili corticis usque ad *Myriactula*.

Figure 11,A; Plate 6, A.

Thallus pulvinate, hemispherical, mucose , brown, 0.5-1.5mm, epiphytic on ramuli of *Cystophora polycystidea* (Fig. 11.A.1).

Basal layer a diffuse filamentous system of small irregular cells penetrating the outer layers of host tissue. *Medulla* with a lower section of closely packed subglobose cells, L/B 1-3, 12-15 µm in diameter, and an upper section of subdichotomous filaments of narrow terete cells L/B 1-5, 7-12 µm broad, with a subglobose terminal cell supporting the hairs and sporangiophores.

Assimilatory filaments filiform, arising from lower medullary cells, extending beyond the corona of plurilocular sporangia 1-1½ times the length of the remaining thallus, infrequent; cells cylindrical, L/B 1-3, 12-15 µm wide, with several lenticular phaeoplasts. *Hairs* as for genus, cylindrical cells L/B 3-5, 7-12 µm in diameter.

Unilocular sporangia unknown.

Plurilocular sporangia of two forms. Primary plurilocular sporangia filiform, uniseriate or biseriate, with 8-24 loculi, opening by a terminal pore, outer wall persistent, on corymbose sporangiophores from terminal medullary cell (Fig. 11.A3,4). Secondary plurilocular sporangia multiseriate, borne on upper cells of assimilatory filaments.

Type locality:- Aldinga reef, S. Aust.

Holotype:- ADU, A48582 (*Skinner*, 14.x.1977)

Distribution:- Known only from type locality.

Host range:- *Cystophora polycystidea*

This is a very distinctive taxon. It shares characters with both *Myriactula*, viz.the lack of a real cortex and the presence of epicellular sporangia in the assimilatory filaments, and with *Corynophlaea*, viz.the form of the primary plurilocular sporangia being close to *C. cystophorae* and *C. umbellata*. It does not show the penetrating stoloniferous rhizoids of *Myriactula*, and the medulla, although aberrant for this genus, is organized and external to the host. More collections could have made taxonomic determination much clearer, but it appears to be a very rare species indeed.

5.4.2 *LEATHESIA* Gray 1821:301. J. Agardh 1848:50; 1882:40. Hamel 1935:138. Harvey 1846:56. Hauck 1886:334. Inagaki 1958:100. Kuckuck 1929:43. Kützing 1849:543. Lindauer, Chapman & Aiken 1961:219. Schiffner 1916:159. Setchell & Gardner 1925:510.

Corynephora C. Agardh 1824:xix. Kützing 1843:331.

Clavatella Bory de St. Vincent 1825:470.

Thallus globose to much lobed and aplanate, mucose, compact and firm even in large hollow thalli, yellow-brown to brown, epiphytic or epilithic.

Basal cells short, isodiametric, forming a radiating plate; growth persistent at the margins. *Medullary filaments* with smaller subglobose cells above, forming a "subcortex", and larger, irregular, elongate pyriform or cruciform cells below; anastomosis between adjacent cells frequent throughout. *Assimilatory filaments* borne in twos and threes on terminal subcortical cells, forming a continuous

cortex over the thallus, erect, determinate, with a small number (3-10) of cells per filament. Terminal cell of assimilatory filaments markedly inflated, giving the surface of the thallus a "cobblestone" appearance under low magnification. *Hairs* borne on terminal subcortical cells with the assimilators, infrequent, often in groups, forming false fascicles (not derived from the same terminal subcortical cell, but rather from several adjacent ones). Hair filaments with a basal cell, a short meristem, and long (L/B about 3) cylindrical cells, with the visible cytoplasm restricted to a small region round the central nucleus.

Unilocular sporangia borne on basal cells of assimilatory filaments, ovoid, pyriform or subglobose, with a terminal pore and plug mechanism. A mucilage envelope is formed, at maturity, between the zooids and the outer wall, which is persistent after zooid discharge.

Plurilocular sporangia solitary or in corymbose groups on short sporangiophores from subcortical cells (uniseriate or biseriate), wall persistent, opening by a terminal pore. Both kinds of sporangia may occur on the thallus at the same time in some species.

Type species:- *Leathesia difformis* (L.) Areschoug.

A genus of perhaps 9 or 10 species in the north Pacific, north Atlantic and Australian regions with the type species widespread in cooler waters throughout the world. The numerous taxa from Japanese waters (see Inagaki 1958) may require revision. Two species are known from southern Australia.

Key to the genus *Leathesia* in Southern Australia.

1. Assimilatory filaments of 3-5 (-6) cells, broadly terete below with an inflated ovoid or pyriform terminal cell, 1½-2 times the diameter of lower cells; unilocular sporangia pyriform or ovoid.
. . . . (1) *Leathesia difformis* (L.) Aresch.

1. Assimilatory filaments with 5-10 (-15) cells, narrow terete below, with a much inflated spherical terminal cell, 4-6 times diameter of lower cells; unilocular sporangia globose to elongate ovoid.
. . . . (2) *Leathesia intermedia* Chapm.

(1) *Leathesia difformis* (L.) Areschoug 1847:154. De Toni 1895:442. De Toni & Forti 1923:79. Guiler 1952:78. Inagaki 1958:101. Kuckuck 1929:44, fig. 49-52. Lindauer, Chapman & Aiken 1961:220, fig. 44. Lucas 1909:18; 1929:48; 1936:102. May 1939:196. Setchell & Gardner 1925:511. Womersley 1967:230.

Figure 12,A; Plate 7, A; Pl. 21,C, Pl.22,A.

Thallus either epilithic or epiphytic on seagrasses and algae, forming a firm, mucose, somewhat verrucose and spreading bladder on rock or coralline turf in the lower eulittoral, or more or less globular and saccate on other substrates (from deep pools in the eulittoral into the sublittoral). Thallus 10-50 (-60)mm across, 10-15mm high, yellow-brown (Fig. 12.A5a, b, Pl. 21.C, Pl. 22.A).

Basal layer of small isomorphic cells in closely appressed radiating filaments. *Medulla* filamentous, composed of two zones of non-pigmented, anastomosing cells. Cells of the lower medulla cruciate with three to five (usually four) terete to inflated arms, those in the axis of growth usually longer than those at right angles, L/B 2-10, 15-30 µm in diameter, the whole structure giving the appearance of a net. Cells of the subcortex subglobose, smaller than lower medullary cells and grading in size with the smallest

cells terminal, 15-25 µm in diameter. Meristematic zone partly diffuse and partly at the margins of the thallus at the boundary between the subcortex and the assimilatory filaments.

Assimilatory filaments borne on terminal subcortical cells in groups of two or three, erect, determinate, of 3 to 5 (-6) cells; lower cells with a few discoid phaeoplasts, inflated cylindrical, L/B 1-1½ (-2 in longer filaments of epiphytic forms), 4-6 µm in diameter; terminal cell with numerous discoid phaeoplasts, ovoid to pyriform (especially in epiphytic plants), L/B 1-1¼ , 6-9 µm in diameter. A graded series can be shown from short three-celled assimilators with ovoid terminal cells ("α" form) on plants from the coralline turf (Koonya Bay, Vic.; ADU, A44619) to long, six celled, assimilators with pyriform terminal cells ("β" form) on plants epiphytic on *Posidonia* (Normanville, S. Aust.; ADU, A47844). Other epiphytic specimens, (e.g. Aldinga reef, on *Posidonia* sp.; ADU, A48248) show assimilators similar to the epilithic and coralline turf plants, and several specimens of the aplanate epilithic habit show the 5 or 6 celled long assimilators of the "epiphyte" form (e.g. Pt Westall, S. Aust.; ADU, A48889; Robe, S. Aust., ADU, A50209; or intermediate forms (e.g. Safety Cove, Tas., ADU, A49174). *Hairs*, in false fascicles, borne on terminal subcortical cells, infrequent, with a basal cell, a long meristem of 6-8 cells, and cylindrical cells above, L/B 5-8, 12-20 µm in diameter, the filament extending beyond the thallus up to 10mm.

Unilocular sporangia borne singly and laterally on the basal cell of an assimilatory filament, ovoid to pyriform, L/B 3-4, 15-25 µm broad (Fig. 12.A.1).

Plurilocular sporangia borne singly on a pedicel, lateral to assimilatory filaments or in twos and threes on a short sporangiophore on the terminal subcortical cell, uniseriate, branched, no longer than assimilatory filaments, with 6-8 loculi, opening by a terminal pore, wall persistent (Fig. 12.A2).

Type locality:- Sweden

Type:- ?

Distribution:- (in Australia) from Point Westall, Eyre Peninsula, to Eden, N.S.W., and around Tasmania. Recorded from cool temperate waters throughout the world.

Host range:- (in Australia) articulated members of the *Corallinaceae* (sensu lato); *Gracilaria* spp.; *Laurencia* sp.; *Cladostephus verticillatus; Heterozostera tasmanica; Amphibolis antarctica; Posidonia* sp.

Representative specimens examined:-

Extra-Australian: East Point Rocks, Nahant, Mass., U.S.A., on mussels (*John*, 23.vii.1977; ADU, A50351). Pebble Beach, Monterey Pen., Calif., U.S.A., on rock (*Womersley*, 31.vii.1969; ADU, A34716).

S. Aust.: Point Westall, on rock (*Skinner*, 30.xi.1977; ADU, A48889). Aldinga reef, on *Posidonia* sp. (*Skinner*, 14.xi.1977; ADU, A48248). Normanville, on *Posidonia* sp. (*Skinner*, 6.i.1977; ADU, A47844). Encounter Bay, on *Amphibolis antarctica* (*Skinner*, 7.xii.1976; ADU, A47816); on *Laurencia* sp. (*Skinner*, 28.ix.1977; ADU, A48268); on *Heterozostera tasmanica* (*Skinner*, 23.xi.1977; ADU, A48853); on rock (*Skinner*, 23.xi.1977; ADU, A48854). Robe, on rock (*Skinner*, 13.xi.1978; ADU, A50209).

Victoria: Nelson Bay, Portland, on rock (*Muir*, 10.i.1950; ADU, A15,791);

Apollo Bay, on rock (*Womersley*, 23.i.1969; ADU, A31,755; *Skinner*, 24.ii.1977; ADU, A47960). Point Lonsdale, on rock (*Skinner*, 4.i.1978; ADU, A49071). Queenscliff, on *Caulerpa* sp. (*Skinner*, 4.i.1978; ADU, A49061). Crawfish rock, Western Port Bay, on *Gracilaria* sp. (*Watson*, 27.viii.1971; ADU, A39442). Koonya Bay, on rock (*Womersley*, 15.i.1974; ADU, A44619). Waratah Bay, on *Cladostephus* sp. (*Sinkora*, 21.ii.1972; ADU, A42307).

Tasmania: Wivenhoe Point, on rock (*Bennett*, 31.i.1955; ADU, A20640). Ulverstone, on rock (*Gordon*, 18.i.1966; ADU, A30000). Bridport, on rock (*Wollaston & Mitchell*, 4.iii.1964; ADU, A27962). Orford, on rock (*Skinner*, 22.ii.1978; ADU, A49175). Safety Cove, on rock (*Skinner*, 21.ii.1978; ADU, A49174).

Inagaki (1958) recognizes two forms, *L. difformis* f. *difformis* for the epilithic and coralline turf epiphytic plants, and *L. difformis* f. *globosa* for the globose, saccate epiphytes on seagrasses and some algae. As indicated above, there is a gradient in the morphological differences in the cortical filaments which separate the two forms, and aplanate, convoluted, crassulate plants can be found in the situation where globose, thin, saccate plants are expected to occur (see Appendix IV).

Cultures:-

Although successful germination was achieved on two occasions (LA-I, ADU, A48627; LA-II; ADU, A49781), and the small filamentous plantlets thus derived grew well, sterile tufts resulted after four to six weeks.

Various attempts have been made to culture this alga (see Chapter I above), of which Dangeard (1964, 1965, 1969) is the most recent and comprehensive. However, it is clear from the published results that

the 'in vitro' plants are markedly dissimilar to the field plants, lacking the development of separate zones of medullary and cortical tissues and developing filiform assimilatory filaments with numerous cells and a terminal cell without inflation. Until close morphological correspondence can be achieved between field and 'in vitro' plants, it may be unwise to draw too many conclusions about life histories, as the 'in vitro' results may be artifacts of the culture procedures.

(2) *Leathesia intermedia* Chapman 1961:20, fig. 4. Lindauer, Chapman & Aiken 1961:221. Womersley 1967:230, fig. 6.

Figure 12, B; Plate 7, B, C, Pl. 22, B.

Thallus epiphytic on a wide variety of other algae, in pools of the eulittoral and sublittoral fringe, commonly solid and globose but may be irregularly lobed in larger specimens, mucose, to 25mm high and 20mm broad, brown (Fig. 12.B.1).

Basal layer a filamentous plate of small cells. *Medulla* with small subglobose cells immediately above the basal plate, supporting subdichotomous filaments of inflated pyriform or subcruciate cells, L/B 1-3, 60-120 µm in diameter, with occasional anastomoses, and a subcortex of more closely packed small subglobose cells supporting the cortex (Fig. 12.B.4).

Assimilatory filaments borne on terminal subcortical cells in groups of two or, more rarely, three, 10-15 cells long, the basal one truncated conical, then 8-13 terete cells with several phaeoplasts, L/B 1½-2, 5-6 µm broad, terminal cell pyriform maturing to spherical, with numerous small discoid phaeoplasts, 15-40 µm in diameter. *Hairs* borne singly on terminal subcortical cells, with a basal cell, a meristem of 8-10 (-15) cells and cylindrical cells above L/B 3-8, 6-8 µm in diameter (Fig. 12.B.2).

Unilocular sporangia on a one (rarely two) celled pedicel on terminal subcortical cells among assimilatory filaments or pedicellate and lateral on the basal cell of an assimilatory filament, globose to terminally rounded cylindrical, L/B 2-3, 25-30 µm in diameter, with a terminal pore and plug mechanism, wall persistent (Fig. 12.B.2).

Plurilocular sporangia on short corymbose sporangiophores, two to five or six in a group, uniseriate, filiform, with 8-12 loculi, 30-40 µm long, opening by a terminal pore, outer wall persistent (Fig. 12.B.3).

Plants may have both kinds of sporangia on the same thallus, usually occupying separate but contiguous sections of the one cortex.

Type locality:- Stewart I., New Zealand

Type:- Herb. Lindauer, CHR

Distribution:- From Robe, S. Aust. to Port Phillip, Vic., including the islands of Bass Strait, and Tasmania. Also New Zealand.

Host range:- *Caulerpa papillosa; C. cactoides; C. brownii, C. simpliciuscula; Perithalia caudata; Scytosiphon lomentaria; Zonaria augustata; Halopteris* spp.; *Caulocystis* sp.; *Sargassum* spp.; *Jania* sp.; *Laurencia elata; Plocamium augustatum; Polysiphonia decipiens; Ptilocladia pulchra; Gelidium australe;* and the seagrass *Amphibolis antarctica.*

Representative specimens examined:-

S. Aust:- Robe, S. Aust., on *Caulerpa simpliciuscula* (*Skinner*, 14.xi.1978; ADU, A50216); on *Ptilocladia pulchra* (*Skinner*, 14.xi.1978; ADU, A50217). Nora Creina, S. Aust., on *Perithalia caudata* (*Womersley*, 11.ii.1979; ADU, A50276). Port MacDonnell, S. Aust., on *Caulerpa papillosa* (*Parsons*, 25.i.1967; ADU, A31401).

Vic.:- Apollo Bay, Vic., on *Zonaria augustata* (*Parsons*, 23.i.1967;

ADU, A31410). Point Lonsdale, Vic., on *Caulocystis* sp. (*Skinner*, 4.i.1978; ADU, A49072). Point Roadknight, Vic., on *Plocamium augustatum* (*Skinner*, 6.i.1978; ADU, A49079). Queenscliff, Vic., on *Halopteris* sp. (*Skinner*, 4.i.1978; ADU, A49063).

Tas.:- Safety Cove, Tas., on *Gelidium australe* (*Skinner*, 21.ii.1978; ADU, A49179). Gordon, Tas., on *Polysiphonia decipiens* (*Skinner*, 24.ii.1979; ADU, A49180).

No New Zealand specimens available.

Of the closely related Japanese taxa *L. sphaerocephala* Yamada and *L. pulvinata* Takamatsu, a specimen of the former was kindly forwarded by Dr M.Kurogi(Akkeski, Hokkaido, on *Cystophyllum hakadatense* (Kurogi, 21.vi.1978; ADU, A49425)). In general all structures are smaller than those of *L. intermedia*, the terminal cell of the assimilatory filaments is distinctly pyriform, and the lower cells are inflated, forming a moniliform chain of cells rather than the terete filament of *L. intermedia*; otherwise the two species are very close(Pl. 7.C,D). The distinctions between the two Japanese taxa, as described by Inagaki (1958, p. 119), appear to be related to the habit of the plants and do not appear to be great. Without more specimens of both Japanese taxa, it is not possible to determine whether there is a real overlap between the three species.

5.4.3 *PETROSPONGIUM* Naegeli ex Kützing 1858:2, pl.3, fig. 2. J. Agardh 1882:44. Inagaki 1958:96. Lindauer, Chapman & Aiken 1961:222. Setchell & Gardner 1925:508.

Thallus epilithic, aplanate, foliose, radiating occasionally, epiphytic on other encrusting algae, perennial, spreading at the margins and dying back in the centre, dark brown to black.

Basal system rhizoidal. *Medulla* of branched filaments of closely appressed moniliform of cylindrical cells, giving rise to both rhizoids and hair filaments, rhizoids from lower cells, hairs usually on upper cells; terminal cells support cortex of

assimilatory filaments. Lacunae in older parts of the medulla may become filled with firm gelatinous material, cementing the filaments of the medulla.

Cortex divisible into an inner cortex of ovoid cells with little pigmented cytoplasm and an outer cortex of uniseriate or bifurcate, moniliform, determinate, *assimilatory filaments*, of four to ten cells, terminal cell not greatly inflated, pyriform.

Unilocular sporangia borne laterally on lower cells of assimilatory filaments, elongate reniform, opening by a terminal pore.

Plurilocular sporangia terminal on assimilatory filaments, multiseriate, known for *P. berkeleyi* only (Hanna 1899).

Type species:- *Petrospongium berkeleyi* (Greville) Naegeli.

Two species known, *P. berkeleyi* from the north Atlantic and Mediterranean, and *P. rugosum* (Okamura) S. & G. in the Pacific.

This genus is considered close to *Cylindrocarpus* Crouan & Crouan, and in recent works on European (Parke & Dixon 1976) and north Pacific American (Abbott & Hollenberg 1976) algae, *Petrospongium* has been submerged in that genus. The difference between the taxa involved can be seen in the table below. *Cylindrocarpus microscopicus* may well be better placed in the Ectocarpales, while the morphology of the two species of *Petrospongium* follows the same pattern as other members of the Corynophlaeideae. The two genera should be separated and *Petrospongium* retained.

TABLE V.iii

Comparison of *Cylindrocarpus microscopicus* with the two species of *Petrospongium*

Cylindrocarpus microscopicus	*Petrospongium berkeleyi*	*P. rugosum*
Unilocular sporangia terminal on medullary filaments; sessile, ovoid	Unilocular sporangia lateral at the base of assimilatory filaments, reniform, pedicellate	Unilocular sporangia lateral at base of assimilatory filaments, sessile, reniform
Medullary filaments with cylindrical cells	Medullary filaments with cylindrical to ovoid cells	Medullary filaments with ovoid to elongate ovoid cells
Rhizoidal filaments arise throughout the medullary filaments	Rhizoidal filaments are modified medullary cells	Rhizoidal filaments in lower medulla only
Plurilocular sporangia uniseriate, filiform	Plurilocular sporangia multiseriate, conical-terete	Not known
Whole thallus microscopic, epiphytic, pulvinate, of loosely interwoven filaments	Whole thallus macroscopic, epilithic, almost crustose, compact, with regularly arranged filaments. Distinct cortex and medulla.	Whole thallus macroscopic, epilithic, almost crustose, compact, with regularly arranged filaments. Distinct cortex and medulla.

5.4.4 *Petrospongium rugosum* (Okamura) Setchell & Gardner 1924:12; 1925:509, Pl. 39, figs 42 & 43. Inagaki 1958:97, figs 1-3. Lindauer, Chapman & Aiken 1961:222, fig. 46. MacLennan 1956:1, fig. 1. May 1947:273. Womersley 1967:231.

Cylindrocarpus rugosus Okamura 1907:20, Pl. 5, figs 1-6. Abbott & Hollenberg 1976:177, fig. 144.

Petrospongium berkeleyi Harvey in Hooker 1855:220.

Figure 12,C; Plate 7, E, F, Pl. 22, C.

Thallus epilithic, spreading, undulate aplanate, spongy, redbrown to very dark brown (Fig. 12.C.3).

Rhizoidal filaments arising from cells of the lower medulla, branched, forming a mat between the thallus and the rock; cells cylindrical L/B 5-10, 10-20 µm in diameter. *Medulla* of branched filaments, cells ovoid, uniform, L/B 1½-2½, lower cells closely appressed, with intercellular spaces gelatinized.

Assimilatory filaments borne on medullary filaments, determinate, forked once or twice, forming an even cortex; cells of inner cortex 7-10, ovoid, L/B 1½-2, 18-30 µm in diameter; cells of outer cortex 3-5 per fork, terete, densely pigmented, L/B 1-1½, 10-15 µm in diameter, terminal cell rounded. *Hairs* arise from cells of inner cortex or upper medulla, infrequent, narrow, with a basal cell, a long meristem, and cylindrical cells above, L/B 3-6, 5-8 µm in diameter.

Unilocular sporangia attached submedianally to basally to inner cortical cells, elongate reniform, L/B 3-4, 15-25 µm in diameter, opening by terminal rupture (Fig. 12, C.1,2). Inagaki (1958) illustrates *in situ* germination of the spores; this has not been observed in material examined. *Plurilocular sporangia* unknown.

Type locality:- Japan

Type:- S A P. ?

Distribution:- (in Australia) sporadic, from Apollo Bay, Victoria, to Port Hacking, New South Wales. Also recorded from New Zealand, Japan and the west coast of North America. Grows in the lower eulittoral to sublittoral on rock, and occasionally on limpets.

Representative specimens examined:- Apollo Bay, Vic. (*Womersley*, 23.i.1967; ADU, A31188). Point Roadknight, Vic. (*Skinner*, 6.i.1978; ADU, A49080). Point Lonsdale, Vic. (*Skinner*, 17.i.1979; ADU, A50231). Also La Jolla, Calif., U.S.A. (*Womersley*, 1.xi.1962; ADU, A25871).

5.5 Summary

The family Corynophlaeaceae can be divided into two tribes based both on the habit of the plants and the form of the medullary system. The tribe Myriactuleae contains the two endophytic genera with a ramifying rhizoidal system, *Strepsithalia* Sauv. and *Myriactula* Kuntze. The tribe Corynophlaeideae contains the four (or five) genera of epiphytic or epilithic plants with little or no rhizoidal system and a well developed medulla directly supporting the cortex of the plants, *Corynophlaea* Kütz., *Microcoryne* Strömf., *Leathesia* Gray, *Petrospongium* Naegeli (and *Cylindrocarpus* Crouan & Crouan). While this division is artificial it reflects the two distinct lines of development within the family.

The genus *Strepsithalia* Sauv. is included with the genus *Myriactula*, and not in the *Myrionemaceae* as has often been the case in the past, because of its similarity in form, especially the development of a sporangiophore for plurilocular sporangia, and the presence of secondary plurilocular organs lateral to the cells of cortical filaments,

at least in *S. clavata* sp. nov. This genus represents an advance in development from *Myrionema* towards *Myriactula*. The life history of *Strepsithalia liagorae* has again been investigated; the results obtained were similar to those of Sauvageau (1925a).

The genus *Myriactula* Kuntze continues to present difficulties as to the precise limits of species. *Myriactula rivulariae* is described as having three varieties in southern Australia, corresponding to the three taxa *M. rivulariae* (Suhr) Feldm., *M. chordae* (Aresch.) Levring and *M. arabica* (Kütz.) Feldm. The life history described for the last variety is direct and asexual, and so is similar to that of members of *Elachista*. The other taxon present in southern Australia corresponds to *M. haydenii* (Gatty) Levring.

The genus *Corynophlaea* Kütz. has three representatives in southern Australia, *C. cystophorae* J. Ag. (incl. *C. longifila* (Reinb.) Chapm.), *C. cristata* sp. nov. and *C. filiformis* sp. nov. The differences between these three species, and extra-Australian taxa, can most readily be demonstrated by examination of the structure of the medulla. Cultures of *C. cystophorae* were unsuccessful in obtaining a life history for this species, but demonstrated that both plurilocular and unilocular sporangia of the macrothallus produced zooids which germinated individually to give a microthallial plant. Some indication of regeneration of the macrothallus by microthalli derived from plurilocular sporangial zooids was found.

The genus *Leathesia* Gray contains the very variable, cosmopolitan species *L. difformis* (L.) Aresch. as well as *L. intermedia* Chapm., in southern Australia. Neither species responded well to culture.

The genus *Petrospongium* Naegeli, which is distinguished from *Cylindrocarpus* Crouan & Crouan by its macroscopic thallus and extensive medullary development, is represented by one species, *P. rugosum* (Okam.) S. & G., in southern Australia.

CHAPTER VI

GIRAUDYACEAE HYGEN 1934

6.1 The Giraudyaceae previously consisted of only one monospecific genus, but two further taxa are here placed in the family. The thallus has a compact or loosely filamentous fanlike or discoid basal plate, from which arise the multicellular erect axes (with cells in tiers of three or more) either directly (as in *Flabellonema codii* gen. et sp. nov.) or from a medulla of branched uniseriate filaments (as in the two species of *Giraudya*). The cells in the tiers of the erect axes are box-like and are arranged in more or less conformable ranks. The cells have numerous discoid phaeoplasts and a large nucleus. The meristem of the erect axis is a zone of cells between the medulla or disc and the first whorl of assimilatory cells. Hairs are exhibited by all three taxa; those of *Flabellonema* are terminal to erect axes, those of the two species of *Giraudya* may be terminal but are also formed laterally on the axes, or from the basal plate or the medulla.

Giraudya sphacelarioides Derbès & Solier, the oldest recognized taxon, had been placed in the Elachistaceae by most workers prior to Kylin (1933). There is an apparent relationship between *G. sphacelarioides* and the various members of the genus *Halothrix*, because both genera share the tapering erect assimilators, buttress rhizoids, a distinctive basal meristem to the assimilators, and, importantly, circumaxial plurilocular sporangial sori which involve the subdivision of the assimilatory cells into numerous sporangial mother cells. Sauvageau (1927, 1928) suggested that *G. sphacelarioides*, with its three kinds of plurilocular structures and its "polysiphonous"

erect axes, with basal rather than internal "medullary" cells (cf. Goebel 1878)[1] was sufficiently different from most other brown algae to warrant a separate family. Kylin (1933) removed *Giraudya* from the Elachistaceae and placed it in his Punctariales on account of its life cycle as then understood, but not in any particular family. Hygen (1934) created a family for *G. sphacelarioides*, the Giraudyaceae. Hamel (1937) placed the new family in the polystichous Ectocarpales near the Punctariaceae. Kylin (1947) placed the family Giraudyaceae before the Striariaceae in his (Kylin 1937) Punctariales. Papenfuss (1951) placed the Punctariales in an enlarged Dictyosiphonales, and included Giraudyaceae as the second family in that order.

The life history studies of Goebel (1878) and Sauvageau (1927), although not complete, indicate that *Giraudya sphacelarioides* has a similar kind of life history to that of *Striaria* and *Stictyosiphon*[2] (Caram 1965, 1966, 1972; Caram & Nygren 1970; Kornmann & Sahling 1973; Sauvageau 1929) and *Asperococcus* (Kylin 1933; Sauvageau 1929). The morphology of the polystichous axes of *Giraudya* is similar to juvenile axes in *Scytosiphon* and *Asperococcus* and also *Desmotrichum*. The lack of a medulla in the axis is an important distinction, but the four primary cells, with smaller subsidiary cells, seen in cross-section of erect axes of *Giraudya* (cf. Goebel 1878, Pl. 17, fig. 22, and Pl. 9, C below) suggest a developmental stage from *Myriotrichia* through *Giraudya* and towards the internal arrangement exhibited by members of the Striariaceae and Scytosiphonaceae (see Chapter VII below for a more detailed discussion of this point). The plurilocular

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1. Goebel, K. 1878: Pl. 7, fig. 22, 23, 24. Goebel implies from figures 23 and 24 that there is an internal medulla in the erect axis in *G. sphacelarioides*, which structure has not been revealed either under light or electron microscopy in the present study.

2. See also South and Hooper 1976.

sporangia in short linear sori are similar to those of many of the Dictyosiphonales *sensu lato*.

The family now contains two genera:-

*Giraudya** Derbès & Solier (2 species), and

Flabellonema gen.nov. (1 species)

Giraudya sphacelarioides occurs in the Mediterranean Sea, on both sides of the north Atlantic, and in southern Australian waters from at least Streaky Bay in the west to northern Tasmania in the east. *Giraudya robusta* sp. nov. has a similar range in southern Australia but extends further to the west, while *Flabellonema* has so far only been found in the Gulf of St Vincent, Encounter Bay and Kangaroo Island.

6.1.1. Key to the taxa of Giraudyaceae in southern Australian waters

1. Erect axes filiform, with two or three cells per tier; axes terminated by a single hair; basal plate monostromatic and fan-like; plurilocular sporangia of one kind only, intercalary or falsely terminal. *Flabellonema* gen.nov.
(1 species, *F. codii* sp. nov.)

1. Erect axes widest near the base and tapering terminally, with five to sixteen cells per tier; axes without hairs or with one to several terminal or lateral hairs; basal plate diffusely filamentous or discoid; plurilocular sporangia of several kinds, basal, lateral or in intercalary sori.
. . . . . *Giraudya* Derbès & Solier (to 2)

2. Erect axes with lateral single hairs and terminal fascicles of hairs; cells of erect axes four sided in face view, 10-12 (-15) cells/tier; basal plurilocular sporangia branched,

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* The orthography follows Sauvageau (1927, p. 1) and Papenfuss (1955).

lateral plurilocular sporangia in short sori developed from one or two assimilatory cells, and intercalary sori in upper sections of erect axes, involving several whorls of cells; no unilocular organs known. (1) *Giraudya sphacelarioides* Derbès & Solier

2. Erect axes with solitary lateral and terminal hairs, basal hairs (from the basal plate or medulla) also present; cells of erect axes with six sides in face view, cells in whorls of 5-7 (-9); basal plurilocular sporangia unbranched, lateral plurilocular sporangia solitary, no intercalary sori formed; unilocular sporangia basal, elongate ovoid.

(2) *Giraudya robusta* sp. nov.

6.2 *FLABELLONEMA* gen. nov.

Diagnosis:-

Thallus cum disco flabelliformi agnascante in externa hospite atque axibus patentibus paucis, ferrugineus; medulla abscenda (esse); axes filiformis cum duabus aut tribus cellulis in verticello et solo pilo terminale in axe; sporangiis unilocullariis ignotis; sporangia plurilocularia aut intercalaria aut subterminalia ovoidis multis cum loculis inflatis.

Thallus an irregular fanlike disc with a few erect axes, epiphytic on the outer surface of the host, red-brown.

Basal plate a single layer of closely appressed subdichotomous filaments of pigmented cells which divide more quickly along one margin, thus forming a fanlike structure on the host surface. The meristem is marginal and no medulla occurs. *Erect axes* arising from individual cells of basal plate behind the meristematic margin, filiform, terete,

patent, tapering very gradually, with cells in tiers of two or three, with numerous small, discoid phaeoplasts. *Hairs* terminal on erect axes, which taper to a single cell, with a short meristem and long cylindrical cells above, without phaeoplasts.

Unilocular sporangia unknown.

Plurilocular sporangia intercalary and formed subterminally on erect axes by the transverse and longitudinal division of two or sometimes all three cells of each whorl, for upwards of a dozen whorls, individual loculi inflated and opening by rupture.

Type species:- *Flabellonema codii* sp. nov.

Only one species, which has been found in southern Australian waters. The generic name is chosen for the fanlike form of the basal system (Φλαβιλλιον Gk. = Flabellum L. = a fan).

(1) *Flabellonema codii* sp. nov.

Thallus parvus; discus partim ex summa utriculis (*Codium mamillosum*) vestiens, flabelliformis; axes filiformis teretis humilior 5mm alto; cellulae axis, duas tresque in vertice, L/B 2-3, 15-25 µm longe atque 30-35 µm late.

Figures 13, 14; Plate 8, Pl. 23, A.

Thallus epiphytic, partially covering the tops of single utricles of *Codium mamillosum*, to 1.5mm across the disc and usually less than 5mm high in the erect axes, red-brown (Fig. 13.1, Pl.8.B).

Basal plate with cells trapezoid in face view, L/B 1-2, 8-15 µm in diameter, 3-5 µm thick, with numerous discoid phaeoplasts. The plate is fan shaped due to the differential meristem favouring growth along one side of the margin at the expense of the others. No *medulla* is formed.

Erect axes borne directly on individual cells of basal plate behind the meristem, occasionally branched, filiform, terete, tapering gradually to an apical rounded cell or hair, growth sub-apical; cells in tiers of two or three, L/B 1½-3, 15-25 µm in diameter, with numerous small discoid phaeoplasts and a single large central nucleus; short, upwardly recurved, laterals may occur, after damage of the tip. *Hairs* formed terminally on erect axes, with a meristem of 2-6 cells and cylindrical, non-pigmented cells above, L/B 3-5, 15-20 µm in diameter.

Unilocular sporangia unknown.

Plurilocular sporangia formed subterminally in erect axes or occasionally on lateral axes by the transverse and longitudinal division of two, occasionally all three, cells of from three to twelve or more tiers; the loculi are all of a similar size and each ruptures individually (Fig. 13.2b,d,e,3, Pl. 8.F).

Vegetative reproduction by the formation of a filamentous stolon-like filament, which forms a new fan, usually on a different part of the same host utricle, may also occur (Fig. 14.3, Pl. 8.C).

Type locality:- Stanley Beach, Kangaroo Island, S. Aust.

Holotype:- ADU, A20906 (*Womersley*, 6.ii.1957)

Host range:- *Codium mamillosum*

Distribution:- Type locality, Waterloo and Encounter Bays and the Gulf of St Vincent, S. Aust., in sublittoral reefs.

Representative specimens examined:- Type and Waterloo Bay, S. Aust. (*Womersley*, 13.i.1951; ADU, A13593). Seaford, S. Aust. (*Skinner*, 14.ix.1976; ADU, A47272). Lady Bay, Normanville, S.Aust. (*Skinner*, 5.vii.1977; ADU, A48123); (*Skinner*, 10.xi.1977; ADU, A48828*). Encounter Bay, S. Aust. (*Womersley*, 5.ii.1978; ADU, A49142).

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* Specimen used for culture.

Cultures:-

Several attempts were made to establish cultures of *Flabellonema codii*, but most were unsuccessful as release of zooids could not be readily induced. On one occasion (ADU, A48828) zooids were released in hanging drop culture and these germinated, without fusion, by a tube and formed loose filamentous plantlets which were sterile when an electrical fault in the culture chamber caused the loss of the culture.

Discussion:-

Plants of *Codium mamillosum* which may be carrying *Flabellonema* can be recognized in the field by a patch of reddish brown colour in the lower regions of the thallus. *F. codii* was first recognized by Professor Womersley on plants of *Codium mamillosum* from Waterloo Bay, South Australia, who placed it with and noted

the similarity in form of the erect axes to those of *Giraudya*, and the presence of intercalary plurilocular sporangia, which closely resemble the sori of plurilocular sporangia involving the whole upper axis in some plants of *G. sphacelarioides*.

These two morphological characters form the basis of the association of *Flabellonema* with the Giraudyaceae. The absence of a meristematic zone at the base of erect axes, together with apical growth and lateral branching of these axes, suggests the possible association of *Flabellonema* with the Sphacelariales. Another similarity with the Sphacelariales is the presence of ranked phaeoplasts in the cells of *Flabellonema*.

Prud'homme van Reine (1978) emphasizes that members of the Sphacelariales show an apical cell directly behind which new cells are formed, and that all taxa, with the exception of one tenuously

included family, react positively to staining with Eau de Javelle. Although growth is apical in *Flabellonema*, the apical cell, when present, does not behave in a *Sphacelaria*-like manner. When the apical tip is lost or damaged, the axis grows through the broken cell wall, and the apical cell is often replaced by a hair, reflecting the behaviour of both species of *Giraudya*. The cell walls of *Flabellonema codii* do not stain black in Eau de Javelle.

The basal meristem in species of *Giraudya* remains active only in the initial stages of growth of axes. Later extension of the axis may be either intercalary, by secondary lateral or longitudinal division of cells, or, especially in *G. robusta* sp. nov., apical. A single apical cell and lateral branching of axes occurs in *G. robusta*, but the lateral axes are biseriate with much further branching, rather than formed of tiers of cells similar to the main axis. Both species of *Giraudya* show some degree of alignment of phaeoplasts in axillary cells. These latter features are shown by *Flabellonema*.

It is therefore concluded that, until more is known of the life history of this taxon, *Flabellonema codii* should be placed in the family Giraudyaceae.

Flabellonema codii is one of several algae which exploit the outer utricle surface of *Codium mamillosum*. Although no great confusion is possible between *F. codii* and the various filamentous bluegreen algae or encrusting red algae, there is often present a microscopic (possibly undescribed) species of *Sphacelaria* with discoid basal system and descending biseriate filaments, with propagules, and infrequently branched erect axes, bearing unilocular sporangia, which in the sterile state may be confused with *F. codii*.

6.3 *GIRAUDYA* Derbès & Solier 1851:101. Hamel 1937:189; Kjellman 1897:221. Kuckuck 1929:28. Newton 1931:185. Sauvageau 1927:1.

Thallus pulvinate with free polystichous erect axes, arising directly or via a medullary stalk from a basal plate of radiating filaments, epiphytic on a number of hosts, especially on the blades of the seagrass *Posidonia*, often in large numbers, red-brown to brown.

Basal plate either compactly or diffusely discoid, of branched radiating filaments, single layered, adnate to host surface, cells isodiametric. *Medullary filaments* uniseriate, irregularly branched, subglobose or terete to pyriform depending on species.

Erect axes terete, polystichous, narrowed at the base and tapering terminally; cells in tiers. Transverse sections of erect axes reveal a group of three or four major cells with the common walls forming a cross, present alone in the tip area and immediately above the basal meristem, with slightly smaller cells cut off successively in the arms of the cross.[2] All cells with a large central nucleus and a number of large discoid phaeoplasts (with associated pyrenoids). Developing erect axes show a uniseriate zone of short, broad, meristematic cells immediately above the base of the axis, but upper cells retain the capacity of division. Thus secondary transverse walls may be formed, as well as lateral hairs and plurilocular sporangia, from these cells. Branching in the terminal region of erect axes of *G. robusta* is not uncommon. Buttress filaments terete, usually secund, arising from the cells below the meristematic zone

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2. A similar segmentation, except proceeding inwards to form the medulla, occurs in *Litosiphon yezoensis* Yamada & Nakamura according to Miyaji (1978, fig.11-16). This secondary division of cells may be thought of as the method of construction of most Dictyosiphonales *sensu lato*.

or the upper medulla of outer erect axes, more common in *G. sphacelarioides*. *Hairs* with a basal cell, a meristematic zone and cylindrical cells without phaeoplasts above, arising from the medulla or the erect axes, depending on the species.

Unilocular sporangia found only in *G. robusta*.

Plurilocular sporangia various, depending on species.

Microthallus discoid with uniseriate assimilatory filaments, long narrow ascocysts and hairs. *Plurilocular sporangia* uniseriate, filiform, opening terminally. Epiphytic on seagrasses, before macrothalli appear. As erect axes may arise directly from the microthallus the ploidy of the two phases is probably the same.

Type species:- *Giraudya sphacelarioides* Derbès & Solier.

A genus of two species, *G. sphacelarioides* from the Mediterranean, the channel coast of both France and Britain, the North Sea coast as far north as Denmark, and the New England coast of the United States, as well as southern Australia; and *G. robusta* sp. nov. from southern Australia.

(1) *Giraudya sphacelarioides* Derbès & Solier 1851:101.

Fritsch 1945:71. Hamel 1937:189, fig. 42. Kuckuck 1929:28, figs 19-25. Newton 1931:135. Sauvageau 1927:1. Womersley 1967:243.

Figure 15; Plate 9, Pl. 23, B.

Thallus epiphytic on the upper blades and flowerstalks of *Posidonia* species, and occasionally on Fucales, pulvinate with separate, polystichous, flexible axes arising from a narrow base, 2-15mm high, red-brown to brown.

Basal system monostromatic, either a discrete disc of small isodiametric cells or a loosely compacted, radiating, branched filamentous system, adnate to the host surface.

Medullary filaments (frequently absent in young plants) uniseriate, irregularly branched, cells weakly pigmented, subglobose, L/B 1-1½, 15-20 µm in diameter. The terminal cells of medullary filaments bear either the erect axes or the branched basal plurilocular sporangia.

Erect axes terete, filiform, tapering gradually above, to 10mm long, more or less flexile, polystichous. The base, below the meristem, consists of several tiers of two cells, without phaeoplasts, terete, L/B 2-3, 5-8 µm broad; meristem of 4-10 short, broad, cells, becoming less numerous as axis matures, L/B ½-½, 20-30 µm; assimilatory cells in tiers of 10-12 (-15), almost rectangular in face view, L/B 2-2½, 5-10 µm, with numerous large discoid parietal phaeoplasts and a large central nucleus. Secondary division of assimilatory cells may occur. Buttress rhizoids develop from the basal cells of erect axes and occasionally from cells of the medulla, usually on outer axes only, and in a secund manner; cells of rhizoids narrow cylindrical, L/B 2-5, 2-5 µm in diameter. *Hairs* either solitary and lateral on erect axes, often subtending sporangial sori, or terminal on erect axes and then fasciculate; with a short pedicel, a meristem of 4-6 cells and above terete cells L/B 3-8, 8-10 µm in diameter, without phaeoplasts. The number of hairs in the terminal fascicle depends on the number of cells in the terminal tier; where the axis is undamaged these may be a solitary hair or two to four hairs, but where damage has occurred larger numbers of hairs may be present.

Unilocular sporangia unknown. Newton (1931, fig. 81, C) appears to confuse young plurilocular sporangia in lateral sori with unilocular organs.

Plurilocular sporangia of three kinds (see below for notes on phenology).

(1) Basal plurilocular sporangia borne on upper medullary cells near the bases of erect axes, multiseriate, bifurcate or trifurcate, each branch more or less elongate-ovoid, coalescent at the bottom, about 80-100 µm long and 5-18 µm broad (Fig. 14.8, Pl. 9.B,F).

(2) Individual lateral plurilocular sporangia in sori which develop from one to four assimilatory cells in a rank, in the middle and lower erect axis; each sporangium multiseriate, terete to conical-terete, 10-15 µm long and 4-5 µm broad; sorus often subtended by a hair (Fig. 14.7, Pl.9.D).

(3) Sporangia in intercalary sori involving several tiers of assimilatory cells in upper erect axes; each sporangium uniseriate, short, with a very small number of loculi, in groups of 4 to 8, involving the subdivision of the outer surface of an assimilatory cell (Fig. 14.6, Pl. 9.E).

The description by Womersley (1967) of a fourth kind of plurilocular sporangium was due to confusion between this and the following species, to which plants with that kind of sporangium are now referred.

Microthallus as described for the genus.[3] Found on *Posidonia* blades prior to the reappearance of the macrothallial stage.

Type locality:- France.

Type:- ?

Distribution:- The Mediterranean, English Channel and the North Sea, the New England (U.S.A.) coast and from Eyre Peninsula

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3. It is not at present possible to ascribe microthalli to one or other taxon with certainty, except when the microthallus acts as a base for new erect axes.

to nothern Tasmania in southern Australia.

Host range:- *Posidonia* species; *Cystophora brownii*.

Representative specimens examined:- American River inlet, Kangaroo I., S. Aust., 2-3m deep (*Kraft, Johnson & Wickes*, 16.iv.1973; ADU, A43735). Troubridge Light, S. Aust. 17m deep (*Shepherd*, 4.ii.1969; ADU, A33441). Myponga Beach, S. Aust., 3-4m deep, on *Cystophora brownii* (*Mazola*, 23.x.1977; ADU, A48591). Aldinga reef, S. Aust. (*Skinner*, 16.viii.1977; ADU, A48226, A48230), (*Skinner*, 25.vii.1978, 4.viii.1978, 15.ix.1978, 31.x.1978; ADU, A49433, A49504, A49557, A49782 resp.). Portsea, Vic. 5-6m deep (*Kraft & Ricker*, 12.v.1978; MELU, s.n.). Bridport, Tas. (*Skinner*, 23.ii.1978; ADU, A49181). For a more complete list of specimens see Appendix V, giving the data for comparison by statistical analysis of *G. sphacelarioides* and *G. robusta*.

The group of four specimens from Aldinga reef (ADU, A49433, A49504, A49557, A49782) provide a sequential set of collections, upon which the following phenological comments are largely based. The earliest erect axes which are usually less than 5mm high show little or no medullary development and only lateral sori. Within the first month of growth the erect axes become much more numerous and longer, and the longest axes, while showing lateral sori in lower sections of the axis, have intercalary sori which involve much of the upper axis. The basal sporangia appear later, after the formation of the medulla. This is a general pattern but numerous exceptions can be found. Some plants show all three kinds of sporangia at the same time. (Table VI.i)

TABLE VI.i

ALDINGA REEF, S. AUST. *GIRAUDYA SPHACELARIOIDES*

Specimen No. & Date	State of erect axes; incl. length and width	Kind and commonness of plurilocular organs
A48226 16.viii.77	c. 4mm; narrow; 8-10 cells/whorl.	long active sori to tips common, with some multi-seriate lateral sporangia
A48245 14.ix.77	c. 4mm; a little broader; 9-16 cells /whorl.	sori common - with sometimes second lot of sporangia
A48579 14.x.77	5-8mm; broad (+new narrow ones); + 16 cells/whorl	whole sections of axis a sorus, v. common
A48636 26.x.77	→ 8mm; broad; → 16 cells/whorl	older plants = upper 1/3 = sorus; younger plants numerous scattered sori
A49433 25.vii.78	2.5-3mm; narrow; 5-10 cells/whorl	sterile
A49504 4.viii.78	c. 4mm; narrow; 8-10 cells/whorl	mainly lateral sori
A49557 15.ix.78	→ 8mm; variable, but narrow; 10 + cells /whorl	lateral sori + young whole axial sori
A49782 31.x.78	→ 10mm; broad, 16 cells / whorl	mostly whole axis sori, some lateral sori.

Cultures:- Figure 19, A: Plate 15.

The life history of *Giraudya sphacelarioides* is complicated by the presence of three different forms of plurilocular sporangia on the macrothallus. No other brown alga displays this phenomenon. Sauvageau (1927) isolated zooids from each of these sporangia, and described their germination and the growth of the prothalli, with, in some cases, the production of narrow, erect axes with only one or two cells in each tier. He did not complete the life history.

Results:-

Three cultures of *G. sphacelarioides* were successfully established. Culture AG-I (A48226, Aldinga reef, S. Aust. 16.viii.1977) was established from sporangia from lateral sori. Settling and germination of negatively phototrophic zooids occurred within 24 hours of excision of sori. There was no fusion of zooids. Both amoeboid germination leading to pseudo-discoid plants and tubular germination leading to filamentous plants occurred. Both forms produced very fine hairs (narrower than hairs of field plants) as the first erect processes (after 6 days). New, broader hairs appeared on the little cushion-like plants by the twentieth day, as well as basal sporangial initials. After one month, new plants, similar to the cultured plants from which they came, were present in the cultures. After 3½ to 4 months in culture normal erect axes were observed at the margins of older plants.

Culture GA-II (ADU, A49504, Aldinga reef, S. Aust., 4.viii.1978) was established from plurilocular sporangia of lateral intercalary sori. Culture GA-III was established from multiseriate plurilocular sporangia of plants collected from the same site on the same date. As no difference was found in the germlings from these cultures, the culture was not treated as two, and the results will be discussed together. Following the successful administration by Pedersen (1968,1973) of Kinetin to cultures of *Ectocarpus siliculosus* and other small browns, to obtain the production of normal erect processes,

20μM Kinetin was added to the Provasoli's Enriched Seawater in which the cultures were established. Germination and early growth followed the pattern shown in AG-I. Production of healthy erect axes with all three forms of plurilocular organs occurred within the first month of growth. The products of these sporangia were similar to the parents. This establishes that an asexual life history is the predominant one, at least from lateral and intercalary sori.

(see Table VI.1.9 and B)

Culture GA-V (Aldinga reef, S. Aust., 31.x.1978; ADU, A49782) was conducted under four temperature/day length systems, with Provasoli's Enriched Seawater with and without added hormones. The zooids were derived from sporangia in lateral sori. Both tubular and amoeboid germination occurred, in about equal proportions, tubular germination being marginally more frequent. The plantlets were either filamentous and tuft-like when derived from tubular germination or pseudodiscoid when derived from amoeboid germination. After a very short period (9 days), the subsamples having been transferred to the various growth conditions, erect axes began to appear on plantlets in all subsamples. Two forms of erect processes could be distinguished; erect axes, similar in form to axes on field plants but with fewer cells per tier, on plants grown under long days, and, in both day lengths, irregularly biseriate filaments, showing determinate growth. Erect axes were present in short day samples after a further two weeks of growth. The plants became fertile rapidly, displaying first basal and lateral sporangia, and subsequently intercalary sporangia (an apparent reversal of the phenology of the parent plants). The influence of hormones, besides Kinetin which was present in the germination medium, was to enhance the speed of development, sometimes leading to less well

TABLE VI.1.A.

GIRAUDYA SPHACELARIOIDES, GA-V, WITHOUT HORMONES

	16°C, 8:$\overline{16}$ h	16°C, 14:$\overline{10}$ h	20°C, 8:$\overline{16}$ h	20°C, 14:$\overline{10}$ h
after 18 days	discoid plants erect filaments; no erect axes			discoid plants with erect axes
	tuft-like plants, hairs terminal on erect filaments, basal conical plurilocular sporangia; no erect axes	tuft with well developed erect axes, 300-500 µm long; terminal hairs; no sporangia	tuft with narrow erect axes, similar to 16°C, 14:$\overline{10}$ h. No sporangia	tuft with erect axes (800-1000 µm long) and intercalary sporangia
after 26 days	disc and tuft - no erect structures			discoid plants with erect axes and intercalary plurilocular sporangia.
		tuft with normal erect axes, long and inflated; sporangia intercalary and plurilocular	tuft with narrow erect axes and filiform filaments (not frequent); sporangia intercalary and plurilocular	tuft plants like the discs, with some erect axes showing secondary meristematic zone and new erect axes above the older ones.
after 32 days	infertile discs and tufts			disc and tuft plants, very rapid growth, highly fecund, many axes with secondary stolonlike meristems.
		tuft plants with normal growth. New plants tuft-like.	tuft plants with narrow normal erect axes. New plants tuft-like or discoid.	
after 39 days	disc plants with normal erect axes, new plants of either form. tuft sterile	tuft plants, new and old, normal and healthy	tuft plants (older) normal. New plants of both types normal.	plants of both types and generations normal, with stolon-like behaviour of erect axes. Signs of nutrient depletion.

TABLE VI.1.B.

GIRAUDYA SPHACELARIOIDES, GA-V, WITH THREE HORMONES

	16°C, 8:$\overline{16}$ h	16°C, 14:$\overline{10}$ h	20°C, 8:$\overline{16}$ h	20°C, 14:$\overline{10}$ h
after 18 days	disc myrionemoid, erect filaments and hairs			disc plants with erect axes
	tuft with initial erect axes; conical basal plurilocular sporangia	tuft sterile with only erect biseriate filaments and hairs	tuft with broad erect axes, and hairs and filaments.	tuft with erect axes; both plant kinds with lateral sori of plurilocular sporangia
after 26 days	very narrow erect axes (2-5 cells/tier) on both kinds of plants. Immature lateral sori of plurilocular sporangia	no erect axes; irregular plurilocular sporangia on tuft.	tuft with narrow erect axes with intercalary plurilocular sporangia	disc and tuft plants; secondary meristems in erect axes. branching where lateral sori were; new plants with erect axes and basal sporangia.
after 32 days	infrequent fertile axes - most of tuft is filaments	no erect axes. New plants similar to parents	both generations with narrow erect axes and intercalary plurilocular sporangia	signs of nutrient depletion. Plants similar to previous observations.
after 39 days	tuft plants only in original stock. New stock with some myrionemoid plants, these with erect axes with intercalary plurilocular sporangia.	both generations of tuft plants; some juvenile erect axes	plants similar to previous observations	plants similar to previous observations.

formed plants. The occurrence of secondary meristems in erect axes, with subsequent stolon-like behaviour (as noted for *Elachista orbicularis* above) was noted in 20°C, 14:$\overline{10}$ h subsamples both with and without hormones.

Among the plants derived from the zooids released by the cultured plants were plants which developed a discrete, ordered disc (Pl. 15.D,F). These were most frequent among zooids derived from long-day plants. These plants supported erect axes in the same fashion as the parent plants, often without the filamentous erect processes. The most interesting feature is that they bore basal uniseriate filiform plurilocular sporangia, and ascocysts. Before they produced erect axes, they were similar in morphology to "*Ascocyclus*" plants found on *Posidonia* at times of the year when normal tuft macrothalli were absent. Careful germination of zooids from these sporangia showed no fusion of zooids, but both amoeboid and tubular germination. The amoeboid germlings retained the discoid form to maturity.

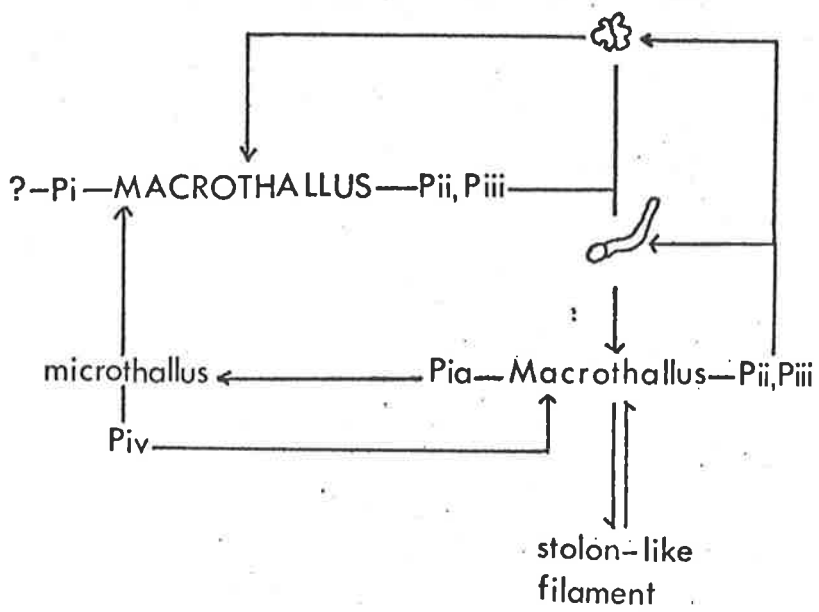
A subsequent experiment involving plants derived from GA-V, indicated that at 16°C, 14:$\overline{10}$ h, with 1.7 ug.l^{-1} Indole Acetic Acid added to the medium (in the absence of other hormones), the plants derived from discoid parents, either tubular or discoid in origin, resembled very closely ordinary field plants (compare Pl. 16.D,E,F).

No cultures were successfully established from basal plurilocular sporangia of field plants.

Summary:-

From these experiments, an asexual life history can be established for *Giraudya sphacelarioides*, involving the two forms of sporangia on erect axes. The life history is direct, but the germlings require an external source of Kinetin for the promotion of formation of erect

axes, and a source, internal or external, of IAA for the maintenance of habit. The growth rate of the plant is promoted by long days, in a water temperature between 16° and 20°C, which after extended growth promotes the release of zooids which form a fertile *"Ascocyclus"* stage. This later stage may either give directly the macrothallus or reproduce itself and subsequently produce the macrothallial stage. The opportunity to test the behaviour of the *"Ascocyclus"* stage at lower temperatures was not available. It is interesting to note that both Sauvageau (1927) and Feldmann (1937) comment that *Giraudya sphacelarioides* grows on *Ascocyclus (= Myrionema) orbicularis* and not directly on the blades of *Posidonia*.



Textfigure VI.i. Life history diagram for *Giraudya sphacelarioides*.
Pi = basal; Pii = lateral sori; Piii = intercalary sori;
Pia basal (culture); Piv uniseriate plurilocular sporangia.

(2) *Giraudya robusta* sp. nov.

Giraudya sphacelarioides Womersley 1967:243, in part.[1]

Diagnosis:-

Thallus epiphyticus, plerumque in laminas *Posidonia*, pulvinatus, ad 8mm altus; axes patentes, teretes, contrahentes, cum base inflato super meristeme, interdum multa in fila biseriata subtermine radians; pili soli base, laterale aut terminale; sporangia unilocularia ad basem axis, elongato-teretia; sporangia plurilocularia basalia multiseriata elongato-teretia, L/B 5-8; lateralia usque ad *Ectocarpus*.

Figures 16, 17; Plate 10, Pl. 23, C.

Thallus pulvinate with individual, patent, polystichous, erect axes on a short, sometimes forked, medullary stalk or occasionally sessile, up to 6 (-8)mm high, yellow brown to brown. Epiphytic on seagrasses or occasionally fucoids, from deeper eulittoral pools to 15m deep.

Basal layer monostromatic, usually a plate of loosely appressed, irregularly branched, radiating uniseriate filaments, or, infrequently, a compact disc, adnate to the host surface, from the small isodiametric cells of which arise the medullary filaments.

Medulla of loosely aggregated subdichotomous filaments of weakly pigmented cells; cells terete below, becoming pyriform to ovoid above, L/B 1-6, 20-35 µm broad. The medulla forms a short (1-2mm) erect stalk, sometimes once or twice forked, with occasional lateral erect axes and a terminal group of radiating erect axes. Immediately below the bases of erect axes one or two rows of colourless, reniform, "buoyancy" cells are formed lateral to the main axis of the medullary filament; these anastomose with nearby cells (cf. medullary cells of species of *Gobia* and *Dictyosiphon*, Rosenvinge & Lund 1947)(Fig. 17.2). Filiform, terete,

1. In later collections Womersley recognized the distinctiveness of *Giraudya* plants with unilocular sporangia and the "fourth" kind of plurilocular sporangium. The name *robusta* describes the rigidly erect habit of the whole thallus.

rhizoidal filaments sometimes are produced in the upper medulla or near the bases of erect axes.

Erect axes patent, conical-terete, basally inflated and tapering rapidly to a terminal cell or hair. The base of the erect axis is narrowed and consists of tiers of two or three cells below the meristematic zone; the meristematic zone, which persists to maturity but not beyond, has a row of 5 or 6 short broad cells, 30-45 µm wide, from which the inflated tiers are formed; beyond the inflated "bulb" the axis tapers rapidly. The assimilatory cells are arranged in tiers of 5-8 (-9); cells are six-sided in face view, L/B 1½-2½, 15-30 µm in diameter, with numerous parietal discoid phaeoplasts and a large central nucleus. In mature plants, uniseriate or biseriate branched filaments, bearing hairs and plurilocular sporangia, may arise from just below the tip of erect axes (Fig. 17.6, Pl. 10.A). *Hairs* are borne on the basal plate, laterally from the medulla and at the bases of erect axes, and also laterally and terminally on the erect axes; always solitary, they have a basal cell, a short meristem, and above terete cells, without pigmented cytoplasm, L/B 3-8, 15-25 µm broad.

Unilocular sporangia borne on medullary cells at the base of erect axes, ovoid, pedicellate, L/B 3-6, 30-40 µm in diameter, with a terminal pore and plug, wall persistent (Fig. 16.1, Pl. 10.C).

Plurilocular sporangia of two kinds:

(1) elongate, conical-terete, basal plurilocular sporangia, multiseriate, L/B 8-12, 10-20 µm wide, borne laterally to the bases of erect axes (and resembling the new erect axes); and (Fig.16.2, Pl.10.D)

(2) elongate ovoid to conical, pedicellate plurilocular sporangia L/B 2-4, 25-30 µm wide, formed laterally on assimilatory cells (Fig.16.3,4, Pl.10.E,F.)

of erect axes, or on the cells of the subterminal branching systems of erect axes.

Microthallus, as for the genus, on *Posidonia* species, found prior to the appearance of new macrothalli.

Type locality:- Pennington Bay, Kangaroo I., S. Aust.

Holotype:- ADU, A20123 (*Womersley*, 11.ii.1956).

Distribution:- From Cape le Grand, near Esperance, to Bridport in Tasmania (no records from the Victorian coast).

Host range:- species of *Posidonia; Amphibolis antarctica; Scaberia agardhii;* and species of *Sargassum*.

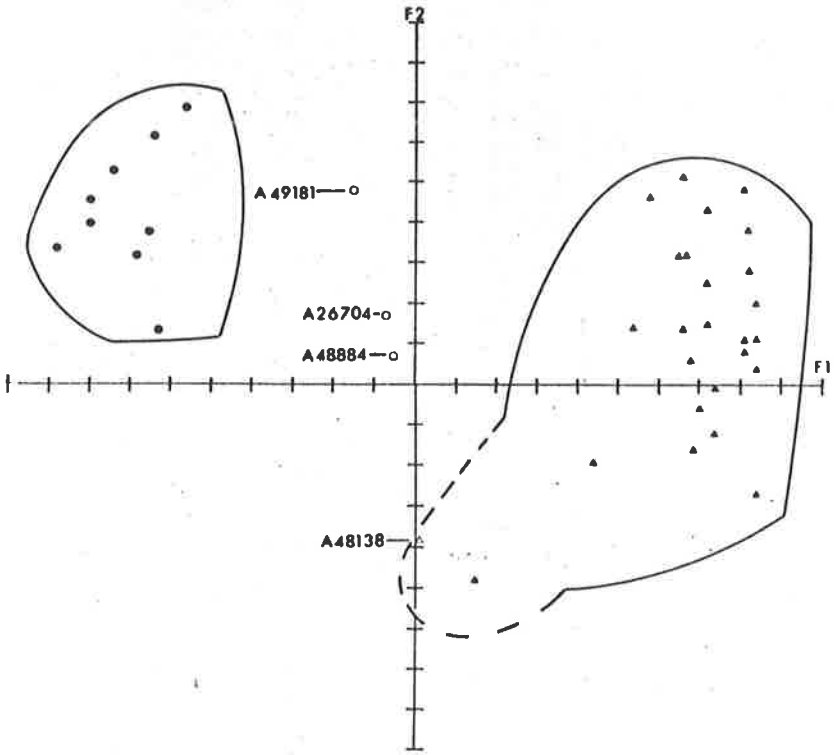
Representative specimens examined:- Type material and North Twin Peaks I., Archipelago of the Recherche, W. Aust. (*Willis*, 20.xi.1950; ADU, A15860). Lucky Bay, Cape le Grand, W. Aust. (*Woelkerling*, 30.i.1978; ADU, A49268). Petrel Bay, St Francis I., 3m deep (*Shepherd*, 7.i.1971; ADU, A38425). Arno Bay, S. Aust. (*Skinner*, 5.xii.1977; ADU, A48915). Tipara reef, S. Aust., 11m deep (*Shepherd*, 31.x.1970; ADU, A37653); 5m deep, on *Sargassum* sp. (*Shepherd*, 11.i.1978; ADU, A49400). Stanley Beach, Kangaroo I., S. Aust. (*Womersley*, 27.i.1957; ADU, A20821). Antechamber Bay, Kangaroo I., S. Aust. (*Womersley*, 25.i.1948; ADU, A8195). Barkers Rocks, Yorke Peninsula, S. Aust. (*Womersley*, 24.ix.1967; ADU, A31963). Aldinga reef, S. Aust. (*Skinner*, 26.x.1977; 31.x.1978; 15.ix.1978; ADU, A48637, A49783, A49558). Normanville, S. Aust. (*Skinner*, 14.ix.1977, 16.viii.1977; ADU, A48243, A48227), on *Scaberia* sp. (*Skinner*, 12.x.1977; ADU, A48575). Encounter Bay, S. Aust. on *Amphibolis antarctica* (*Skinner*, 28.ix.1977; ADU, A48262). Bridport, Tasmania (*Skinner*, 23.ii.1978; ADU, A49182).

As *Giraudya robusta* and *Giraudya sphacelarioides* commonly occur

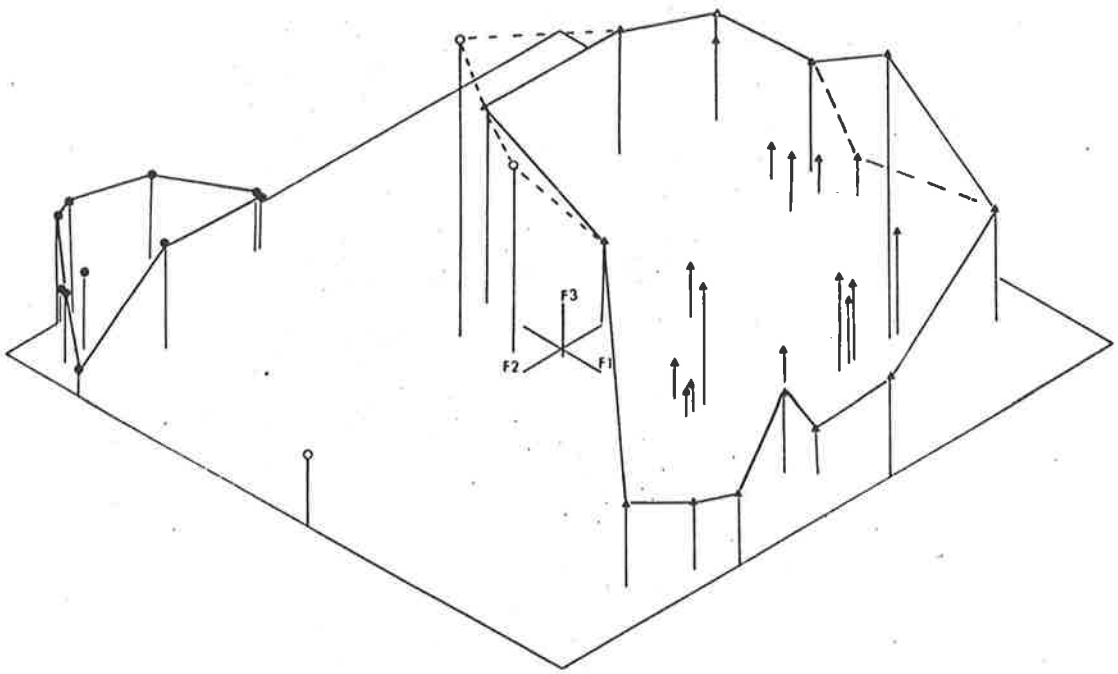
together on their hosts, and considerable confusion is possible between juvenile plants, it was decided to subject the 51 specimens available at the time to principal components analysis. The data sheets for this will be found in Appendix V, below. The results showed two clumps (Graph A, p.165) which corresponded with *Giraudya sphacelarioides* and *G. robusta* respectively, with five unaligned specimens. Two of these (ADU, A49181, and ADU, A29636) while showing basal hairs in the former case and rectangular cells in filiform axes in the latter case, could be assigned to one or other species on sporangial morphology. ADU, A48138 is a very young plant, but has more in common with *G. robusta* than *G. sphacelarioides*. The two remaining specimens, ADU, A26704 and A48884, possess vegetative characters which would place them in *G. sphacelarioides*, but have solitary lateral plurilocular sporangia similar to those found in *G. robusta*. These two specimens have been left as possible hybrid forms (Graph B).

For field recognition, those plants which remain erect after removal from the water, are a darker brown and may appear to be stalked and hairy, are usually *Giraudya robusta*. Plants with flaccid, lighter brown erect axes, which are often longer than the stiffly erect plants, are usually *Giraudya sphacelarioides*. However, microscopic examination is always necessary, as *Sphacelaria biradiata* and *S. furcigera* may also be found on *Posidonia* on occasions, and neither species of *Giraudya* is wholly consistent in the characters given above.

On sterile plants, usually juvenile, which may occasionally be encountered, the presence of a bulbous swelling of the erect axis above the meristem, cells with a six-sided face view and either a solitary terminal hair or rounded terminal cell, together refer the specimen to *Giraudya robusta*. Where there is no inflation of the cells in the tiers immediately above the meristem, these cells are rectangular in



Graph A. Two-Factor grouping of specimens of *Giraudya*.



Graph B. Three-Factor grouping of specimens of *Giraudya*, singleton is A49181.

Key:- ●,○ *G. sphaeelarioides*
▲,△ *G. robusta*

face view, and the erect axes have fascicles of hairs at the tip, the specimen is likely to be *Giraudya sphacelarioides*.

When fertile plants are collected, those with intercalary or lateral sori of plurilocular sporangia on erect axes, or branched basal plurilocular sporangia are *Giraudya sphacelarioides*. Specimens with unilocular sporangia, or terete unbranched basal plurilocular sporangia are *Giraudya robusta*. Specimens which have branched development of the terminal region of erect axes with discrete lateral plurilocular sporangia either from the cells of the erect axes or on the distromatic filaments of the branches, and agree in vegetative characters with *Giraudya robusta*, are that species. As noted above, hybrid specimens display lateral plurilocular sporangia from cells of erect axes, but agree in vegetative characters with *G. sphacelarioides*.

Culture studies:- Figure 19, B; Plate 16.

Giraudya robusta has, as stated above, two forms of plurilocular sporangia, essentially similar, and unilocular sporangia. The macrothallus may bear all three forms of sporangia at once, and separation of the basal plurilocular sporangia and the unilocular sporangia is extremely difficult.

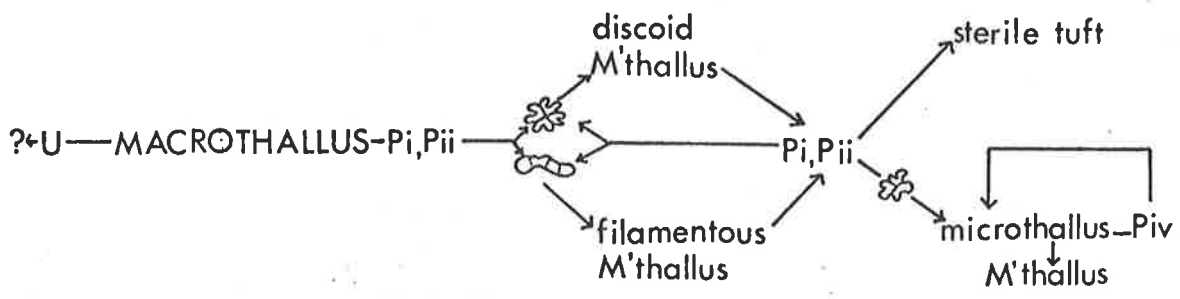
Four cultures of *Giraudya robusta* have been obtained successfully. The first two cultures, grown in Provasoli's Enriched Seawater, were obtained from ADU, A47500, and A48227, collected on 27.x.1976 and 16.viii.1977 respectively at Normanville, S. Australia. The lateral plurilocular sporangia were used, and the results were similar. GSL-I (= GR-I) showed a predominance of tubular-germinated, filamentous plantlets. After one month, basal plurilocular sporangia and poorly developed erect axes were present; the second generation plantlets were similar to the first generation parents. Both plants never reached field form.

GR-II subsamples failed to show high germination rates. However, three subsamples were obtained. These grew from tubular germlings into small filamentous plants which after sixteen days showed erect filaments with occasional longitudinal divisions of the cells, and basal plurilocular sporangia, as well as hairs. These plants were fertile and produced similar plants.

Culture GR-III (ADU, A48859, Aldinga reef, 23.xi.1977) was grown in Provasoli's Enriched Seawater with 20 uM Kinetin. The basal plurilocular sporangia were the source of inoculum. The zooids showed tubular or amoeboid germination, which resulted in essentially similar filamentous plantlets. However, within the first month new erect axes and basal plurilocular sporangia had developed from the filamentous plantlets. These plants went on to reproduce themselves in a similar manner.

Culture GR-IV (ADU, A49783, Aldinga reef, 31.x.1978) was set up similarly to GA-V above. The long day treatments with added hormones were the first subsamples to produce new erect axes. The occurrence of the *"Ascocyclus"* stage was in the long day cultures, after several weeks of culture. Unilocular sporangia developed on 16°C, 14:$\overline{10}$ h plants, but were of a deformed nature. No plants showed production of a medullary stalk.

The life history, at least that part not involving the unilocular sporangia, is a direct one, wholly asexual. The "Ascocyclus" stage - which has been collected on host plants in the late winter - may be an over-wintering strategy, to avoid loss of plants during the heavier winter seas.



Textfigure VI.iii Life history diagram for *Giraudya robusta*.
Pi = basal plurilocular sporangia; Pii = lateral plurilocular sporangia; Piv = uniseriate plurilocular sporangia.

TABLE VI.2.A.

GIRAUDYA ROBUSTA, GR-IV, WITHOUT HORMONES

	16°C, 8:$\overline{16}$ h	16°C, 14:$\overline{10}$ h	20°C, 8:$\overline{16}$ h	20°C, 14:$\overline{10}$ h
after 18 days	tuft plants - only erect filaments, hairs common, occasional conical basal plurilocular sporangia	tuft plants - long erect filaments and hair; sterile	discrete tuft plants with interconnecting filaments; hairs long erect filaments, initial erect axes; occasional plurilocular sporangia	tuft plants with branched long filaments, hairs and common plurilocular sporangia; initial erect axes.
after 26 days	new narrow erect axes, without leading hairs; plurilocular sporangia on base of plant.	disorganized erect axes, with sub-terminal hairs.	some narrow erect axes; sterile	disorganized erect axes; sterile
after 32 days	little change; erect axes with only two or three cells/tier	still disorganized erect axes; a few plurilocular sporangia	occasional initial normal erect axes; most plants tuft only	old plants with narrow erect axes (of 2-3 cells/tier), and plurilocular sporangia. new generation plants with myrionemoid base.
after 39 days	occasional erect axes, plurilocular sporangia. new generation plants tuft-like	some new normal erect axes; plurilocular sporangia. new generation plants tuft-like with basal plurilocular sporangia	little change new generation plants also tuft-like	old plants normal (nutrient depletion) new generation plants normal - with myrionemoid base.

TABLE VI.2.B.

GIRAUDYA ROBUSTA, GR-IV, WITH HORMONES

	16°C, 8:$\overline{16}$ h	16°C, 14:$\overline{10}$ h	20°C, 8:$\overline{16}$ h	20°C, 14:$\overline{10}$ h
after 18 days	tuft-like plants; initial erect axes, hairs common, occasional plurilocular sporangia	tuft-like plants short, robust erect filaments; hairs; sterile	tuft-like plants; long erect filaments; hairs; sterile	tufts; initial erect axes; branching erect filaments; hairs; common plurilocular sporangia
after 26 days	narrow erect axes, without terminal hairs; basal plurilocular sporangia	some normal erect axes; hairs basal or subterminal; basal plurilocular sporangia	rare narrow erect axes; sterile	initial erect axes only; branched erect filaments; basal plurilocular sporangia
after 32 days	little change	highly fecund normal plants, with some branching of erect axes. new generation plants similar to parent plants	little change	little change in older plants. new generation plants both myrionemoid and tuft-like
after 39 days	initial erect axes, with basal plurilocular sporangia new generation plants similar to parent plants.	lateral and basal plurilocular sporangia, and branching of erect axes. new generation plants similar to parents	little change	little change in older plants. new generation plants of myrionemoid plants with ascocytes = to "*Ascocysts*". New tufts also present.

6.4 Summary

The family Giraudyaceae has been expanded by the addition of one new monospecific genus, *Flabellonema*, and a new species of *Giraudya*, *G. robusta*. *Giraudya sphacelarioides* and *G. robusta* occur in similar habitats in southern Australia growing mainly on the blades of the seagrass, *Posidonia* spp.

Flabellonema codii gen. et sp. nov. is a semi-macroscopic epiphyte, growing on the utricles of *Codium mamillosum*. It has a fan-like basal disc and branching erect axes with tiers of two or three cells each. Only plants with plurilocular sporangia have been found. No successful cultures of this taxon have been achieved.

The southern Australian race of *Giraudya sphacelarioides* is morphologically very similar to the European plant of that name. Culture studies reveal an asexual life history involving both a direct regeneration of the macrothallus and the development of an "Ascocyclus" - like microthallus which either subsequently supports normal erect axes or regenerates the macrothallus via zooids from uniseriate plurilocular sporangia.

Giraudya robusta differs from *G. sphacelarioides* in developing a medullary system which supports patent erect axes with tiers of five to nine cells, which are six-sided in face view. The reproductive organs included elongate-ovoid unilocular sporangia, and two forms of discrete, terete, almost conical, multiseriate plurilocular sporangia. Although the products of the unilocular sporangia were not obtained in culture, the asexual life history (derived from zooids from plurilocular sporangia) is similar to that of *G. sphacelarioides*, and also involves an "Ascocyclus" stage. Both taxa require the addition of Kinetin to the culture medium to stimulate the production of erect axes.

CHAPTER VII

CONCLUSIONS AND PHYLOGENETIC CONSIDERATIONS

7.1 An assessment of the value of culture studies

Among the larger brown algae (Laminariales and Fucales in particular), where reproduction is by and large sexual and involves readily separable gametes or gametophytes, studies can be conducted of both the normal reproductive pattern and of breeding and hybridization (cf. A.R.O. Chapman 1978). This situation makes it possible to draw far-reaching phylogenetic conclusions with concrete experimental evidence to back up hypotheses and speculations. Such studies can also be made, with a little more dexterity on the part of the experimenter, with those smaller taxa which show anisogamy or separation into distinct male and female thalli, viz. Hoek & Flinterman (1968) with cultures of *Sphacelaria furcigera* and Müller (1972) with *Ectocarpus siliculosus*.

But for the great majority of the smaller (and some not so small) taxa, the reproductive behaviour, *in vitro*, is more complex and presents greater mechanical difficulties as well as raising a number of significant theoretical problems.

7.1.0. Sexual and asexual reproduction.

In the classical assessment of sexuality in brown algae, it was assumed that the flagellated products of unilocular organs were the products of meiosis and, having germinated singly, would produce the haploid or gametophyte generation. This generation produced plurilocular organs which released flagellated gametes that formed a zygote by fusion and, after germination, formed the diploid, or sporophyte generation, which bore the unilocular organs. Superimposed on this basic life history in several groups of Phaeophyta were accessory cycles in which plurilocular organs bore neutral spores (the products of mitosis) which

recycled the generation bearing them. However, it has been demonstrated many times that this theoretical life history is not conformed to by very many species of brown algae. Frequently it is the sexual phase of the life history which has been supressed, being either totally lost or only expressed as a response to narrowly defined environmental conditions.

It is apparent that zooids from haploid plants of many species act as asexual zoospores under usually prevailing field conditions, but may act as sexual gametes under suitable conditions (e.g. *Colpomenia peregrina* as described by Clayton 1979). The nature of such zooids cannot be inferred without evidence of their fusion or non-fusion and subsequent germination to a recognised phase of the species.

The maintenance of one ploidy level, even when several morphologically distinct generations may be formed, indicates an asexual life history by a particular species. Where meiosis and zygote formation can be demonstrated, a species has a sexual phase in its life history. Conflicting reports of life histories of the same species from different parts of the world suggest that the delicate environmental responses needed to trigger one or other phase in the overall life history do not occur evenly across the globe [e.g. the discussion of the life histories of certain of the Scytosiphonales in Wynne and Loiseaux (1976), and Clayton (1976a,b,1978)].

In all the taxa which were successfully cultured from field plants in the present study, no zygote formation was demonstrated. In the case of *Myrionema strangulans*, where no evidence of plurilocular sporangia has been found for Australian populations, the life history for Australian populations is dissimilar to that outlined by Loiseaux (1967c) for French populations. The absence of a phase bearing plurilocular sporangia in field plants precludes a life history similar to the French populations. The filamentous phase which bore plurilocular sporangia (found in culture) did not appear to be fertile. Thus, for Australian populations, the life history of *M. strangulans* is asexual.

The results of life history studies of *Elachista orbicularis* confirm that members of this genus so far studied show asexual life histories, even when, in the case of *E. orbicularis* it is the plurilocular sporangia which have been retained.

The two species of *Giraudya* represent a slightly different position. *Giraudya* is remarkable in that three types of reproductive organ may be formed on the one plant. All appear to produce asexual zooids, with no evidence of gamete and zygote formation. Yet, in both species, the asexual cycle is complex and involves the products of several of their various plurilocular organs. However, the existance of a sexual phase in their respective life histories cannot be ruled out, as plants with certain reproductive organs in mature state were not obtained during the study. Some related organisms have been shown to have a sexual phase in their life histories (cf. Wynne & Loiseaux 1976), and so further investigation of both *Giraudya sphacelarioides* and *G. robusta* may ellucidate a sexual phase.

It is clear that much remains to be learned about the reproduction and the conditions controlling this in these groups of Phaeophyta.

7.1.1 Do *in vitro* results really reflect *in vivo* behaviour?

As has been stated several times above, it is not uncommon to find that cultures made from different parts of the world of the same morphological taxon will provide different patterns of life history. Clayton (1978) discusses this phenomenon for *Scytosiphon*. In the present study, the life history of the Australian race of *Myrionema strangulans* differs markedly from that obtained for the French race by Loiseaux (1967c). Field observations of *M. strangulans* suggest

a third possible life history, direct reproduction of the macrothallus, at least some of the time.

There are two problems involved in the comparison of cultures from different parts of the world. The first is the lack of a convention on a standard medium for the comparative studies of life histories. This might easily be overcome by requesting that in future everyone use for example Provasoli's Enriched Seawater for unialgal cultures and Fries Modified Artificial Seawater Preparation 6 for axenic cultures. This has the inherent problem that some algae will not grow well in either or both of these media, and, as well, there is little real understanding of the roles of even the major nutrients in the promotion of both growth and fecundity in species of brown algae.

The second problem is that little is known about phenotype/genotype responses among brown algae in culture. Russell (1978) reviews this situation, and points out that with some species one isolate may show little change under culture, while another is very likely to show wide variation. He cites examples of this among the Scytosiphonales and Ectocarpales.

7.1.2 What are pseudo-discoid thalli, plethysmothalli, and other aberrant microstages, and why do they occur in cultures?

It is not adequate to give an empirical reply that they are developmental stages of the life history seldom if ever encountered in field collections. Where it has been possible to exclude the occurrence of such developmental stages by continued subculturing (e.g. Clayton (1972) for various species of *Giffordia* and *Ectocarpus*), the assumed integral role of such a microstage can be dismissed but its occurrence remains unaccounted for. Where, as is seen above with *Myrionema latipilosum*

and both species of *Giraudya*, the behaviour of the pseudodiscoid or other different developmental stage is seen to parallel a regular field observable form, it can be judged to be a result of the culture conditions, but its induction remains a problem. When, as is the case with the Australian race of *M. strangulans*, such a pseudo-discoid developmental stage appears to replace the field form, it may either be due to lack of the real culture requirements of the plant, or a phenotypic response to culture conditions. Either case makes comparison with other workers' results difficult.

Other, apparently sterile, growths are even more difficult to interpret. Where they occur as an alternative to gamete fusion, they can readily be accounted for as the naturally sterile products of germinated solitary gametes. But when they occur as an alternative to asexual zooid behaviour, they may be assumed to have some form of "resting stage" role, if consequent culturing can induce the production of normal vegetative forms directly from them. An alternative suggestion is that they are artifacts of the culture methods. But the question, as with the pseudo-discoid stages, arises as to why both kinds of response should occur under the one set of conditions. There is some slight evidence to suggest, from the present studies of *Myrionema* and *Giraudya*, that their occurrence may be linked to later settled or later germinated zooids.[1] This evidence itself presents the problem of "staleness" of zooids, which, while known to have some consequences in mammalian embryology and that of higher plants, has seldom been posed in the study of microorganisms. Sequential removal before settling of zooids (or gametes) from the

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1. In culture ME-III (Table III.ia, p. 46 above), the earliest removed samples showed the highest proportions of amoeboid germination, while later ones showed more tubular germination, which led to plethysmothalli, or filamentous plantlets which produced aberrant plurilocular organs. Similar results were found with *M. latipilosum* and both *Giraudya* species.

mother culture would be one way of testing this problem, especially if the zooids could be induced to remain active for longer periods than normal.

7.1.3 The *in vitro* induction of field form

Among the Corynophlaeaceae, and to some degree the Elachistaceae, one of the significant difficulties in culture work is the failure of induction of the various tissue types, especially the medulla. The results of Dangeard (1964, 1969) for *Leathesia difformis* in culture are difficult to interpret because the plants described from culture bear little real resemblance to the field morphology of the same species. Similar patterns have been found with *L. difformis* and *Corynophlaea cystophorae* in the present study.

The form in culture of facultative endophytes, i.e. those which use the host cortex and medulla as a substrate (e.g. *Strepsithalia*) rather than a source of nutrition, is often nearer that of epiphytes than their normal form, but this is a natural and expected consequence of cultural isolation.

The tendency for taxa not to form proper medullary tissues when the macrophyte developmental stage is achieved in culture may be due to a number of causes. One of the principal causes may be the static nature of most culture procedures, which may indicate that the formation of the medulla is a response to wave action and the need for cushioning of natural mechanical stresses on the thallus. Another possibility is that we do not know how to set in motion the regulatory chemical mechanisms which induce the meristematic zones of *Corynophlaea* or *Elachista* for the production of medullary tissue. Until this mystery is better understood, the results of *in vitro* experiments with plants in which we cannot induce fully mature macrothalli may tell us much about

the life history, but leave us with morphogenetic problems.

7.1.4 Unialgal or Axenic Cultures

Loiseaux & Rozier (1978) have discussed both the methods for obtaining axenic cultures of small brown algae and the effects on the vitamin and hormone requirements of such cultures. Using *Pylaiella littoralis* they demonstrated that, in the absence of bacteria, this alga shows an absolute requirement for thiamine and/or vitamin B12. The growth rate of axenic cultures appeared to be less rapid than unialgal nonaxenic cultures, but showed a pronounced response to the administration of vitamins. The lack of responses to hormone treatments (Kinetin and PAA) may be specific for this organism.

The advantage of axenic culture is the complete assurance that all developmental stages and effects of treatments apply to the test organism alone. But in clean unialgal cultures, where the bacterial contaminants may alleviate the necessity to add vitamins to the medium, the same certainty applies, at least as far as life history results are involved.

Indeed, the importance of bacterial contaminants in the induction of various morphological effects has been demonstrated with some morphologically plastic algae. Provasoli and Pintner (1980) have recently conducted exhaustive tests of the effects of numerous bacteria on the polymorphism of an axenic strain of *Ulva lactuca*. They comment (p.200):

> 'The effects of bacteria on morphology may explain the findings that many seaweeds have different and typical morphs depending upon locality of collection. This indicates that these species may be unable to govern their own morphology and that they depend upon the action of the microbial biocenosis of each locality.'

This has important implications in laboratory replication of field behaviour of algae.

While it may or may not be best to use axenic cultures, the results obtained from pure unialgal cultures provide a satisfactory first approximation for life history studies.

Despite the imperfections, unialgal cultures of the smaller brown algae provide at least an insight into the life histories of these algae, and where field confirmation of the results of culture is available, a very close approximation to the naturally occurring life history. Further investigation of the sports of culture will make it possible some day to explain them.

7.1.5 Epiphyte - Host specificity

Field observations and examination of herbaria suggest that the range of hosts available for exploitation by an epiphytic species is usually confined to one species or a small number of related taxa. However, this may be due to poor documentation of the range of the epiphyte's host tolerance. It can result in Feldmann's (1943) concept of species in the genus *Myriactula*, and the treatment of Japanese taxa in *Leathesia* by Inagaki (1958). There are, moreover, many epiphytes which do not show a restricted host range.

Recently some elegant experimental work has been done to test the validity of the *one epiphyte - one host* proposal. This work has been made possible by advances in isotope and fluourescence chemistry, and use of the electron microscope. Harlin (1973a, 1975) has shown that *obligate* epiphytes of the seagrasses *Phyllospadix* and *Zostera* will readily colonize polypropylene strips placed in the same field conditions. Further to this, Harlin (1973b) has demonstrated exchange of ^{14}C and ^{35}P between host and epiphyte. But the generality of this exchange, and its importance in the growth and maturity of the epiphyte, has been questioned for some host-epiphyte relationships (Harlin & Cragie 1975). In the case of *Smithora naiadum*, the epiphyte most intensely investigated, Harlin (1973a) has demonstrated that, given the same field situation, there appear to be no direct dependence of this epiphyte on its host for triggers for substrate selection and adhesion, growth of basal cushion and young blade, nor maturation of the cushion. However, this needs to be tested *in vitro* also.

Among the epiphytic taxa described here, some appear to be obligate epiphytes, being associated with one host or a restricted range of hosts. Examples are *Elachista orbicularis* on *Ecklonia radiata* in southern Australia (and two or three similar Laminariales in Japan); *Portphillipia australis* on *Xiphophora* species; and the various species of *Myrionema* and *Strepsithalia*

found in southern Australian waters. Most other taxa appear to be adventitious, since they can be found on a wide selection of suitable hosts in similar habitats. Such epiphytes are *Corynophlaea cystophorae* (Appendix III) and *Leathesia intermedia* (p. 130), and, in a more restricted sense, *Leathesia difformis* (Appendix IV) when it occurs as an epiphyte. The above observations are based on field data.

The results from culture studies are somewhat different. *Myrionema latipilosum* grew successfully on both an artificial substrate (polyethylene strips) and glass. The plants used for culture were obtained from tanks of *Zostera* plants grown in controlled conditions in water from the Onkaparinga River. Thomas (pers. comm.) noted *M. latipilosum* on *Zostera* blades, strips of polyethylene and the glass walls of the tanks. *M. latipilosum* also grew well in unialgal culture in artificial media. *Elachista orbicularis* is another *obligate* epiphyte which responds well to unialgal culture in glass containers. Apart from the lack of production of an organized medulla, it developed a morphology close to the field form.

The two species of *Giraudya* show a host preference for species of seagrass (particularly *Posidonia*) in the field, but may be found on various fucalean taxa growing in association with *Posidonia* beds, in southern Australia. Under culture conditions both these *Giraudya* species require the presence, in the initial medium, of very low concentrations of kinetin to stimulate the production of erect axes. Thereafter they grow satisfactorily *in vitro*, regaining and maintaining field morphology. The studies of M. Pedersen (1968) first demonstrated the requirement for this group of hormones by some brown algae. Pedersen (1973) isolated and identified such a kinetin from seawater - the *Fucus-Ascophyllum* zone - and demonstrated its ability to elicit the same responses as synthetic kinetins. No evidence is available on the presence of exudates of kinetin-like substances in seawater from similar zones in southern Australia, but their presence might be expected. A direct association between the epiphyte (*Giraudya* spp.) and the host community

(*Posidonia* dominated seagrass beds) may be indicated here, but the question of specific host choice remains unanswered.

It is paradoxical that those species (*Corynophlaea cystophorae*, *Leathesia difformis* and *L. intermedia*) for which the field information indicates a wide selection of hosts are those which were found most difficult to establish successfully in culture, and which did not retain field morphology when cultured.

It is clear that the subject of epiphytes and their substrate and ecological requirements is deserving of much further study. Each epiphyte species must have strict, if often broadly based, requirements for suitable ecological conditions at a site where potential hosts grow. As well, epiphytes grow on hosts which offer benefits to the successful growth and reproduction of the epiphyte, even though these benefits may be very subtle and oblique. As is discussed above, the requirements of the epiphyte include nutritional or growth regulating substances, either provided directly by the host or present in the environment in which both grow. Similar interrelationships of host and environment may be demonstrated for many of the requirements of epiphyte.

7.2 Phylogenetic relationships between the four families and the Chordariales and Dictyosiphonales

The main criteria available for phylogenetic views about the Myrionemaceae, Elachistaceae and Corynophlaeaceae remain within the confines of comparative morphology and, to a lesser extent, comparison of life histories. Some information may be gleaned from such ultra-structural information as is available.

The Giraudyaceae, the members of which have a rather more complex anatomy, has also to be compared to related groups using ontogenetic and comparative morphological arguments. However, a wider selection of comparisons is open for association between this and related families in the Dictyosiphonales.

7.2.1 The Myrionemaceae

The first problem to be confronted in any discussion of the Myrionemaceae, as presently restricted, is an assessment of whether it is a natural group or an artificial assemblage imposed by systematists in a desire to clarify the origins of more advanced and supposedly related groups.

The generic limits imposed on *Myrionema* and *Compsonema* appear at first artificial and in the latter genus are very likely so. In *Myrionema* sensu Loiseaux (1967a), and as used here, several characters found consistently in the Chordariales can be seen. The monostromatic basal layer, the truly "phaeophytan" hair, the filiform uniseriate plurilocular sporangia, and the determinate, often few-celled, cortical assimilatory filaments with small discoid phaeoplasts in the upper cells and lower terete cells with parietal (? coalesced) phaeoplasts, all show anatomical similarity to those found in most taxa in the

Corynophlaeaceae and Chordariaceae. The suggestion that the life form is the neoteny of a developmental stage of Chordariaceae life cycles (Kylin 1933) is only acceptable in part, as the occurrence of a monostromatic discoid microthallus of the *Myrionema* form is found in several related genera.

Compsonema presents a problem both systematically and phylogenetically. There would be justification on the grounds of comparative morphology, e.g. the indeterminate, often ectocarpoid erect filaments and multi-seriate plurilocular sporangia, for placing it with *Herponema* J. Ag. and *Hecatonema* in the Ectocarpales. Loiseaux (1967a) treats it with *Hecatonema* in that section of the family Myrionemaceae. The suggestion of *Compsonema*-like stages in the life history of a species of *Scytosiphon* (Loiseaux 1970a) add further to the contention that *Compsonema* may be associated with *Hecatonema*. However, this link is not a strong one, as the microthalli of various taxa of *Scytosiphon* have been compared with a wide range of genera in several families, including the Ralfsiaceae (see Clayton 1978). Hecatonemoid microthalli are also frequently associated with Dictyosiphonales life histories (Wynne and Loiseaux 1976, Clayton 1974). If *Compsonema* is placed in the Ectocarpales, then the Myrionemaceae becomes a monotypic family (see however, discussion p. 60), with quite close association with the Chordariales. In the present treatment, *Compsonema* is retained in Myrionemaceae as a possible forerunner to the *Myrionema*-type, following the criteria used for its generic separation by Kuckuck (1953).

7.2.2 The Elachistaceae

The Elachistaceae is one of the neat natural groups within the Phaeophyta, like the Sphacelariales, where a consistent set of morphological characters prevail, as does the habit. The lack of hairs, and the presence of both short cortical and long extended assimilatory filaments, mark this family off as a separate but parallel group to the Corynophlaeaceae although they do not show the aplanate, encrusting form of *Leathesia* and *Petrospongium*. There is a clear progression in

form from *Halothrix*, where little medullary development is present, through *Elachista* to the form of *Elachista lindaueri* Chapman and *Portphillipia australis*, which is very close to *Corynophlaea* in habit. The parallels in form between the various species of *Elachista* and *Myriactula* have been the cause of much confusion in the past.

The origins of the Elachistaceae, since there is no ontogenetic evidence to support a close connection with the Myrionemaceae, probably lie close to the Streblonemaceae and *Pylaiella* in the Ectocarpales. The cell structure in long assimilatory filaments is similar to that of *Giffordia*, *Feldmannia* and *Pylaiella* in the Ectocarpaceae. The phaeoplasts are discoid and parietal and often show projecting pyrenoids in all of these genera. The presence of a meristem, either just above the medulla in the Elachistaceae, or intercalary in the Ectocarpaceae is a feature suggesting a common ancestral linkage between the two groups of taxa. The Elachistaceae also share this form of meristem with *Giraudya* and some species of *Myriotrichia*. As only Maŧkey & Wilce (1975, 1976a and b) have produced high grade pictures of the ultrastructure of *Pylaiella*, and the other algae mentioned are not known at this level, light microscopal comparison is all that is available, and the conformability may be another demonstration of general uniformity of the brown algal assimilatory cell, rather than either an indication of alliance or parallel development.

However, it is interesting to speculate on the removal of the Elachistaceae from near the Corynophlaeaceae and their repositioning towards the base of the line of development which leads to the Dictyosiphonales. While *Myriotrichia*, *Leptonematella* and perhaps *Litosiphon* (at least in juvenile stages) show a closer resemblance

to *Feldmannia* and *Giffordia*, the Elachistaceae could fit in as a side-branch here almost as consistently as with Corynophlaeaceae, except for the uniseriate form of the plurilocular sporangium, which is consistent with that borne by most taxa in the Chordariales.

The origins of the Elachistaceae do seem separate from the *Myrionema/Hecatonema* complex, but to create a separate order for this one family appears unjustified for the present.

7.2.3 The Corynophlaeaceae

The Corynophlaeaceae consists of two groups of genera which are internally consistent and one outlying genus, *Cylindrocarpus*. The origin of *Strepsithalia* from a *Myrionema*-like ancestral form is not hard to imagine. The form and nature of the assimilators is similar in both cases, and the plurilocular sporangia, and in culture the unilocular sporangia, are similar in form and position. The production of new sporangia within the old empty wall is a feature in both, although it occurs in other unrelated genera. It is a short step from *Strepsithalia clavata* to the pattern of growth shown by most species of *Myriactula*.

An alternative approach to the origins of the Myriactuleae may involve their derivation from a *Corynophlaea*-like ancestral form which, in exploiting the endophytic habit, has lost its compact medullary tissue. One important function of the medulla in *Corynophlaea* and *Leathesia* is to provide mechanical support for the assimilatory and reproductive functions of the cortex. If the tissues of a host organism provide a similar degree of mechanical support for an endophyte, then the endophyte may evolve a medulla which functions as an interconnecting tissue between parts of the endophyte thallus and serves little further function. It is also an advantage for an endophyte to cause minimum disturbance of its host,

in an effort to retain host compatability. Thus a progression may be seen from *Myriactula*, with a partially endophytic habit and a reduced medulla, through *Strepsithalia clavata*, to the wholly endophytic *S. liagorae*, where the medulla is indistinguishable from a rhizoidal system linking cortical branches.

The change from the endophytic life style to the epiphytic life style is a dramatic one, even for a facultative, i.e. non parasitic, endophyte. It is possible that the ancestral form of the remainder of the Corynophlaeaceae was an epiphyte, but with a morphology similar to *Strepsithalia*. As several authors (Kylin 1933, Rosenvinge & Lund 1943, Fritsch 1945) have noted, *Microcoryne*, *Corynophlaea*, *Leathesia* and *Petrospongium* conform to a graded series, with increasing complexity and diversity of form upwards to the perennial *Petrospongium*, well protected against predation and climate by its habit and the close

packing of its medullary and cortical structures.

Apart from the ability to branch freely, provided by the longitudinal rather than radial growth pattern, the Chordariaceae are hardly more advanced than the Corynophlaeaceae. Apart from differences in thallus form, the various taxa in the Corynophlaeideae could be placed in morphologically similar genera in the Chordariaceae: *Corynophlaea cristata* in *Bactrophora*, near *B. filum*; *C. filiformis* in *Tinocladia*; *Leathesia intermedia* and *L. sphaerocephala* in *Polycerea*; and *Petrospongium* in *Suringaria*, and so on. If one does this, the parallels between the two families are clear, and the division between them is seen to be one of convenience following a general difference in growth habit. The taxa involved often share similar habitats, being inhabitants of the lower eulittoral and upper sublittoral in particular. The close morphological parallels between the Corynophlaeaceae and Chordariaceae, and the similarity between *Myrionema* and *Strepsithalia*, present an evolutionary series, with increasing morphological complexity in the lower part of the Chordariales. The Elachistaceae form a parallel line to the Corynophlaeaceae, but may have a different origin within the same general part of the proto-Ectocarpus-like algae.

7.2.4 The Giraudyaceae

The internal relationships within the Giraudyaceae, although there are only two genera, are interesting and a little difficult to assess. On page 147 above, the relationship between *Giraudya* and *Flabellonema* is discussed in detail. The main characters shared by the two genera are the ordered ranks of tiers of cells in the erect axes, the presence of terminal hairs on those axes and the similarity between the intercalary plurilocular sporangia in *F. codii* and

the intercalary sori of plurilocular sporangia in *G. sphacelarioides*. The similarity in form of branching of erect axes between *Flabellonema* and the Sphacelariaceae is also discussed there (compare branching in Pls 8.E and 18.A).

Kylin (1933) based his removal of *Giraudya sphacelarioides* from the Elachistaceae in the Chordariales to the Dictyosiphonales on the ontogenetic similarities between *Giraudya*, as demonstrated in culture by Sauvageau (1927), and the Striariaceae. While recent studies of *Striaria* and *Stictyosiphon* (Caram 1965, Caram & Nygren 1970, Kornmann & Sahling 1973, Nygren 1975) have produced inconsistent information as to whether the lifecycle involves an alternation of generations or is direct in these two genera, various morphological stages in the life history agree well with those found for *G. sphacelarioides* and *G. robusta* in Australia. The form of the juvenile thallus of *Striaria* is very similar to that of *Giraudya robusta* (cf. Caram and Nygren 1970, fig. 4). The mature erect axes of both species of *Giraudya* show close similarities to the juvenile axes of *Striaria* (Caram & Nygren 1970; Nygren 1975) and *Asperococcus* sp. (Pl. 18, E.) as well as the juvenile laterals of *Stictyosiphon* sp. (Pl. 18, C, D.). The life history, as far as is presently known, is direct for both species of *Giraudya* in Australia. This is a form of life history common in the Dictyosiphonales (Wynne & Loiseaux 1976).

However, the three taxa in the family Giraudyaceae differ from most other members of the Dictyosiphonales in one important respect, the division of the primary tier cells leads to the development of further tier cells, not to the formation of a tiered medulla. In two of the taxa a medulla is formed, consistently in *Giraudya robusta*, only in older plants bearing basal sporangia in *Giraudya sphacelarioides*,

at the base of the erect axes, below the meristematic zone. In *Flabellonema codii* no medulla is formed. Each of these taxa indicate a different origin for the family. *Flabellonema codii* shows features, especially in the branching of erect axis and the form of the basal disc, which indicate a possible relationship to the Sphacelariales, although the discoid base is common in the Punctariaceae. *Giraudya sphacelarioides* may be seen as a reduced, neotenic form of *Striaria*. *G. robusta* has a medullary system and unilocular sporangia reminiscent of those shown by the pulvinate Chordariales, although the buoyancy cells in the medullary filaments are similar to those described by Rosenvinge & Lund (1947) for *Dictyosiphon*, and the uniseriate or biseriate laterals towards the tip of the main axes are not unlike similar laterals in some species of *Myriotrichia*.

So the relationships between the Giraudyaceae and other families in the Dictyosiphonales are not clear. A position close to the Striariaceae is indicated by the life history and the general morphological form, but the exact relationship of this family to the whole order may require considerable revision. The form of both species of *Giraudya* suggests that neoteny has occurred, and the exhibition of juvenile features may indicate that a separate line of development, parallel to the main developmental lines of the Dictyosiphonales, may be involved.

7.3 Summary

The present investigation has shown that each of the four families, Myrionemaceae, Elachistaceae and Corynophlaeaceae in the Chordariales, and Giraudyaceae in the Dictyosiphonales, is represented by various taxa exploiting the different habitats available to pulvinate algae.

The Myrionemaceae has been expanded to include three previously undescribed species of *Myrionema*, one in each section of the genus, and an uncommon *Compsonema*. The Elachistaceae has representatives of all three genera in southern Australia. *Elachista secundata* shows affinities with north Atlantic taxa, while *E. orbicularis* is a species shared between Australia and Japan, and may prove to be an introduced species from the north west Pacific.

Each genus of the Corynophaeaceae (except *Microcoryne* and *Cylindrocarpus*) has one or more representative in southern Australia. The occurrence of three species of *Strepsithalia* in southern Australia is remarkable, and the selection of a fucalean host by one of these taxa is equally interesting. The other taxa in *Strepsithalia*, both in Europe and southern Australia, select non-parenchymaceous, filamentous hosts, but *S. clavata* successfully invades the upper ramuli of *Caulocystis*, not only penetrating the conceptacles but also the vegetative tissue between them.

Myriactula has always presented taxonomic problems, not least in the limits of species. In the present study two species are recognized for southern Australia, *Myriactula haydenii* and *M. rivulariae* with three varieties. *Corynophlaea* has three species in southern Australia, distinguishable clearly on differences in medullary structure. *Corynophlaea longifila* has been reincluded in *C. cystophorae* because extensive collections have shown that there is a continuum of characters from those of the small "type" of *C. cystophorae* to the very large "type" of *C. longifila*. The presence of two species of *Leathesia* and of *Petrospongium rugosum* is confirmed.

Culture studies of taxa in the three families in the Chordariales, have usually shown close agreement between southern Australian species

and the same or comparable species from elsewhere. A notable exception is *Myrionema strangulans*, where there is close morphological correspondence between southern Australian specimens and those from elsewhere, but the results of the culture of southern Australian specimens differ from those found for specimens from France (Loiseaux 1967c), in that no return to field form was obtained from southern Australian specimens. The various taxa in the Corynophlaeaceae from southern Australia did not respond well to attempts to culture them.

The Giraudyaceae has been increased by the addition of a new species to the genus *Giraudya* and a new genus and species to the family. While culture studies of both species of *Giraudya* have demonstrated a life history which is similar to various strains and species of *Striaria* and *Stictyosiphon*, the various morphological features of the three taxa in the family indicate that this family is distinct from the general phylogenetic line in the Dictyosiphonales, from *Myriotrichia* to *Dictyosiphon*.

The comparison of the southern Australian flora in these four families to floras in other parts of the world shows that there are similarities between this flora and those of the Mediterranean basin and the Japanese region.

Summary of Culture Results

The results obtained from culture studies of southern Australian taxa included here agree, on the whole, with those found for the same related taxa in other part of the world. The demonstration of a direct life history in a species of *Elachista* which only forms plurilocular sporangia is a further indication that this family shows a dominantly asexual life history pattern. A direct life history has also been demonstrated for both species of *Giraudya*.

In fact, life histories of the plants in this study appear to be asexual. There is an absence of fusion of zooids from plurilocular sporangia. The zooids, whether produced by unilocular or plurilocular sporangia, are similar in their behaviour and settle individually. While cytological confirmation of this was attempted with both field and cultured material, it was unfortunately never achieved.

The Myrionemaceae. Two taxa were successfully cultured. *Myrionema latipilosum*, a southern Australian representative of the *M. balticum* complex, has a life history closely comparable with those demonstrated by Loiseaux (1967c) for *M. orbicularis* and *M. magnusii*. Plurilocular sporangia have not been found on Australian plants of *M. strangulans*, and cultures established from zooids released from unilocular sporangia behaved differently from those reported by Loiseaux (1967c). The zooids of Australian material settle individually and the majority of plants produced also bore unilocular sporangia only. The absence of field form in cultures, even when amoeboid germlings formed, indicates that further research into the nutritional and environmental requirements of this taxon is needed. Within the limits of the culture facilities that were available, the strategies that were tried demonstrated that there was a link between daylength and the culture morphology of the plant, including the kind of sporangium formed.

The Elachistaceae. Elachista orbicularis, although only known to produce plurilocular sporangia, has a direct, asexual life history in agreement with the other members of the genus cultured previously. It is the first member of the *E. intermedia* section of the genus to have been followed in culture.

The Corynophlaeaceae. The members of this family presented the greatest problems in culture. When successful zooid release was obtained the resulting cultured plants showed little resemblance to parent stock and usually remained infertile. The results of cultures of *Strepsithalia liagorae* and *Myriactula rivulariae* var. *arabica* are insufficient from which to draw

conclusions.

The Giraudyaceae. After the initial difficulties of culture establishment and induction of erect axes were overcome (by the addition of kinetin to the medium), cultures of both species of *Giraudya* provided much information on their asexual behaviour and phenology. The results built on the information already obtained by Sauvageau (1927). Both lateral kinds of plurilocular sporangia developed by *G. sphacelarioides* provided similar results in culture. The life history is asexual and direct, with the addition of an *Ascocyclus* phase. The *Ascocyclus* phase also arose from individually settled zooids of plurilocular sporangia and either produced uniseriate plurilocular sporangia which replicated the phase, or acted as a base for normal erect taxes, or both. This result is significant in that it shows that Feldmann (1937) and Sauvageau (1927) may have been mistaken in their conclusion that *Giraudya sphacelarioides* grew on *Ascocyclus (= Myrionema) orbicularis* on *Posidonia*, and not directly on the seagrass itself. Similar results were obtained for the products of the plurilocular sporangia of *G. robusta*, once again with an *Ascocyclus* phase. The one successful germination of zooids from the unilocular sporangia of *G. robusta* was prematurely terminated by mechanical fault before this possibly sexual phase of the life history could be fully examined. Cytological examination of both species of *Giraudya* was unsuccessful.

The life histories of both species of *Giraudya* follow similar patterns to the asexual phases of related genera in the Dictyosiphonales as summarised by Wynne & Loiseaux (1976).

Phenological studies of many of the taxa discussed here were not possible as the available specimens were fully grown, and many taxa appear to have a very short life span. In *Leathesia difformis* and the two species

of *Giraudya*, the available information has been presented. For *L. difformis* (Appendix IV) no clear cut trends in development can be determined, although shorter assimilators (α form) and unilocular sporangia are perhaps more common in plants found in October, November and December, while the β form and/or plurilocular sporangia appear more commonly in specimens collected later in the summer.

The culture results and the phenology shown by both species of *Giraudya* have been discussed above. The comparison is close, although slight variations occur in the sequence of appearance of the sporangial forms. The details of phenology of *Myrionema* species are described in the literature and compare closely with observation of southern Australian material. *Elachista orbicularis* and *Corynophlaea cystophorae* mature very quickly and retain the same morphology throughout their active life.

Cytological and Ultrastructural examination of several of the taxa discussed in this thesis was attempted following the methods indicated above, but without success.

APPENDIX I

KEY TO THE DISCOID, SACCATE AND PULVINATE CHORDARIALES IN SOUTHERN AUSTRALIAN WATERS

1. Thallus consisting of a conspicuous disc with erect filaments arising directly from cells of the disc. (Myrionemaceae) 2

1. Thallus with an inconspicuous or fragmented basal system, an intermediate medullary system, and a cortex of assimilatory filaments. 7

2. Disc strictly monostromatic; erect assimilatory filaments with determinate growth, simple or occasionally bifurcate above the basal cell of the filament; plurilocular sporangia sessile, on a one-celled pedicel or in a sporangiophore, uni- or biseriate. . . . . *Myrionema* Grev. . . . 4

2. Disc mono- to distromatic; erect assimilatory filaments of indeterminate growth, sometimes branching irregularly above the basal cell of the filament; plurilocular sporangia on a one to several-celled pedicel or lateral and/or terminal on erect filaments, multiseriate. 3

3. Disc monostromatic with two cells, arising from each disc cell, which are closely appressed, giving the appearance of two layers in the base; erect assimilatory filaments short (usually less than 10 cells, not becoming ectocarpoid; plurilocular sporangia on a one to several celled pedicel, multiseriate. . . . . *Compsonema* Kuck.

(one species, *C. compactum* (Lindr.) comb. nov.)

3. Disc distromatic; erect assimilatory filaments either short, with a few cells, or ectocarpoid, on same thallus; plurilocular sporangia on a multicellular pedicel or lateral or terminal to erect filaments, multiseriate. . . . . *Hecatonema* Sauv.

(Ectocarpales; three common species *H. maculans; H. streblonemoides;* and *H. stewartense.*)

4. Each cell of basal system able to support only one erect filament. 5

4. Each cell of basal system able to support two erect filaments. 6

5. Erect assimilatory filaments numerous, of 4-6(-10) cells, terminal cell inflated; ascocyst absent; hairs narrow, cells 10-12 µm in diameter; only unilocular sporangia in Australian material. *Myrionema strangulans* Grev.

5. Erect assimilatory filaments infrequent, of 3-5 cells, terminal cell not inflated; ascocysts numerous, terete, as long or longer than plurilocular sporangia; hairs broad, cells 15-20µm in diameter; unilocular sporangia rare, plurilocular sporangia long, with sixteen or more loculi. *Myrionema magnusii* (Sauv.) Lois.

(The taxon known as *M. incommodum* Skottsb., semi-endophytic on *Adenocystis* in Tasmania, has a filamentous rhizoidal system and the form of a species of *Streblonema*).

6. Erect assimilatory filaments narrow, short, patent, of 3-5 cells; hairs with a single basal cell and short meristem; unilocular sporangia clavate; plurilocular sporangia formed on branched, modified erect filaments, of 4-8 loculi..... *Myrionema ramulans* sp. nov. —

6. Erect assimilatory filaments broader than above, long, flexible, of 8-20 cells; hairs with a 2 or 3 celled pedicel and long meristem; unilocular sporangia elongate-ovoid; plurilocular sporangia unknown.

Myrionema myriodesmae sp. nov.

7. Growth of thallus radial, form of thallus usually hemispherical and pulvinate. 8

7. Growth of thallus longitudinal, form of thallus terete and ramifying. . . . . larger Chordariales.

8. Thallus without hairs; erect assimilatory filaments of two forms, a cortex of determinate filaments and long filaments extending beyond the main thallus; thallus not mucilaginous.

(Elachistaceae) 9

8. Thallus with hairs; erect assimilatory filaments determinate, forming the cortex beyond which the hairs extend; thallus mucilaginous.

(Corynophlaeaceae) . . 12

9. Cells of long assimilatory filaments as short or shorter than broad at least in the lower filament; plurilocular sporangia formed in a sorus by the repeated division of a group of cells of long assimilatory filaments. . . . . *Halothrix*

(one species, *H. ephemeralis* sp. nov.; report of *H. lumbricalis* from Victoria).

9. Cells of long assimilatory filaments as long or longer than broad; plurilocular sporangia uniseriate, formed on corymbose sporangiophores in the cortex, or absent. 10

10. Cortical assimilatory filaments recurved, subtending unilocular sporangia; (buttress or) rhizoidal filaments arising from medullary filaments through the tissue; plurilocular sporangia unknown.

. . . . *Portphillipia* Silva

(one species *P. australis* (J. Ag.) Silva).

10. Cortical assimilatory filaments erect, not directly subtending sporangia; no buttress or rhizoidal filaments, one celled rhizoidal pegs from basal cells present in some species; plurilocular sporangia uniseriate, filiform, formed on corymbose sporangiophores in cortex. . . . *Elachista* Duby . . .11

11. Long assimilatory filaments arising from unbranched medullary filaments, cortical assimilatory filaments and sporangiophores arising from branched medullary filaments; unilocular sporangia unknown. . . . *Elachista orbicularis* (Ohta) comb. nov.

11. Long assimilatory filaments, cortical assimilatory filaments and sporangiophores arising from branched medullary filaments; unilocular sporangia elongate-ovoid. . . . *Elachista secundata* sp. nov.

12. Thallus pulvinate, partly endophytic, with medullary filaments restricted to a few cells. . . . Tribe I Myriactuleae... 13

12. Thallus globose and compact, or coarsely aplanate, epiphytic or epilithic, with medullary filaments forming at least half the thallus tissue. . . . Tribe II Corynophlaeideae . . . 17

13. External thallus covering an extensive irregular area of the host surface; medulla reduced to one or two cells between the rhizoidal filaments and the cortical tissue. . . *Strepsithalia* Bornet in Sauv. . . . 14

13. External thallus in discrete patches; medulla branched and forming a distinct tissue between the rhizoidal filaments and the cortex. . . . *Myriactula* Kuntze . . . 16

14. Terminal cell of assimilatory filaments pyriform, filaments tapering towards the base; partly endophytic in *Caulocystis* spp. . . . *Strepsithalia clavata* sp.nov.

14. Terminal cell of assimilatory filaments not inflated, filaments terete, filiform; partly endophytic in Helminthocladiaceae. 15

15. Assimilatory filaments long, 70-130 µm; partly endophytic in *Liagora* spp. . . . . *Strepsithalia liagorae* Sauv.

15. Assimilatory filaments short, 40-55 µm long; partly endophytic in *Helminthocladia* sp. . . . . *Strepsithalia aemula* sp. nov.

16. Assimilatory filaments of moniliform cells of inflated cells, cells narrow, to 15 µm wide. . . . . *Myriactula haydenii* (Gatty) Levring.

16. Assimilatory filaments terete or with inflated cells confined to just above the meristematic zone, cells broader, to 25 µm wide. . . . . *Myriactula rivulariae* (Suhr) J. Feldm.

(three varieties in southern Australia, see pp. 100-1)

17. Medullary filaments closely compacted, without fluid-filled lacunae between the cells; cortical filaments bifurcate at about half their length. . . . . *Petrospongium* Naegeli

(one species, *P. rugosum* (Okam.) S. & G.)

17. Medullary filaments loosely compacted, with fluid filled lacunae between the cells; cortical filaments undivided. 18

18. Medullary cells pyriform or terete, not forming anastomoses with adjacent cells; cortical filaments of six to more than fifty cells, terminal cell not inflated with respect to other cells of filament. . . . . *Corynophlaea* Kütz. 19

18. Medullary cells subglobose, cruciate or stellate, forming anastomoses with adjacent cells; cortical filaments of 3-10 (-15) cells, terminal cell markedly inflated. . . . . *Leathesia* Gray 21

19. Cells of cortical filaments terete throughout the filament.
. . . . *Corynophlaea filiformis* sp. nov.

19. Cells of cortical filaments subglobose or laterally expanded, at least in upper filament. 20

20. Medullary filaments subdichotomous; plurilocular sporangia uniseriate, filiform on corymbose sporangiophores in the cortex.
. . . . *Corynophlaea cystophorae* J. Ag.

20. Medullary filaments polychotomous at nodes, with two or more cells in internodes; plurilocular sporangia multiseriate, arising laterally from upper cells of cortical filaments, forming a crest together. . . . . *Corynophlaea cristata* sp. nov.

21. Cortical filaments of 3-8 cells, terminal cell inflated to twice the size of that below it.
. . . . *Leathesia difformis* (L.) Aresch.

21. Cortical filaments of 8-15 cells, terminal cell inflated to five times the size of that below it.
. . . . *Leathesia intermedia* Chapm.

APPENDIX II

CORYNOPHLAEA CYSTOPHORAE; COMPARATIVE CELL NUMBERS OF ASSIMILATORY FILAMENTS

SPECIMEN NO.	LOCALITY	RANGE OF CELL NO.	MODE	CELL SHAPE IN UPPER FILAMENT
A30129	Bicheno, Tas.	4 - 8	6	deltoid
A49170	Low Head, Tas.	6 - 11	7	"
A48906	Wanna, S. Aust.	5 - 10	8	"
A48896	Elliston, S. Aust.	6 - 10	8	"
A49054	Queenscliff, Vic.	6 - 10	8	"
A49171	Low Head, Tas.	6 - 10	8	"
A48899	Sheringa Beach, S. Aust.	7 - 10	8	"
A50271	Nora Creina, S. Aust.	6 - 10	9	"
A48825	Normanville, S. Aust.	7 - 10	9	"
A48902	Avoid Bay, S. Aust.	7 - 10	9	"
A48888	Point Westall, S. Aust.	8 - 11	9	"
A49075	Point Roadknight, Vic.	8 - 11	9	"
A49173	Gordon, Tas.	8 - 11	9	"
A46767	Point Avoid, S. Aust.	8 - 12	9	"
A48900	Sheringa Beach, S. Aust.	8 - 12	9	"
A49077	Point Roadknight, Vic.	8 - 13	9	"
A48831	Encounter Bay, S. Aust.	6 - 10	10	"
A48882	Blanche Port, S. Aust.	6 - 11	10	"
A48898	Sheringa Beach, S. Aust.	7 - 11	10	"
A48908	Fishery Bay, S. Aust.	8 - 10	10	"
A49070	Point Lonsdale, Vic.	8 - 11	10	"
A47271	Encounter Bay, S. Aust.	8 - 12	10	"
A48833	Encounter Bay, S. Aust.	8 - 12	10	"
A48834	Encounter Bay, S. Aust.	8 - 12	10	"
A48909	Fishery Bay, S. Aust.	8 - 12	10	"
A48910	Port Neil, S. Aust.	9 - 11	10	"
A48892	Venus Bay, S. Aust.	9 - 12	10	"
A30026	Safety Cove, Tas.	8 - 14	10	"
A48835	Encounter Bay, S. Aust.	9 - 11	11	"
A31173	Cape Naturalist, W. Aust.	8 - 12	11	"
A32184	Pennington Bay, K.I.	8 - 12	11	"
A48893	Venus Bay, S. Aust.	9 - 12	11	"
A50272	Cape Lannes, S. Aust.	10 - 12	11	"
A28057	Port Campbell, Vic.	9 - 16	11	rounded
A31759	Apollo Bay, Vic.	8 - 12	12	deltoid
A48894	Venus Bay, S. Aust.	8 - 12	12	"
A49172	Woodbridge, Tas.	9 - 13	12	"
A49197	Aldinga reef, S. Aust.	9 - 13	12	"
A48895	Venus Bay, S. Aust.	10 - 12	12	"
A47965	Robe, S. Aust.	10 - 14	12	"
A47966	Little Dip, S. Aust.	10 - 15	12	"
A48832	Encounter Bay, S. Aust.	10 - 15	12	"
A48891	Venus Bay, S. Aust.	10 - 15	12	"

APPENDIX II Cont'd

SPECIMEN NO.	LOCALITY	RANGE OF CELL NO.	MODE	CELL SHAPE IN UPPER FILAMENT
A49253	Aldinga reef, S. Aust.	10 - 15	12	deltoid
A48897	Sharinga Beach, S. Aust.	11 - 15	12	"
A47963	Skene's Ck., Vic.	10 - 16	12	"
A48887	Pt. Westall, S. Aust.	11 - 16	12	"
A49076	Point Roadknight, Vic.	9 - 17	12	"
A48263	Encounter Bay, S. Aust.	10 - 20	12	"
A2752	Pennington Bay, K.I.	8 - 15	13	rounded
A33330	Rottnest I., W. Aust.	9 - 15	13	deltoid
A47499	Encounter Bay, S. Aust.	10 - 16	14	rounded
A28907	Sou'West R., K.I.	8 - 18	15	"
A48830	Aldinga reef, S. Aust	10 - 16	15	deltoid
A49169	Bicheno, Tas.	12 - 16	15	"
A49056	Queenscliff, Vic.	12 - 16	16	"
A48592	Myponga Beach, S. Aust.	15 - 20	16	rounded
A49778	Aldinga reef, S. Aust.	13 - 20	17	deltoid
A48631	Aldinga reef, S. Aust.	15 - 20	18	"
A49057	Queenscliff, Vic.	16 - 20	19	"
A48904	Wanna, S. Aust.	16 - 23	19	rounded
A49055	Queenscliff, Vic.	17 - 20	19	deltoid
A48251	Normanville, S. Aust.	15 - 25	20	rounded
A49074	Point Roadknight, Vic.	17 - 23	20	deltoid
A49552	Aldinga reef, S. Aust.	18 - 21	20	"
A48265	Encounter Bay, S. Aust.	18 - 25	20	rounded
A48824	Encounter Bay, S. Aust.	18 - 25	20	"
A50232	Point Lonsdale, Vic.	17 - 22	21	"
A48923	Reevsby I., S. Aust.	18 - 24	21	"
A48581	Aldinga Beach, S. Aust.	15 - 25	22	"
A37705	Tipara reef, S. Aust.	20 - 25	22	"
A48582	Aldinga reef, S. Aust.	20 - 30	22	deltoid
A32188	Balgowan reef, S. Aust.	20 - 35	27	rounded
A49096	Point Lonsdale, Vic.	24 - 33	30	"
A48851	Robe, S. Aust.	25 - 35	30	"
A47858	Marengo, Vic.	25 - 35	30	"
A48590	Myponga Beach, S. Aust.	25 - 35	30	"
A48638	Cape Liptrap, Vic.	30 - 45	35	"
A21051	Tathra, N.S.W.	30 - 50	40	rounded
A48905	Wanna, S. Aust.	40 - 70	55	deltoid
A48907	Wanna, S. Aust.	40 - 60	55	rounded
A29839	Stewart Is., N.Z.	45 - 75	60	deltoid

APPENDIX III

HOST RANGE OF *CORYNOPHLAEA CYSTOPHORAE* (based on collection at ADU)

Rhodophyta	
Gigartinales	
Osmundaria prolifera . . .	Balgowan reef, S. Aust.
Corallinaceae	
Metagoniolithon	Tipara reef, S. Aust.; Reevesby Is., Yorke Peninsula, S. Aust.
Phaeophyta	
Dictyotales	
Dictyota sp.	Encounter Bay, S. Aust.
Zonaria angustata	Port Campbell, Vic.; Skene's Ck., Vic.; Point Roadknight, Vic.
Fucales	
Xiphophora	Apollo Bay, Vic.
Sargassum spp.	Queenscliff, Vic.; Pennington Bay, K.I., S. Aust.; Normanville, S. Aust.; Aldinga reef, S. Aust.; Robe, S. Aust.; Encounter Bay, S. Aust.
Caulocystis sp.	Normanville, S. Aust.; Encounter Bay, S. Aust.; Little Dip, Robe, S. Aust.; Venus Bay, S. Aust.
Cystophora brownii	Tipara reef, S. Aust.; Point Avoid, S. Aust.; Encounter Bay, S. Aust.; Venus Bay, S. Aust.; Fishery Bay, WhalersWay, S. Aust.; Wanna, S. Aust.; Myponga Beach, S. Aust.; Rottnest Is., W. Aust.
C. expansa	Vivonne Bay, K.I., S. Aust.; Sheringa, S. Aust.
C. intermedia . .	Low Head, Tas.; Pennington Bay, K.I., S. Aust.; Cape du Couedic, K.I.; Sou'west Rocks, K.I.; Robe, S. Aust.; Venus Bay, S. Aust.; Wanna, S. Aust.
C. monilifera . .	Point Roadknight, Vic.; Encounter Bay, S. Aust.
Cystophora moniliformis .	Bicheno, Tas.; Low Head, Tas.; Gordon, Tas.; Safety Cove, Tas.; Point Lonsdale, Vic.; Queenscliff, Vic.; Western River, K.I., S. Aust.; Point Avoid, S. Aust.; Encounter Bay, S. Aust.; Point Westall, S. Aust.; Venus Bay, S. Aust.; Elliston, S. Aust.; Sheringa Beach, S. Aust.; Port Neil, S. Aust.; Myponga Beach, S. Aust.

APPENDIX III Cont'd.

Cystophora polycystidea . . .	Aldinga reef, S. Aust.; Encounter Bay, S. Aust.; Streaky Bay, S. Aust.; Point Westall, S. Aust.
C. retorta	Venus Bay, S. Aust.; Sheringa Beach, S. Aust.; Fishery Bay, Whalers' Way, S. Aust.; Avoid Bay, S. Aust.; Encounter Bay, S. Aust.
C. retroflexa . . .	Tathra, N.S.W.
C. siliquosa . . .	Pennington Bay, K.I., S. Aust.; Wanna, S. Aust.; Meelup, W. Aust.
C. subfarcinata . .	Rocky Cape, Tas.; Bicheno, Tas.; Cape Liptrap, Vic.; Queenscliff, Vic.; Point Roadknight, Vic.; Aldinga reef, S. Aust.; Encounter Bay, S. Aust.; Robe, S. Aust.; Venus Bay, S. Aust.; Sheringa Beach, S. Aust.
C. torulosa	Rocky Cape, Tas.; Wood Bridge, Tas.; Waratah Bay, Vic.; Point Lonsdale, Vic.; Queenscliff, Vic.; Point Roadknight, Vic.; Marengo, Vic.

APPENDIX III Cont'd

HOST	W.AUST.	S.AUST.	VIC.	TAS.	N.S.W.	TOTAL
Metagoniolithon sp.		2				2
Osmundaria prolifica		1				1
Dictyota sp.		1				1
Zonaria sp.			3			3
Caulocystis sp.		4				4
Sargassum spp.		5	1			6
Xiphophora sp.			1			1
Cystophora brownii	1	7				8
C. expansa		1				1
C. intermedia		7		1		8
C. monilifera		1	1			2
C. moniliformis		9	2	4		15
C. polycystidea		4				4
C. retorta		5				5
C. retroflexa					1	1
C. siliquosa	1	2				3
C. subfarcinata		5	3	2		10
C. torulosa			5	2		7
	2	54	16	9	1	82

APPENDIX IV

TABLE OF COMPARISONS OF CORTICAL FILAMENT FORM AND HABITAT, THALLUS MORPHOLOGY AND DATE OF COLLECTION OF *LEATHESIA DIFFORMIS*

	HERB NO.	LOCALITY	HABIT	DATE	SPORANGIUM	FORM	CORT.FIL.FORM
South Australia	A48889	Pt. Westall;	on rock	30.xi.1977	Plurilocular	brainlike	β
	A48901	Sheringa;	drift	2.xii.1977	U/P	"	β
	A48126	Aldinga reef;	on *H. tasmanica*	5.vii.1977	-	globose	α
	A48229	" " ;	" " "	16.viii.1977	-	"	α
	A48247	" " ;	" " "	14.ix.1977	-	"	α
	A48248	" " ;	on *Posidonia* sp	14.ix.1977	Unilocular	both	both
	A48578	" " ;	on *H. tasmanica*	14.x.1977	U	globose	β
	A48626	" " ;	on rock	26.x.1977	U	"	α
	A48627	" " ;	on *Posidonia* sp	26.x.1977	U	brainlike	β
	A48628	" " ;	on *Amphibolis* sp	26.x.1977	U	globose	intermediate
	A49556	" " ;	on *H. tasmanica*	15.ix.1978	-	"	α
	A49574	" " ;	" " "	2.x.1978	U	"	intermediate
	A49780	" " ;	" " "	31.x.1978	-	"	α
	A49781	" " ;	on rock	31.x.1978	U	brainlike	intermediate
	A47844	Normanville ;	on *Posidonia* sp	6.i.1977	U	globose	β
	A49777	" ;	" " "	31.x.1978	-	both	α
	A47678	Encounter Bay;	on *H. tasmanica*	26.x.1976	U	globose	β
	A47816	" " ;	on *Amphibolis* sp	7.xii.1976	U	"	β
	A47817	" " ;	on *H. tasmanica*	7.xii.1976	U	"	β
	A48267	" " ;	on *Cladophora* sp	28.ix.1977	U	"	β
	A48268	" " ;	on *Laurencia* sp	28.ix.1977	-	"	α
	A48853	" " ;	on *H. tasmanica*	23.xi.1977	-	"	α
	A48854	" " ;	on rock	23.xi.1977	-	brainlike	intermediate
	A50209	Robe ;	on rock	13.xi.1978	P	"	β
Victoria	A47960	Apollo Bay ;	on rock	24.II.1977	P	"	α
	A47961	" " ;	on *Cladostephus* sp	24.II.1977	P	"	intermediate
	A47962	" " ;	on coralline	24.II.1977	P	"	α
	A49071	Pt. Lonsdale ;	on rock	4.I.1978	-	"	α
	A49060	Queenscliff ;	on rock	4.I.1978	-	"	α
	A49061	" ;	on *Caulerpa* sp	4.I.1978	-	globose	α

APPENDIX IV Cont'd

	HERB.NO.	LOCALITY	HABIT	DATE	SPORANGIUM	FORM	CORT.FIL.FORM
Victoria	A50233	Queenscliff	; on rock	17.I.1979	-	brainlike	intermediate
	A39,442	Crawfish Rock	; on *Gracilaria* sp	27.viii.1971	U	globose	α
	A44619	Koonya Bay	; on rock	15.I.1974	P	brainlike	α
Tasmania	A49177	Georgetown	; drift	23.II.1978	P	"	β
	A30123	Bicheno	; on *Cystophora* sp	16.I.1966	-	globose	intermediate
	A49176	"	; on rock	22.II.1978	P	brainlike	β
	A49175	Orford	; on rock	22.II.1978	-	"	β
	A49174	Safety Cove	; on rock	21.II.1978	P	"	β

APPENDIX V

DATA FOR PRINCIPAL COMPONENTS ANALYSIS PROGRAM, *GIRAUDYA SPHACELARIOIDES AND G. ROBUSTA*

Key

Medullary cells subglobose	=	MEDSUB
Medullary cells pyriform	=	MEDPYR
Basal meristem for erect axes	=	BASMER
Bulbose base for erect axes	=	BASBUB
Basal hairs present	=	BASHAIR
Lateral hairs present	=	LATHAIR
Terminal hairs (solitary) present	=	TERHAS
Terminal hairs (fasciculate) present	=	TERHAF
Branching of erect axes	=	ERECB
Basal plurilocular sporangia branched	=	BASAPB (0 = Basal plurilocular sporangia unbranched)
Lateral solitary plurilocular sporangia	=	LATERAL
Sori of multiseriate lateral sporangia	=	MULTI
Sori of uniseriate intercalary sporangia	=	UNIS
Solitary lateral plurilocular sporangia on branches	=	LATB
Unilocular sporangia	=	UNILOC
Axillary cells rectangular in face view	=	CRECT
Axillary cells hexagonal in face view	=	CHEX

APPENDIX V Cont'd

MORPHOLOGICAL CHARACTERS

FACTOR MATRIX USING PRINCIPAL FACTOR

	FACTOR 1	FACTOR 2	FACTOR 3
MEDSUB	.47641	-.18403	.38468
MEDPYR	-.94101	-.16401	-.07673
BASMER	.61245	.27211	-.23257
BASBUB	-.73855	-.17556	.45875
BASHAIR	-.91608	-.05145	.06568
LATHAIR	.47431	.64548	.04739
TERHAS	-.47675	.50304	-.03958
TERHAF	.93865	-.00996	-.05212
ERECB	-.25005	.80063	-.05134
BASAPB	.67600	-.07785	.14655
LATERAL	-.44325	.69487	.18141
MULTIS	.82245	-.05644	.48094
UNIS	.48100	.04520	-.45317
LATB	-.18717	.71160	.19718
UNILOC	-.48098	-.13407	-.03025
CRECT	.89134	.19062	.12615
CHEX	-.90382	-.01904	.00624

CONVERGENCE REQUIRED 8 ITERATIONS.

APPENDIX V Cont'd

Specimen No. (ADU)	MED SUB	MED PYR	BAS MER	BAS BUB	BAS HAIR	LAT HAIR	TER HAS	TER HAF	ERE CB	BAS APB	LATE RAL	MUL TI	UNIS	LATB	UNI LOC	CRE CT	CHE X
A48579			1			1		1					1			1	
A49181	1			1	1					1		1				1	
A48210			1			1		1		0		1				1	
A48912			1			1		1	1				1			1	
A48859		1		1	1	1									1		1
A26704			1	1	1	1		1	1		1	1		1		1	1
A6559		1	1	1	1	1	1			0					1		1
A37710		1		1	1					0							1
A47500		1		1	1		1		1	0							1
A48244		1	1	1	1	1	1		1	0	1						1
A48911		1		1	1					0	1				1		1
A31963		1	1	1	1		1			0					1		1
A48884				1		1			1		1	1		1		1	1
A47252			1			1		1				1				1	
A48591			1			1		1				1				1	
A48226			1			1		1				1				1	
A48245			1			1		1				1				1	
A48636	1		1			1		1		1		1	1			1	
A48138			1		1	1	1		1	0	1			1		1	
A48913		1		1	1	1			1	0	1						1
A29617	1		1	1		1		1		1		1				1	
A29636			1			1	1		1	0	1			1			1
A33441			1	1		1		1				1				1	
A35104			1			1		1	1				1			1	
A38460	1		1			1		1				1				1	
A39238		1	1	1	1	1	1		1	0	1					1	1
A41266	1		1	1		1		1		1		1				1	
A42871		1		1	1	1	1		1		1						1
A43735			1			1		1				1	1			1	
A48926		1		1	1					0							1

APPENDIX V Cont'd

Specimen No.(AUD)	MED SUB	MED PYR	BAS MER	BAS BUB	BAS HAIR	LAT HAIR	TER HAS	TER HAF	ERE CB	BAS APB	LATE RAL	MUL TI	UNIS	LATB	UNI LOC	CRE CT	CHE X
A49182		1		1	1										1		1
A2273		1		1	1					0							1
A8195		1		1	1					0					1		1
A15860		1		1	1										1		1
A20123		1		1	1	1	1		1	0	1			1	1		1
A20821		1		1	1		1			0							1
A29566		1		1	1	1	1		1	0	1			1		1	
A37313		1		1	1						1						1
A37653		1	1	1	1		1			0							1
A37706		1		1	1					0							1
A38261		1		1	1					0							1
A38425		1		1	1										1		1
A39167		1		1	1	1			1	0	1			1			1
A39735		1		1	1					0	1				1		1
A46932		1		1	1	1	1			0	1				1		1
A48227		1	1	1	1	1	1		1	0	1				1		1
A48243		1		1	1	1	1		1	0	1			1	1		1
A48262		1		1	1		1			0	1						1
A48266		1	1	1	1	1	1		1	0	1			1			1
A48575		1		1	1	1	1		1		1			1	1		1
A48637		1		1	1		1			0					1		1

APPENDIX V Cont'd

SPECIMENS

FACTOR MATRIX USING PRINCIPAL FACTORS

	FACTOR 1	FACTOR 2	FACTOR 3
A48579	-.67796	.32341	.21552
A49181	-.15159	.49040	-.24243
A48210	-.64748	.38443	.87996
A48912	-.63318	.13831	.33427
A48859	.71775	.42793	-.02879
A47252	-.73868	.53050	.32957
A48591	-.73868	.53050	.32957
A48226	-.73868	.53050	.32957
A48245	-.73868	.53050	.32957
A48636	-.88092	.34016	-.03471
A29617	-.63590	.62122	.11661
A33441	-.55854	.69260	.31550
A35104	-.63318	.13831	.33427
A38460	-.80386	.45541	.12166
A41226	-.63590	.62122	.11661
A42871	.66456	.14191	.44117
A43735	-.80270	.39670	.15669
A48138	.00754	-.38009	.73118
A26704	-.07244	.17068	.68359
A48884	-.04839	.07454	.40204
A48913	.72061	.14616	.41819
A29636	.15372	-.47873	.70052
A29566	.43947	-.18920	.53184
A39238	.53699	.13925	.68100
A02273	.81233	.48071	-.09323
A06559	.64669	.31834	.16929
A08195	.81935	.38131	-.31813
A15860	.66282	.50910	-.34362
A20123	.83687	-.26935	.29817
A20821	.82389	.28140	-.00139

APPENDIX V Cont'd

SPECIMENS

FACTOR MATRIX USING PRINCIPAL FACTORS

	FACTOR 1	FACTOR 2	FACTOR 3
A31963	.71141	.25256	-.07895
A37313	.58344	.46059	.23961
A37653	.67372	.32132	.12720
A37706	.81233	.48071	-.09323
A37710	.81233	.48071	-.09323
J38261	.81233	.48071	-.09323
A38425	.66282	.50910	-.34362
A39167	.69665	-.05705	.41185
A39735	.83597	.19654	-.18405
A46932	.80899	.11499	.15379
A47500	.80692	.08438	.13305
A48227	.74107	-.00095	.41591
A48243	.83687	-.26935	.29817
A48244	.67763	.05998	.62798
A48262	.84406	.10830	.11016
A48575	.73942	-.12219	.25172
A48637	.84222	.02171	-.07702
A48911	.83597	.19654	-.18405
A48926	.81233	.48071	-.09323
A49182	.66282	.50910	-.34362
A48266	.67566	-.14821	.64408

REFERENCES

Abbott, I.A. & Hollenberg, G.J. (1976). - *Marine Algae of California.* Stanford University Press, Calif.; 827 pages.

Agardh, C.A. (1824). - *Systematica algarum.* Lund; 312 pages.

Agardh, J.G. (1842). - *Algae Maris Mediterranei et Adriatici.* Paris.

Agardh, J.G. (1848). - *Species, Genera et Ordines Algarum.* Vol. 1. Lund; 363 pages.

Agardh, J.G. (1882). - Till algernes systematik. Nya bidrag. *Acta Univ. Lund,* 17 : 1-136, plates 1-3.

Arasaki, S. (1948). - On the life history of *Acrothrix pacifica, Myriocladia kuromo* and *Petrospongium rugosum. Seibutu,* 3 : 95-102 (with English résumé).

Areschoug, J.E. (1842). - Algarum minus rite cognitarum pugillus primus. *Linnaea,* 16 : 225-236, plate 7.

Areschoug, J.E. (1843). - Algarum minus rite cognitarum pugillus secungundus. *Linnaea,* 17 : 257-269, plate 9.

Bailey, A. & Bisalputra, T. (1969). - Some structural aspects of the cell wall of *Ectocarpus acutus* Setchell & Gardner and *Elachista fucicola* (Valley) Areschoug. *Phycologia,* 8 (1) : 57-63.

Batters, E.A.L. (1902). - Catalogue of British Marine algae. *J. Bot.,* (London), 40 : Supplement.

Bisalputra, T. (1974). - Plastids, p. 124-160, *IN* W.D.P. Stewart, *Algal Physiology and Biochemistry,* Blackwell, London, 989 pages.

Blackler, M.C.H. (1961). - The algal herbarium of Mrs. Gatty, 1809-1873. *Rep. Challenger Soc.* 3, No. XIII.

Blackler, H. & Katpitia, A. (1963). - Observations on the life-history and cytology of *Elachista fucicola. Trans. Bot. Soc. Edinb.,* 39 : 392-395.

Bold, H.C. & Wynne, M.J. (1978) - *Introduction to the algae.* 706p. Prentice Hall, Englewood Cliffs, New Jersey.

Bory de St. Vincent, J. - B.G.M. (1825). - *Dictionnaire classique d'histoire naturelle.* 7. Paris.

Bouck, G.B. (1965). - Fine structure and organelle associations in brown algae. *J. Cell Biol.,* 26(2) : 523-537.

Børgesen, F. (1934). - Some marine algae from the northern part of the Arabian Sea with remarks on their geographical distribution. *D. Kgl. Danske Vid. Sels., Biol. Medd.,* 11 (6): 72 pages, Pl. I-II.

Calvert, H.E., Dawes, C.J. & Borowitzka, M.A. (1976). - Phylogenetic Relationships of *Caulerpa* (Chlorophyta) based on Comparative Chloroplast Ultrastructure. *J. Phycol.,* 12 (2) : 149-162.

Caram, B. (1957). - Sur la sexualité de le developpement d'une Phéophycée: *Cylindrocarpus berkeleyi* (Grev.) Crouan. *C.R. Acad. Sci., Paris,* 245 : 440-443.

Caram, B. (1965). - Recherches sur la reproduction et le cycle sexué de quelques Phéophycées. *Vie et Milieu,* 16 (1, A-C): 21-221.

Caram, B. (1966). - Sur la reproduction de deux Striariacées des eaux danoises. *C.R. Acad. Sci., Paris,* 262 (D) : 2333-2335.

Caram, B. (1972). - Le cycle de reproduction des Phéophycées, Phéosporées et ses modifications. *Mém. Soc. bot. Fr.,* 1972 : 151-160.

Caram, B. & Nygren, S. (1970). - A propos de la reproduction comparée en France et en Suède d'une Phéophycée - Phéosporée : le *Striaria attenuata. Helgol. wiss. Meeresunters,* 20 : 130-135.

Chapman, A.R.O. (1978). - Experimental and Numerical Taxonomy of the Laminariales: A Review., P. 428-432 *IN* Irving, D.E.G. & Price, J.H. *Modern Approaches to the Taxonomy of Red and Brown Algae.* Academic Press, London & New York, 484 pages.

Chapman, V.J. (1961). - New entities and Combinations in the Phaeophyceae of New Zealand. *Bull. Res. Counc. Isr.,* sect. D Bot., 10D : 15-28.

Clayton, M.N. (1972). - The occurrence of variant forms in cultures of species of *Ectocarpus* and *Giffordia. Br. phycol. J.,* 7 : 101-108.

Clayton, M.N. (1974). - Studies on the development, life history and taxonomy of the Ectocarpales (Phaeophyta) in southern Australia. *Aust. J. Bot.,* 22 : 743-813.

Clayton, M.N. (1976a). - The morphology, anatomy and life history of a complanate form of *Scytosiphon lomentaria* (Scytosiphonales, Phaeophyta) from southern Australia. *Mar. Biol.,* 38 : 201-208.

Clayton, M.N. (1976b). - Complanate *Scytosiphon lomentaria* (Lyngbye) J. Agardh (Scytosiphonales : Phaeophyta) from southern Australia: the effects of season, temperature, and daylength on the life history. *J. exp. mar. Biol. Ecol.,* 25 : 187-198.

Clayton, M.N. (1978). - Morphological Variation and life history in cylindrical form of *Scytosiphon lomentaria* (Scytosiphonaceae : Phaeophyta) from southern Australia. *Mar. Bot.* 47 : 349-357.

Clayton, M.N. (1979). - The life history and sexual reproduction of *Colpomenia peregrina* (Scytosiphonaceae, Phaeophyta) in Australia. *Br. phycol. J.,* 14 : 1-10.

Clayton, M.N. & Ducker, S.C. (1970). - The life history of *Punctaria latifolia* Greville (Phaeophyta) in southern Australia. *Aust. J. Bot.,* 18 : 293-300.

Cole, K. (1969). - The cytology of *Eudesme virescens* (Carm.) J. Ag. II Ultrastructure of cortical cells. *Phycologia*, 8 : 101-108.

Cole, K. & Lin, S-C. (1968). - The cytology of *Leathesia difformis* I. Fine structure and vegetative cells in field and cultured material. *Syesis*, 1 (1,2) : 103-119.

Cole, K., Bourne, V. & Lin, S-C. (1968)- Electron microscopic observations on chloroplasts of cultured *Leathesia difformis* (L.) Aresch. *Can. J. Genet. Cytol.*, 10 : 63-67.

Colijn, F. & van den Hoek, C. (1971). - The life-history of *Sphacelaria furcigera* Kütz. (Phaeophyceae) II. The influence of day length and temperature on sexual and vegetative reproduction. *Nova Hedwigia*, 21 (1-4) : 899-922.

Crouan, H.M. & Crouan, P.L. (1867). - Florule du Finistère. Paris.

Dangeard, P. (1964). - Sur le cycle évolutif de *Leathesia difformis* (L.) Aresch. *C.R. Acad. Sci., Paris,* 259 : 2673-2675.

Dangeard, P. (1965a). - Recherches sur le cycle évolutif de *Leathesia difformis* (L.) Areschoug. *Le Botaniste,* 48 (1-6) : 5-43, Pl. I-IV.

Dangeard, P. (1965b). - Sur le nouveau genre *Giraudyopsis* P.D. *Le Botaniste,* 49 : 99-108.

Dangeard, P. (1969). - A propos des travaux récents sur le cycle évolutif de quelques Phéophycées, Phéosporées. *Le Botaniste,* 52 : 59-102.

Dawes, C.J., Scott, F.M. and Bowler, E. (1960). - Light and electron microscopic study of cell walls of brown and red algae. *Science,* 132 : 1663-1664.

Dawes, C.J., Scott, F.M. and Bowler, E. (1961). - A light and Electron-Microscopic Survey of Algal Cell Walls. I. Phaeophyta and Rhodophyta. *Am. J. Bot.,* 48 : 925-934.

Derbès, A. & Solier, A.J.J. (1851). - Algaes, pp. 93-114 *IN* J.L.M. Castagne, *Supplement au catalogue des plantes qui croissent naturellement aux environs de Marseille.* Nicot & Pardigon; Aix.

De Toni, J.B. (1889). - *Sylloge Algarum omnium hucusque Cognitarum,* Vol. 1. Padua, 1315 pages.

De Toni, J.B. (1891). - Systematische Übersicht der bischer bekannten Gattungen der echten Fucoideen. *Flora, Jena,* 74 : 171-182.

De Toni, J.B. (1895). - Sylloge Algarum omnium hucusque Cognitarum, Vol. 3. Padua, 638 pages.

De Toni, G.B. & Forti, A. (1923). - Alghe di Australia, Tasmania, Nuova Zelanda. *Mem. R. Ist. veneto Sci.,* 29 (3) : 1-183.

Dodge, J. (1974). - Fine structure and phylogeny in the Algae. *Sci. Prog.,* Oxf., 61 : 257-274.

Dring, M.J. & Lüning, K. (1975a). - A photoperiodic response mediated by blue light in the brown alga *Scytosiphon lomentaria. Planta (Berl.)* 125 : 25-32.

Dring, M.J. & Lüning, K. (1975b). - Induction of Two-dimensional Growth and hair formation by Blue Light in the Brown Alga *Scytosiphon lomentaria. Z. Plantzenphysiol.,* 75 (2) : 107 : 117.

Duby, S.-E. (1832). - *Botanicon gallicum,* II. Paris.

Edelstein, T., Chen, L. C-M. & McLachlan, J. (1970). - The life cycle of *Ralfsia clavata* and *R. borneti. Can. J. Bot.,* 48 (3): 527-531, + 3 plates.

Edelstein, T., Chen, L. C-M. & McLachlan, J. (1971). - On the life histories of some brown algae from eastern Canada. *Can. J. Bot.,* 49 (7) : 1247-1251.

Evans, L.V. (1974). - Cytoplasmic organelles, p. 86-123 *IN* W.D.P. Stewart *Algal Physiology and Biochemistry*. Blackwells, London, 989 pages.

Feldmann, J. (1937). - Les algues Marines de la Côte des Albères. I-III Cyanophycèes, Chlorophycées, Phéophycées. *Rev. Algol.*, IX, : 141-329, + pls. 8-17.

Feldmann, J. (1943). - Une nouvelle espèce de *Myriactula* parasite du *Gracilaria armata* J.Ag. *Bull. Soc. Hist. Nat. Afr. Nord*, 34 : 222-229.

Feldmann, J. (1954). - Inventaire de la flore marine de Roscoff. Suppl. 6. *Trav. Stat. Biol. Roscoff*, 152 pages.

Feldmann, J. edit. (1972). - Colloque sur les cycles sexuels et l'alternance des generations chez les algues. *Mém. Soc. Bot., Fr.* 1972, 368 pages.

Foslie, M. (1890). - Contribution to knowledge of the marine algae of Norway. I. *Tromso Museums Aarschefter*, 13 : 1-186, + 3 pls.

Foslie, M. (1894). - New or critical Norwegian Algae. *K. norske Vid. Sels. Skr. Trondhjem* 1894 : 114-144, + 2 plates.

Fries, L. (1963). - On the culture of axenic red algae. *Physiol. Plant.*, 16 : 695-708.

Fries, L. & Pettersson, J. (1968). - On the physiology of the red alga *Asterocystis ramosa* in axenic culture. *Br. Phycol. Bull.*, 3 (3) : 417-422.

Fritsch, F.E. (1945). - *The structure and Reproduction of the Algae*. Vol. II. University Press, Cambridge.

Gatty, M. (1863). - *The Seaweeds of Great Britain*. London.

Godward, M.B.E. (1949). - Iron alum acetocarmine method for algae. *Nature*, 161 : 203.

Goebel, K. (1878). - Sur Kenntniss einiger Meeresalgen. *Bot. Zeit.*, 36 (12/13) : 177-184, 193-201.

Gray, S.F. (1821). - *A natural arrangement of British plants*. 2 vols. London.

Greville, R.K. (1827). - *Scottish Cryptogamic Flora*. Vol. 5. Maclachlan & Stewart, Edinburgh.

Guiler, E.R. (1952). - The Marine algae of Tasmania,check list with Localities. *Pap. Proc. R. Soc. Tas.*, 86 : 71-106.

Hamel, G. (1931). - *Phéophycées de France*. I. Paris : 1-80.

Hamel, G. (1935). - *Phéophycées de France*. II. Paris : 81-176.

Hamel, G. (1937). - *Phéophycées de France*. III. Paris : 177-240.

Hamel, G. (1939). - Sur la classification des Ectocarpales. *Bot. Not.*, 1939 : 65-70.

Hanna, H. (1899). - The plurilocular sporangia of *Petrospongium berkeleyi*. *Ann. Bot.*, 13 (51) : 461-464.

Harlin, M.M. (1973a). - "Obligate" algal epiphyte: *Smithora naiadum* grows on a synthetic substrate. *J. Phycol.*, 9 (2) : 230-232.

Harlin, M.M. (1973b). - Transfer of products between epiphytic marine algae and host plants. *J. Phycol.*, 9 (3): 243-248.

Harlin, M.M. (1975). - Epiphyte-Host relations in seagrass communities. *Aquatic Botany*, 1 : 125-131.

Harlin, M.M. & Craigie, J.S. (1975). - The distribution of Photosynthate in *Ascophyllum nodosum* as it relates to epiphytic *Polysiphonia lanosa*. *J. Phycol.*, 11 (1) : 109-113.

Harvey, W.H. (1842). - A Manual of the British Marine algae. Reeve, London.

Harvey, W.H. (1846). - *Phycologia Britannica*, Vol. I., Reeve, London.

Harvey, W.H. (1855). - Algae, pp. 211 - 266. *IN* J.D. Hooker, *The Botany of the Antarctic Voyage*, Vol. II (II). Reeve, London. 378 pages.

Harvey, W.H. (1860). - Algae, pp. 282 - 343. *IN* J.D. Hooker, *The Botany of the Antarctic Voyage*, Part III, Vol. II. Reeve, London, 422 pages.

Harvey, W.H. (1863). - Synopsic Catalogue of Australian and Tasmanian Algae, pp. i - lxii. *IN* W.H. Harvey, *Phycologia Australica*, Vol. V. Reeve, London. Plates ccxli - ccc, and pp. i - lxxii.

Hauck, F. (1885). - Die Meeresalgen, Vol. II. 575 pp + 6 plates. *IN* L. Rabenhorst, *Kryptogamen - Flora von Deutschland, Oesterreich und der Schweiz*. Kummer, Leipzig.

Hoek, C. van den, & Flinterman, A. (1968). - The Life-History of *Sphacelaria furcigera* Kütz. (Phaeophyceae). *Blumea*, 16 : 193 - 242.

Hoek, C. van den, Cortel-Breeman, A.M., Rietema, H. & Wanders, J.B.W. (1972). - L'interprétation des donnés obtenues, par des cultures unialgales, sur les cycles évolutifs des algues. Quelques examples tirés des recherches conduites au laboratoire de Gronuigue. *Mém. Soc. bot. Fr.*, (1972) : 45 - 66.

Hsiao, S.I.C. (1969). - Life history and iodine nutrition of the marine brown alga, *Petalonia fascia* (O.F. Mull.) Küntze. *Can. J. Bot.* 47 : 1611-1616.

Hygen, G. (1934). - Uber den Lebenszyklus und die entwichlungsgeschichte der Phaeosporeen. Versuche an *Nemacystus divaricatus* (Ag.) Kuck. *Nyt Magazin for Naturvidenskaberne*, 74 : 187-268, 16 plates.

Inagaki, K. (1958). - A Systematic Study of the Order Chordariales from Japan and its Vicinity. *Sci. Pap. Inst. Alg. Res.*, Fac. Sci., Hokkaido Univ., 4 (2) : 87-197.

Iwasaki, H. (1965). - Nutritional studies of the edible seaweed *Porphyra tenera* I. The influence of Different Biz analogues, plant hormones, purines and pyramidines on the growth of *Conchocelis*. *Plant & Cell Physiol.* 6 : 325-336.

Jaasund, E. (1951). - Marine algae from North Norway I. *Bot. Not.*, 1951 (2) : 128-142.

Jaasund, E. (1960). - *Elachista lubrica* Ruprecht and *Elachista fucicola* (Vell.) Areschoug. *Bot. mar.*, 1 (3,4) : 101-107.

Jaasund, E. (1965). - Aspects of the Marine Algal vegetation of North Norway. *Acta Bot. Gothoburg.*, 4, 174 pages.

Jaasund, E. (1969). - Marine algae from Tanzania I. *Bot.Mar.*, 12 (1-4) : 255-274.

James, D.E. (1974). - Culturing algae. Carolina Biological Supply Company, Burlington, N.C., 24 pages.

Jennings, R.C. (1968). - Gibberellins as endogenous Growth regulators in Green and Brown algae. *Planta (Berl.)*, 80 : 34-42.

Kjellman, F.R. (1890). - *Handbook i Skandinaviens Hafsalgflora*, Vol. I, Fucoideae. O.L. Lamms, Stockholm.

Kjellman, F.R. (1897). - Phaeophyceae, *IN* A. Engler & K. Prantl. *Die Natürlichen Pflanzenfamilien*, 1 (2).

Kjellman, F.R. & Svedelius, N. (1911). - Chordariaceae, 163-164. *IN* A. Engler & K. Prantl, *Die Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten*. I (2). Engelmann, Leipzig.

Klotzsch, J.F. (1834). - Ericearum cel Adelberto de Chamisso descriptarum. Pars Addita. *Linnaea*, 9 : 350-367.

Knaggs, F.W. (1972). - Cultivation techniques and their application to the study of Rhodophycean life histories. *Mem. Soc. bot. Fr.*, 1972 : 237-246.

Koeman, R.P.T. & Cortel-Breeman, A.M. (1976). - Observations on the life history of *Elachista fucicola* (Vell.) Aresch. (Phaeophyceae) in culture. *Phycologia*, 15 (2) : 107-117.

Kornmann, P. & Sahling, P.-H. (1973). - *Striaria attenuata* (Phaeophyta, Dictyosiphonales), neu bei Helgoland : Entwichlung und Aufbau. *Helgol. wiss. Meeresunters*, 25 : 14-25.

Kuckuck, P. (1899). - Beiträge zur Kenntnis der Meeresalgen, 5-9. *Helgol. wiss. Meeresunters*, 1899 : 47-116.

Kuckuck, P. (1929). - Fragmente einer Monographie der Phaeosporeen. *Wiss. Meeresunters*, N.F., 17 (4): n.s.

Kuckuck, P. (edit. P. Kornmann) (1953). - Ectocarpaceen-Studien I. *Hecatonema, Chilionema, Compsonema. Helgol. wiss. Meeresunters.*, 4 (3) : 316-353.

Kuntze, O. (1891). - Revisio Generum Plantarum. Pars II. Charles Klincksieck, Paris.

Kuntze, O. (1898). - Revision Generum Plantarum, Pars. III (II), Charles Klincksieck, Paris.

Kützing, F.T. (1843). - *Phycologia generalis; oder Anatomie, Physiologie und Systemkunde der Tange*. Leipzig.

Kützing, F.T. (1845). - *Phycologia germanica*. W. Köhne, Nordhausen, 340 pages.

Kützing, F.T. (1849). - *Species Algarum*. Brockhaus, Leipzig, 922 pages.

Kützing, F.T. (1858). - *Tabulae Phycologicae*, Vol. 8. W. Köhne, Nordhausen.

Kylin, H. (1907). - Studien über die Algen flora der schwedischen Westküste. *Akad.. Abhand., Upsala*, 288 pp. + 8 plates.

Kylin, H. (1916). - Über den Generationswechsel bie Laminaria digitata. Sven. bot. Tidskr., *10* : 551-561.

Kylin, H. (1933). - Über die Entwicklungsgeschichte der Phaeophyceen. *Lunds Univ. Arssk.*, N.F. 2, 29 (7) : 1-102.

Kylin, H. (1934). - Zur kenntnis der entwicklungsgeschichte einiger Phaeophyceen. *Lunds Univ. Arssk.*, N.F. 2, 30 (9) : 1-19.

Kylin, H. (1937). - Bemerkungen uber die entwicklungsgeschichte einiger Phaeophyceen. *Lunds Univ. Arssk.*, N.F. 2, 33 (1) : 1-34.

Kylin, H. (1940). - Die Phaeophyceenordnung Chordariales. *Lunds Univ. Arssk.*, N.F. 2, (9) : 1-67, 8 plates.

Kylin, H. (1947). - Die Phaeophyceen der Schwedischen Westküste. *Lunds Univ. Arssk.* N.F. 2, 43 (4) : 92 pp. + 18 plates.

Lessing, C.F. (1831). - Synanthereae Rich. *Linnaea*, 6 : 83-170, pls. I-II.

Levring, T. (1937). - Zur Kenntnis der Algenflora der Norwegischen Westküste. *Lunds Univ. Arssk.*, N.F. 2, 33 (8) : 148 pp.

Leyon, H. & Wettstein, D. von (1954). - Der Chromatophoren - Feinbau bei den Phaeophyceen. *Z. Naturf.*, 9 : 471-475.

Lindauer, V.W. (1949). - Notes on Marine Algae of New Zealand. I. *Pacific Science*, 3 (4) : 340-352.

Lindauer, V.W., Chapman, V.J. & Aiken, M. (1961). - The Marine Algae of New Zealand II : Phaeophyceae. *Nova Hedwigia*, 3 : 129-350. Plates 57-97.

Loiseaux, S. (1964a). - Sur une Nouvelle espèce de *Myrionema* des environs de Roscoff et son cycle. *C.R. Acad. Sci., Paris*, 258 : 2383-2385.

Loiseaux, S. (1964b). - Sur l'hétéroblastie et le cycle de deux *Ascocyclus* de la région de Roscoff. *C.R. Acad. Sc., Paris*, 259 : 2903-2904.

Loiseaux, S. (1966). - Sur le cycle de développement de l'*Ascocyclus hispanicus* (Phéophycées, Myrionématacées) et la formation en culture de stades coccoides. *C.R. Acad. Sci., Paris*, 262 : 68-71.

Loiseaux, S. (1967a). - Morphologie et cytologie de Myrionémacées. Critères taxonomiques. *Rev. gén. Bot.*, 74 : 329-347.

Loiseaux, S. (1967b). - Sur la position systematiques du Genre *Giraudyopsis* P. Dangeard. *Rev. gén. Bot.*, 74 : 389-394.

Loiseaux, S. (1967c). - Recherches sur les cycles de développement des Myrionematacées (Pheophycées). I-II Hécatonematées et Myrionématées. *Rev. gén. Bot.*, 74 : 529-576.

Loiseaux, S. (1968a).- Sur les phénomènes d'heteroblastie et de dimorphisme chez les phéophycées. *Rev. gén. Bot.*, 75 : 229-244.

Loiseaux, S. (1968b). - Recherches sur les cycles de développement des Myrionématacées (Pheophycees). III-IV. Tribu des Ralfsiees, Conclusions générales. *Rev. gen. Bot.*, 75 : 295-318.

Loiseaux, S. (1969). - Sur une espèce de *Myriotrichia* obtenue en culture à partir de zoïdes d'*Hecatonema maculans* Sauv. *Phycologia*, 8 (1): 11-15.

Loiseaux, S. (1970a). - *Streblonema anomalum* S. et G. and *Compsonema sporangiiferum* S. et G. stages in the life history of a minute *Scytosiphon*. *Phycologia*, 9 (2) : 185-191.

Loiseaux, S. (1970b). - Notes on several Myrionemataceae from California using culture studies. *J. Phycol.*, 6 : 248-260.

Loiseaux, S. (1973). - Ultrastructure of zoidogenesis in unilocular zoidocysts of several brown algae. *J. Phycol.*, 9 (3) : 277-289.

Loiseaux, S. & Rozier, C. (1978). - Culture axénique de *Pylaiella littoralis* (L.) Kjellm. (Phéophycées). *Rev. Algol.*, N.S., XIII (4) : 333-340.

Lucas, A.H.S. (1909). - Revised list of the Fucoideae and Florideae of Australia. *Proc. Linn. Soc., N.S.W.*, 34 : 9-60.

Lucas, A.H.S. (1913). - Notes on Australian marine algae. I. *Proc. Linn. Soc., N.S.W.*, 38 : 49-60, Plates 1-5.

Lucas, A.H.S. (1929a). - The marine algae of Tasmania. *Pap. Proc. R. Soc. Tas.*, 1928 : 6-27.

Lucas, A.H.S. (1929b). - A census of the marine algae of South Australia. *Trans. R. Soc. S. Aust.*, 53 : 45-53.

Lucas, A.H.S. (1936). - *The Seaweeds of South Australia*. Part I. Govt Printer, Adelaide.

Lund, S. (1966). - On a sporangia-bearing microthallus of *Scytosiphon lomentaria* from Nature. *Phycologia*, 6 (1) : 67-78.

MacLennan, I.G. (1956). - A brown alga (Petrospongium rugosum) new to Victoria. *Proc. R. Soc. Vic.*, 69: 1-3.

Magnus, P. (1874). - Die botanische Ergebnisse de Nordseefahrt vom 21 July bis 9 September 1872. *II Jahresberichte der Kommission zur Untersuchung der deutschen Meers in Kiel*, Berlin.

Manton, I. & Clark, B. (1951a). - An electron microscope study of the spermatozoid of *Fucus serratus*. *Ann. Bot.*, 15 : 461-471.

Manton, I. & Clark, B. (1951b). - Electron Microscope Observations on the Zoospores of *Pylaiella* and *Laminaria*. *J. Exp. Bot.*, 2 : 242-246, + 8 plates.

Manton, I., Clark, B. & Greenwood, A.D. (1953). - Further observations with the Electron Microscope of spermatozoids in the brown algae. *J. Exp. Bot.*, 4 : 319-329.

Markey, D.R. & Wilce, R.T. (1975). - The ultrastructure of reproduction in the brown alga *Pylaiella littoralis*. I. Mitosis and cytokinesis in the plurilocular gametangia. *Protoplasma*, 85 : 219-241.

Markey, D.R. & Wilce, R.T. (1976a). - The ultrastructure of reproduction in the brown alga *Pylaiella littoralis*. II. Zoosporogenesis in the unilocular sporangia. *Protoplasma* 88 : 147-173.

Markey, D.R. & Wilce, R.T. (1976b). - The ultrastructure of reproduction in the brown alga *Pylaiella littoralis*. III. Later stages of gametogenesis in the plurilocular gametangia. *Protoplasma*, 88 : 175-186.

Mathieson, A.C. (1967). - Morphologie and Life History of *Phaeostrophion irregulare* S. & G. *Nova Hedwigia*, 13 : 293-318, + 15 plates.

May, V. (1939). - A key to the marine algae of New South Wales. Part II. Melanophyceae (Phaeophyceae). *Proc. Linn. Soc., N.S.W.*, 64 :191-215.

May, V. (1947). - Studies on Australian marine algae. III. *Proc. Linn. Soc., N.S.W.*, 71 : 273-277.

Meneghini, G. (1843). - *Algae italiane e dalmatiche*. Trib V. Chordarieae. pp. 257-304; Pl. V. Sicca, Padua.

Miranda, F. (1928). - Sobre una nueva especie de *Strepsithalia*. *Bol. R. Soc. Esp. Hist. Nat.*, 28 : 457-462.

Mishra, A.K. & Kefford, N.P. (1969). - Development studies onthe coenocytic alga, *Caulerpa sertularioides*. *J. Phycol.*, 5 : 103-109.

Miyaji, K. (1978). - On *Litosiphon yezoensis*, Yamada & Nakamura. *Jap. J. Phycol.*, 26 : 165-170.

Mowat, J.A. (1965). - A survey of results on the occurrence of auxins and gibberellins in algae. *Bot. mar.*, 8 : 149-155.

Müller, D.G. (1964). - Life-cycle of *Ectocarpus siliculosus* from Naples, Italy. *Nature*, 203 : 1402.

Müller, D.G. (1967). - Generationswechsel, Kernphasenwechsel, und Sexualität der Braun alge *Ectocarpus siliculosus* im Kulturversuch. *Planta (Berl.)*, 75 : 39-54.

Müller, D.G. (1972). - Studies on reproduction in *Ectocarpus siliculosus*. *Soc. bot. Fr. Mem.* 1972 : 87-98.

Müller, D.G. (1976a). - Relative sexuality in *Ectocarpus siliculosus*. A scientific error. *Arch. Microbiol.*, 109: 59-94.

Müller, D.G. (1976b). - Sexual isolation between a European and an American population of *Ectocarpus siliculosus* (Phaeophyta). *J. Phycol.*, 12 (2) : 252-254.

Nakamura, Y. (1965). - Development of Zoospores in *Ralfsia*-like thallus with special reference to the life cycle of the Scytosiphonales. *The Bot. Mag., Tokyo*, 78 : 109-110.

Nakamura, Y. (1972). - A proposal on the classification of the Phaeophyta 147-156 .*IN Contributions to Systematics of Benthic Marine Algae of the North Pacific*. Jap. Soc. Phycol., Kobe.

Nieuwland, J.A. (1917). - Critical notes on new and old Genera of Plants. IX. *Amer. Midland Nat.*, 5 (30) : 30 only.

Newton, L. (1931). - *A Handbook of the British Seaweeds.* British Museum, London.

Noda, M. (1964). - Marine algae in the vicinity of the Shioyazaki Cape, Fukushima Prefecture. *J. Fac. Sci. Niigata Univ., Ser. II*, 4 : 33-75.

Noda, M. (1969). - The species of Phaeophyta from Sado Island in the Japan Sea. *Sci. Rep. Niigata Univ., Ser. D.* 6 : 1-64.

Noda, M. (1974). - Some marine algae collected on the coast of Kashiwazaki Province facing the Japan Sea. *Sci. Rep. Niigata Univ., Ser. D*, 11 : 65-74.

Noda, M. (1975). - Some marine algae further added to the marine flora of Sado Island in the Japan Sea. *Sci. Rep. Niigata Univ., Ser. D*, 12 : 91-107.

Noda, M. & Kitami, T. (1971). - Some species of Marine Algae from Echigo Province facing the Japan Sea. *Sci. Rep. Niigata Univ., Ser. D*, 8 : 35-52.

Nygren, S. (1975). - Life history of some Phaeophyceae from Sweden. *Bot. mar.*, 18 : 131-141.

Ohta, T. (1973). - Some new and rare marine algae from Tsugara straits between Honshu and Hokkaido. *Sci. Rep. Niigata Univ., Ser. D.* 10 : 11-28.

Okamura, K. (1907). - *Icones of Japanese Algae.* Vol. I (5) : 93-119, plates 21-25.

Oltmanns, F. (1904). - *Morphologie und Biologie der Algen.* Vol. I. G. Fischer, Jena, 733 pages.

Oltmanns, F. (1922). - *Morphologie und Biologie der Algen*, 2nd Edn, Vol. II. Phaeophyceae - Rhodophyceae. G. Fischer, Jena, 439 pages.

Papenfuss, G.F. (1951). - Phaeophyta, 119-158, *IN* G.M. Smith, *Manual of Phycology*, Waltham, U.S.A., 375 pages.

Papenfuss, G.F. (1955). - Classification of the Algae, 115-224, *IN* *A Century of Progress in the Natural Sciences.* California Academy of Sciences, San Francisco.

Parke, M., Dixon, P.S., Russell, G. & Fletcher, R.L. (1976). - Phaeophyta pp. 558-563, *IN* Parke, M. & Dixon, P.S. Checklist of British Marine Algae. Third Revision. *J. mar. biol. Ass. U.K.*, 56 : 52-594.

Pedersén, Marianne (1968). - *Ectocarpus fasciculatus:* Marine brown alga requiring kinetin. *Nature*, 218 : 776.

Pedersén, M. (1969a). - The demand for Iodine and Bromine of three Marine Brown algae grown in Bacteria-free cultures. *Physiol. Plant.*, 22 (4) : 680-685.

Pedersén, M. (1973). - Identification of a Cytokinin, 6-(3 Methyl-2-butenylamino) purine, in sea water and the effect of cytokinins on brown algae. *Physiol. Plant.*, 28 (1) : 101-105.

Pedersen, P.M. (1978). - Culture studies on marine algae from West Greenland III. The life histories and systematic positions of *Pogotrichum filiforme* and *Leptonematella fasciculata* (Phaeophyceae). *Phycologia*, 17 (1) : 61-68.

Pedersen, P.M. (1979). - Culture studies on the brown algae *Halothrix lumbricalis* and *Elachista fucicola* (Elachistaceae). *Bot. Not.*, 132 : 151-159.

Provasoli, L., McLaughlin, J.J.A. & Droop, M.R. (1959). - The development of artificial media for marine algae. *Arch. Mikrobiol.*, 25 : 392-428.

Provasoli, L. & Pintner, I.J. (1980). - Bacteria induced polymorphism in an axenic laboratory strain of *Ulva lactuca* (Chlorophyceae). *J. Phycol.*, 16 : 196-201.

Prud'homme van Reine, W.F. (1978). - Criteria used in systematic studies in the Sphacelariales, pp. 301-323. *IN* Irvine, D.E.C. & Price, J.H. *Modern Approaches to the Taxonomy of Red and Brown Algae*. Academic Press, London & New York, 484 pages.

Rafinesque (-Schmaltz), C.S. (1814). - *Precis decouv. et trav. somiol.* Palermo.

Reinbold, T. (1899). - Ergebnisse einer Reise nach dem Pacific. Meeresalgen. *Abh. Naturwissenschaftlichen Verein, Bremen*, 16 (2) : 287-302.

Reinke, J. (1899). - Algenflora der Westlichen Ostsee. Deutschen Autheils. Eine systematischpflanzen-geographische studie. I. Kiel.

Reynolds, E.S. (1963). - The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. *J. Cell Biol.*, 17 : 208-212.

Rosenvinge, L.K. (1935). - On some Danish Phaeophyceae. *Mem. Acad. R. Sci. Lett. Dan., Copenhague, Sect. Sci.* Sev. 9, 4 (3) : 40 pages.

Rosenvinge, L.K. & LUND, S. (1943). - The marine algae of Denmark, Vol. II Phaeophyceae. II. Corynophlaeaceae - Arthrocladiaceae. *D.K. Dan. Viden. Sels.*, Biol. Skr. II (6) : 59 pages.

Rosenvinge, L.K. & Lund, S. (1947). - The marine algae of Denmark, Vol. II Phaeophyceae. III. Encoeliaceae - Laminariaceae. *D.K. Dan. Viden. Sels.*, Biol. Skr. IV (5) : 99 pages.

Russell, G. (1962). - An aceto-carmine staining technique for the Ectocarpales. *Nature*, 193 : 396.

Russell, G. (1978). - Environment and form in the discrimination of taxa in Brown Algae. pp. 339-369. *IN* Irvine, D.E.C. & Price, J.H. *Modern Approaches to the Taxonomy of Red and Brown Algae*. Academic Press, London & New York, 484 pages.

Sauvageau, C. (1896). - Note sur le *Strepsithalia*, nouveau genre de Phéosporée. *J. Bot.*, 10 (4) : 53-65.

Sauvageau, C. (1897). - Sur quelques Myrionémacées. *Ann. Sci. Nat. Bot.*, Ser. 8, 5 : 161-288.

Sauvageau, C. (1915a). - Sur les débuts du développement d'une Laminaire *(Saccorhiza bulbosa)*. *C.R. Acad. Sci., Paris*, 161 : 5-9.

Sauvageau, C. (1915b). - Sur la sexualité hétérogamique d'une Laminaire *(Saccorhiza bulbosa)*. *C.R. Acad. Sci., Paris,* 161 : 1-4.

Sauvageau, C. (1918). - Recherches sur les Laminaires des côtes de France. *Acad. Sci., Paris, Mem.,* 56 : n.s.

Sauvageau, C. (1924a). - Sur le curieux developpement d'une Algue phéosporée, *Castagnea Zosterae* Thuret. *C.R. Acad. Sci., Paris,* 179 : 1381-1384.

Sauvageau, C. (1924b). - Sur quelques exemples d'hétéroblastie dans le développement des Algues phéosporées. *C.R. Acad. Sci., Paris,* 179 : 1576-1579.

Sauvageau, C. (1925a). - Sur la culture d'une Algue phéosporée epiphyte *Strepsithalia liagorae* Sauv. *C.R. Acad. Sci., Paris,* 180 : 1464-1467.

Sauvageau, C. (1925b). - Sur le développement d'une algue phéosporée *Leathesia difformis* Aresch. *C.R. Acad. Sci., Paris,* 180 : 1632-1635.

Sauvageau, C. (1927). - Sur les Problemes du *Giraudya*. *Bulletin de la Station Biologique d'Arcachon,* 24 : 3-74.

Sauvageau, C. (1928). - Sur les Algues phéosporées à éclipse ou Eclipsiophycées. *Rec. trav. bot., néerlandais,* 25 (A) : 260-270.

Sauvageau, C. (1929). - Sur le développement de Quelques Phéosporées. *Bull. Stat. Biol. d'Arcachon,* 26 : 253-420.

Sauvageau, C. (1933a). - Sur quelques Algues Phéosporées de Guethary. *Bull. Stat. Biol. d'Arcachon,* 30 : 1-126.

Sauvageau, C. (1933b). - Un genre *"Symphoricoccus"* Rke est-il justifié? Sur le *Climacosorus,* nouveau genre de Phéosporée. *Bull. Stat. Biol. d'Arcachon,* 30 : 179-196.

Sauvageau, C. (1936). - Second Mémoire sur les Algues Phéosporées. *Bull. Stat. Biol. d'Arcachon,* 33 : 1-204.

Schiffner, V. (1916). - Studien über Algen des adriatischen. *Meeres. Wiss. Meeresunters,* n.f. Abt. Helgoland., 2 : 129-198.

Setchell, W.A. & Gardner, N.L. (1924). - Phycological Contributions, VII. *Univ. Calif. Publ. Bot.,* 13 (1) : 1-13.

Setchell, W.A. & Gardner, N.L. (1925). - The Marine Algae of the Pacific Coast of North America. Part III. Melanophyceae. *Univ. Calif. Publ. Bot.,* 8 (3) : 383-898, + 74 plates.

Silva, P.C. (1959). - Remarks on algal nomenclature. II. *Taxon,* 8 : 60-64.

Silva, P.C. (1970). - Remarks on algal nomenclature. IV. *Taxon,* 19 : 941-945.

Skottsberg, C. (1907). - Zur Kenntnis der Subantarktischen und Antarkischen Meeresalgen, 1-172, plates 1-10. I. Phaeophyceen. *IN Wissenschaftliche Ergebnisse der Schwedischen Sudpolar - expedition,* 1901-1903, 4.

Skottsberg, C. (1921). - Botanische Ergebnisse der Schwedischen Expedition nach Patagonien und dem Feuerlande 1907-1909. VIII Marine Algae. I. Phaeophyceae. *Kgl. Svenska Vetensk. Handl.,* 61 (11) 1-56.

Skottsberg, C. (1953). - On two collections of Antarctic Marine Algae. *Arkiv. för Botanik,* ser 2, 2 (7) :531-566, 1 plate.

South, G.R. (1974). - *Herpodiscus* gen. nov. and *Herpodiscus durvilleae* (Lindauer) comb. nov., a parasite of *Durvillea antarctica* (Chamisso) Hariot endemic to New Zealand. *J. R. Soc., N.Z.,* 4 (4) : 455-461.

South, G.R, & Hooper, R.(1976). - *Stictyosiphon soriferus* (Phaeophyta, Dictyosiphonales) from eastern North America. *J. Phycol.,* 12 (1) : 24-29.

Spegazzini, (1897). - *Rev. Fae. Agron. y Vet.,* La Plata 1897 : 566.

Stafleu, F.A. *et al.* (1978). - *International code of Botanical Nomenclature. Intern. Ass. Pl. tax..* Bohn, Schelten & Holkema ; Utrecht.

Starr, R.C. (1971). - The Culture Collection of Algae at Indiana University. Additions to the Collection July 1966 - July 1971. *J. Phycol.,* 7 (4) : 350-362.

Strömfelt, H. (1888). - Algae quas ad littora Scandinavia indagavit. *Notarisia,* 1888 : ?

Svedelius, N. (1911). - Elachistaceae, 162. *IN* A. Engler & K. Prantl, *Die naturlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten.* I (2) Engelmann : Leipzig.

Takamatsu, M. (1938a). - *Elachista* aus dem nordöstlichen Honshû, Japan. *Saitô Hô-on Kai Museum, Res. Bull.,* 14 : 145-176, 6 plates.

Takamatsu, M. (1938b). - *Halothrix* aus dem nordöstlichen Honshû, Japan. *Saitô Hô-on Kai Museum, Res. Bull.,* 14 : 181-192, 2 plates.

Takamatsu, M. (1938c). - Eine neue Art von der Gattung *Gonodia. Saitô Hô-on Kai Museum, Res. Bull.,* 14 : 177-180, 1 plate.

Takamatsu, M. (1939). - The species of *Leathesia* from North-eastern Honshû, Japan. *Saitô Hô-on Kai Museum, Res. Bull.,* 17 : 1-19, 4 plates.

Thuret, G. (1849). - Recherches sur les zoospores des algues et les anthéridies des cryptogames. *Ann. Sci., Nat.* ser. 4, Bot. Tom. 14 : 214-260, + 16 plates.

Thuret, G. (1864). - *IN* Le Jolis, A. *Liste des algues marines de Cherbourg. Mem. Soc. imp. Sci. Nat. de Charbourg,* 10:

Toth, R. (1976). - A mechanism of propagule release from Unilocular Reproductive Structures in brown algae. *Protoplasma,* 89 : 263-278.

Wanders, J.B.W., Hoek, C. van den and Schiller-Van Nes, E.N. (1972). - Observations on the life-history of *Elachista stellaris* (PHAEOPHYCEAE) in culture. *Neth. J. Sea Res.,* 5 (4) : 458-491.

Wettstein, D. von (1954). - Form wechsel und Teilung der Chromatopharen von *Fucus vesiculosus*. *Z. Naturf.*, 9 (6) : 476-481.

Womersley, H.B.S. (1950). - The marine algae of Kangaroo Island. III. List of species 1. *Trans. R. Soc. S. Aust.*, 73 : 137-197.

Womersley, H.B.S. (1967). - A critical survey of the marine algae of southern Australia. II. Phaeophyta. *Aust. J. Bot.*, 15 : 189-270.

Woolery, M.L. & Lewin, R.W. (1973). - Influence of iodine on growth and development of the brown alga *Ectocarpus siliculosus* in axenic cultures. *Phycologia*, 12 : 131-138.

Wynne, M.J. (1969). - Life history and systematic studies of some Pacific North American Phaeophyceae (Brown Algae). *Univ. Calif. Publ. Bot.*, 50 : 1-88.

Wynne, M.J. (1972a). - Culture studies of Pacific coast Phaeophyceae. *Mem. Soc. bot. Fr.*, 1972 : 129-144.

Wynne, M.J. (1972b). - Studies on the life forms in nature and in culture of selected brown algae, pages 133-145. *IN* I.A. Abbott & M. Kurogi. *Contributions to the Systematics of Benthic Marine Algae of the North Pacific. Japanese Soc. Phycology*, Kobe.

Wynne, M.J. & Loiseaux, S. (1976). - Recent advances in life history studies of the Phaeophyta. *Phycologia*, 15, 3/4 : 435-452.

Yamada, Y. (1927). - Report of the Biological Survey of Mutsu Bay, 9. Marine algae of Mutsu Bay and adjacent waters, II. *Sci. Rep., Tôhoku Imp. Univ.*, 4th Ser., 3 (4) :

Yendo, K. (1909). - Notes on Algae new to Japan. *The Bot. Mag., Tokyo*, 23 (270) : 117-133.

Figure 1. Generalized Zone Diagrams of Structure

A. Corynophlaeaceae
B. Chordariaceae
C. Myrionemaceae
D. Elachistaceae

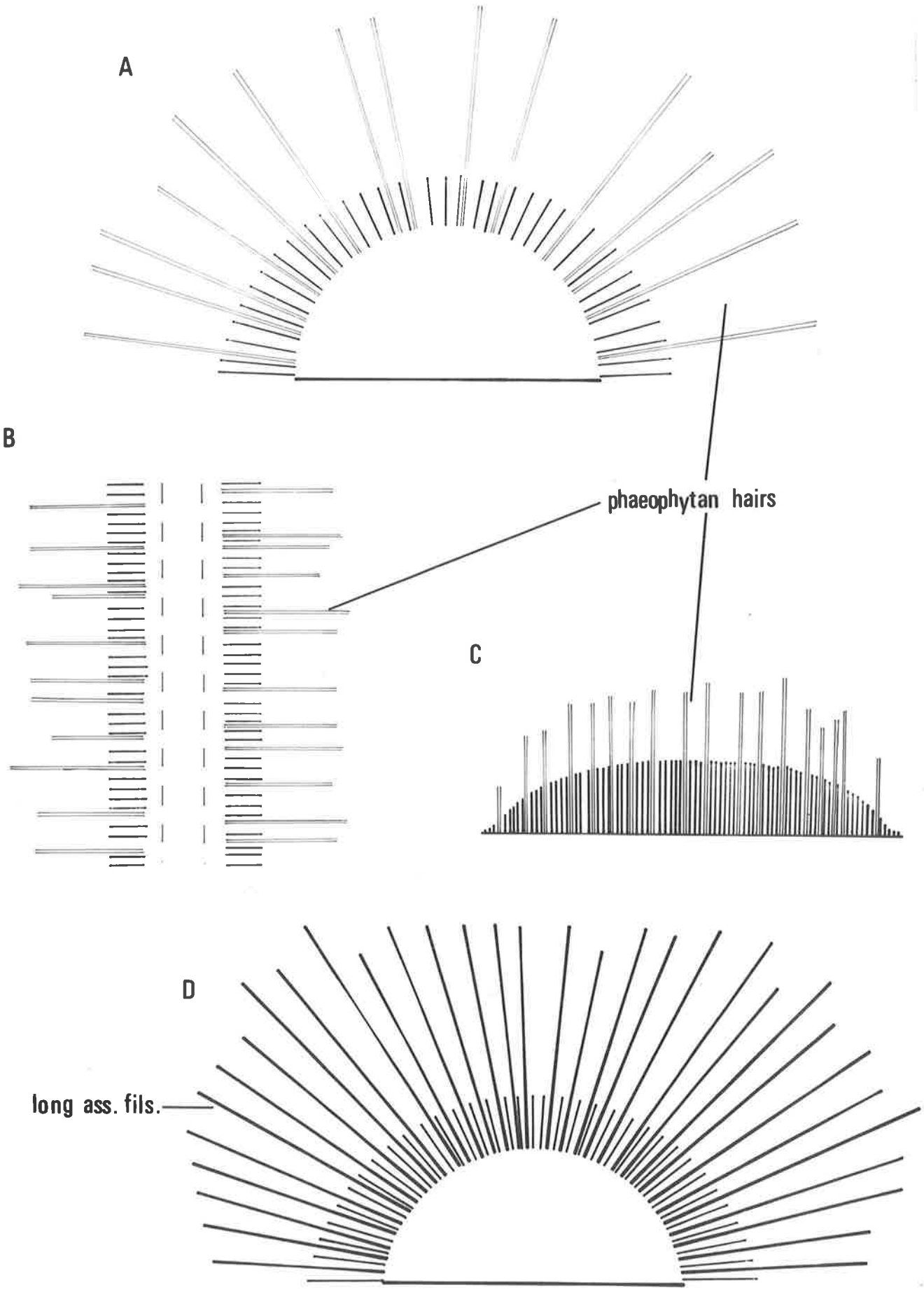

A
B
phaeophytan hairs
C
D
long ass. fils.

Figure 2. Myrionemaceae

A. *Myrionema strangulans* Grev.

1. Assimilatory filaments and unilocular sporangia; (ADU, A29639, Robe, S. Aust.)
2. Juvenile disc; (ADU, A49161, Woodbridge, Tas.)
3. Disc margin; (ADU, A29639)

B. *Myrionema latipilosum* sp. nov. (A48142, Onkaparinga River, S. Aust.)

1. Fragment of thallus with hair, ascocysts and unilocular sporangium.
2. Juvenile disc.
3. Margin of disc.
4. Assimilatory filaments.
5. Plurilocular sporangia, extended.

C. *Myrionema ramulans* sp. nov.

1. Hair, branched assimilatory filament, with plurilocular sporangium; (ADU, A48246, Normanville, S. Aust.)
2. Thallus fragment with short assimilatory filaments and pedicellate ascocysts; (ADU, A49058, Queenscliff, Vic.)
3. Margin of disc; (ADU, A49058)
4. Branched assimilatory filaments as sporangiophores; (ADU, A49058)
5. Unilocular sporangia; (ADU, A49058)

D. *Myrionema myriodesmae* sp. nov. (ADU, A28591, Seal Beach, K.I., S. Aust.)

1. Fragment of thallus, showing variable length of assimilatory filaments.
2. Hair, showing long basal and meristematic section.
3. Unilocular sporangia.

E. *Compsonema compactum* (Chapm.) comb. nov. (ADU, A47831, Encounter Bay, S. Aust)

1. Thallus fragment with hair, assimilatory filaments, and young plurilocular sporangia.
2. Hyaline marginal stoloniferous filaments.
3. Mature plurilocular sporangia and ascocyst.

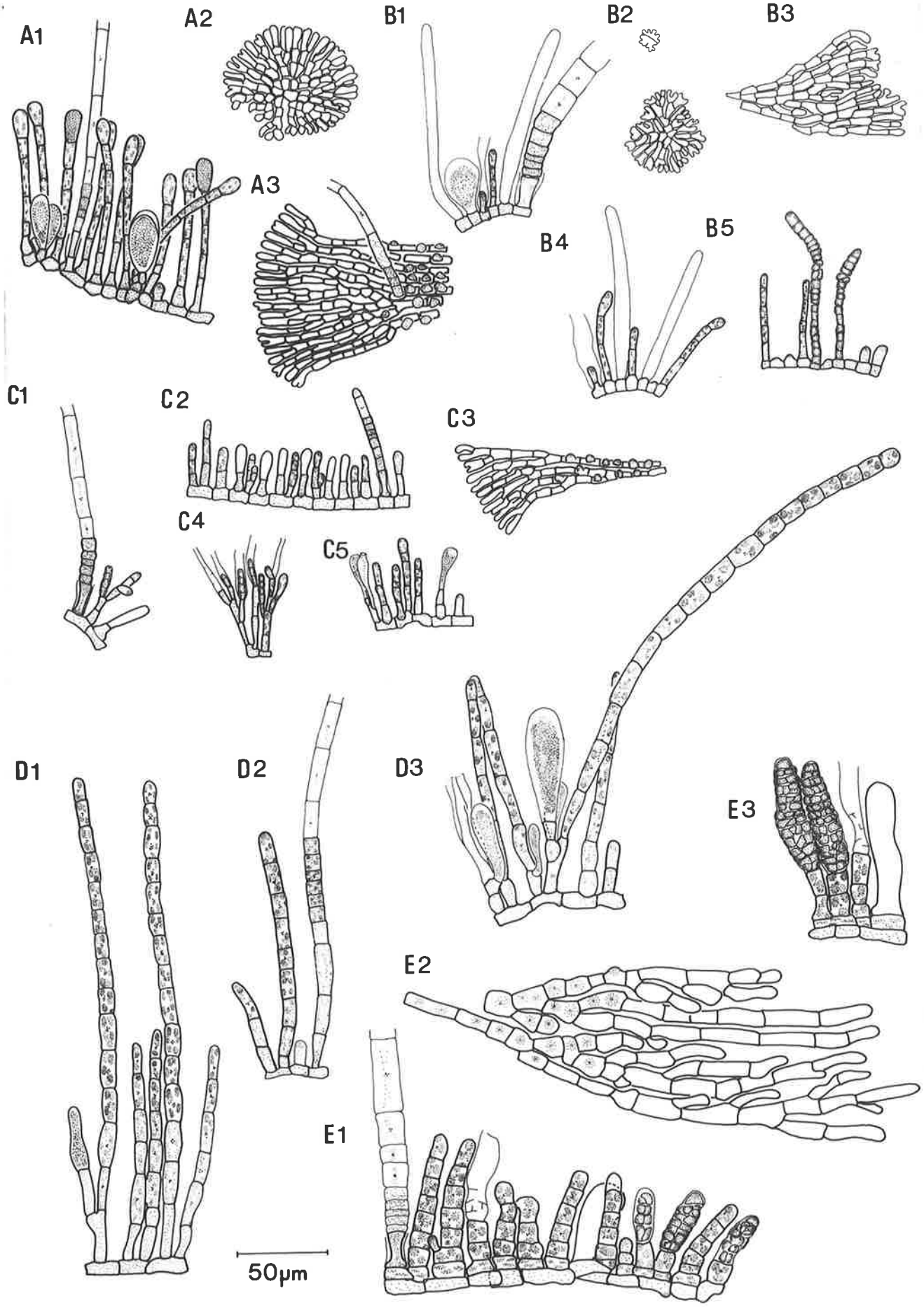

A1
A2
A3
B1
B2
B3
B4
B5
C1
C2
C3
C4
C5
D1
D2
D3
E1
E2
E3
50µm

Figure 3. *Elachista orbicularis* (Ohta) comb. nov.

1. Habit, on *Ecklonia radiata;* (after ADU, A50315, Encounter Bay, S. Aust.)
2. Cortical assimilatory filament and sporangiophores; ADU, A47847, Port Noarlunga, S. Aust.)
3. Fragment of thallus; (ADU, A47215, Port Noarlunga, S. Aust.)
4. Lower medullary cells and base, with rhizoidal pegs; ADU, A49377, type fragment, Tappi, Japan).
5. a. Base of long assimilatory filament, with rhizoidal pegs; (ADU, A49377).
   b. The same, (ADU, A49196, Aldinga reef, S. Aust.).
6. a. & b. Long assimilatory filament, with enlargement of cell to show stellate nucleus and phaeoplasts with pyrenoids; (ADU, A50315, Encounter Bay, S. Aust.).

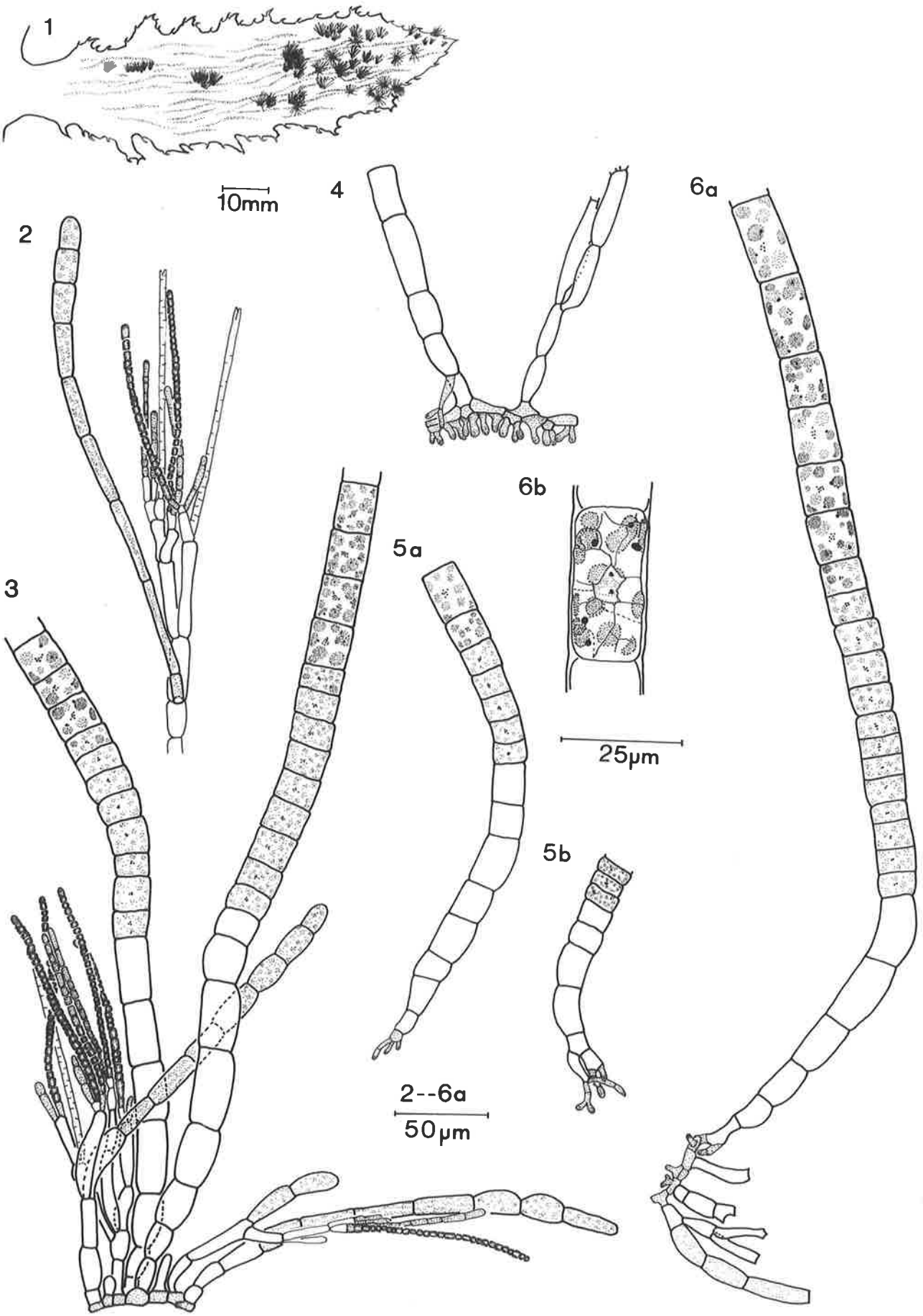

1
10mm
2
3
4
5a
5b
6a
6b
25µm
2--6a
50µm

Figure 4. *Elachista secundata* sp. nov.

1. Habit, on *Sargassum* sp.; (after ADU, A50331, Queenscliff, Vic.)
2, 3. Thallus fragments; (MELU 20520, Sorrento, Vic.)
4. Unilocular sporangium; (MELU 21207, Sorrento, Vic.)
5. Balloon cells and cortical assimilatory filament; (MELU 20520).
6. Lower medullary cells and base of thallus; (ADU, A50331).
7. Secundate sporangiophores on long assimilatory filament; (ADU, A50331).

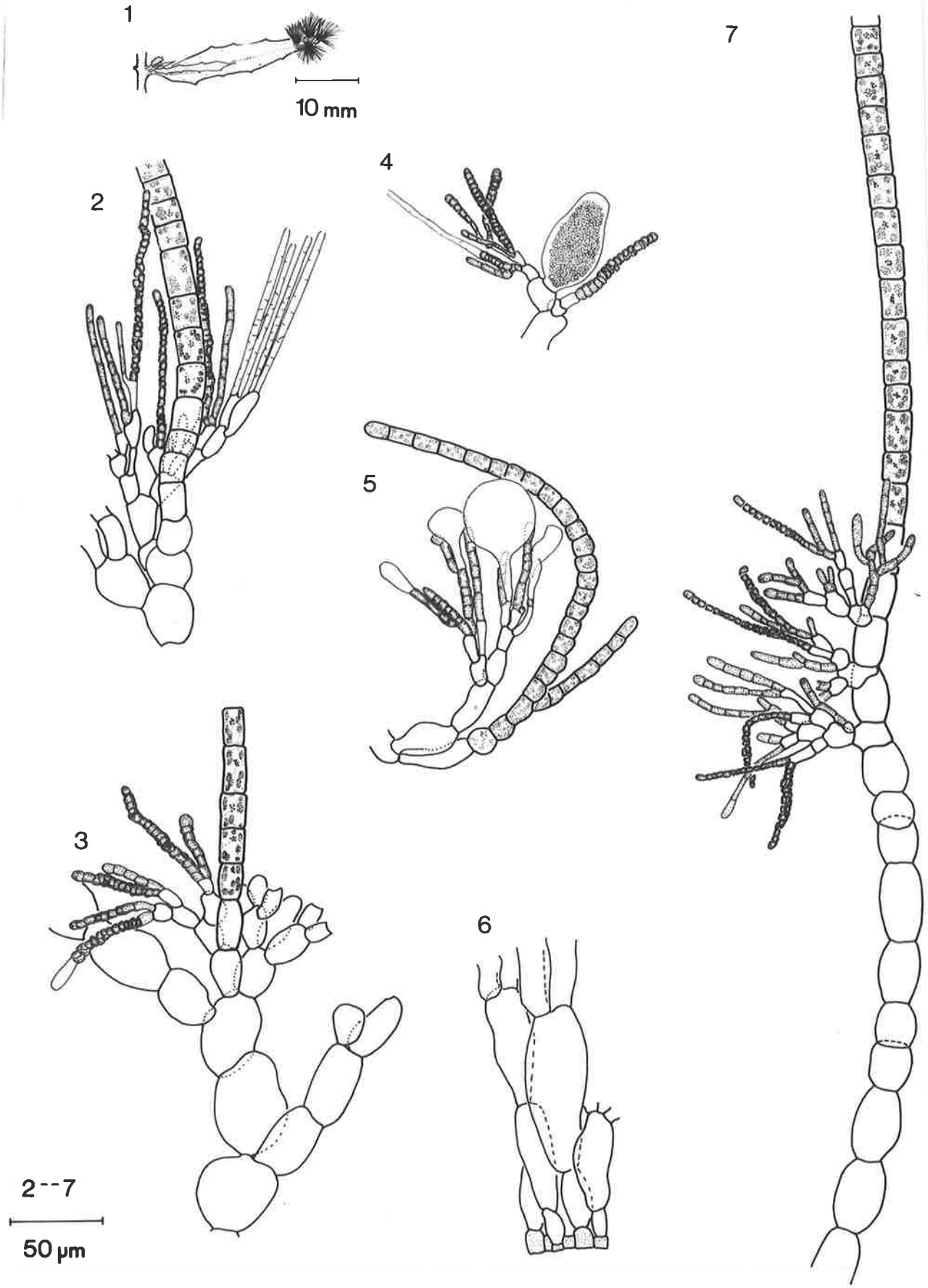

1
10 mm
2
4
5
7
3
6
2--7
50 µm

Figure 5. *Halothrix* species

1. *H. ephemeralis* sp. nov., habit, on *Heterozostera tasmanica;* (after ADU, A32664).
2. *H. ambigua* Yamada, cortical assimilatory filaments; ADU, A49376, Muroran, Japan).
3. *H. ephemeralis*, cortical assimilatory filament;(ADU, A32664, Aldinga reef, S. Aust.)
4. *H. ephemeralis*, plurilocular sporangia; (ADU, A32664).
5. *H. ephemeralis*, unilocular sporangia; (ADU, A32664).

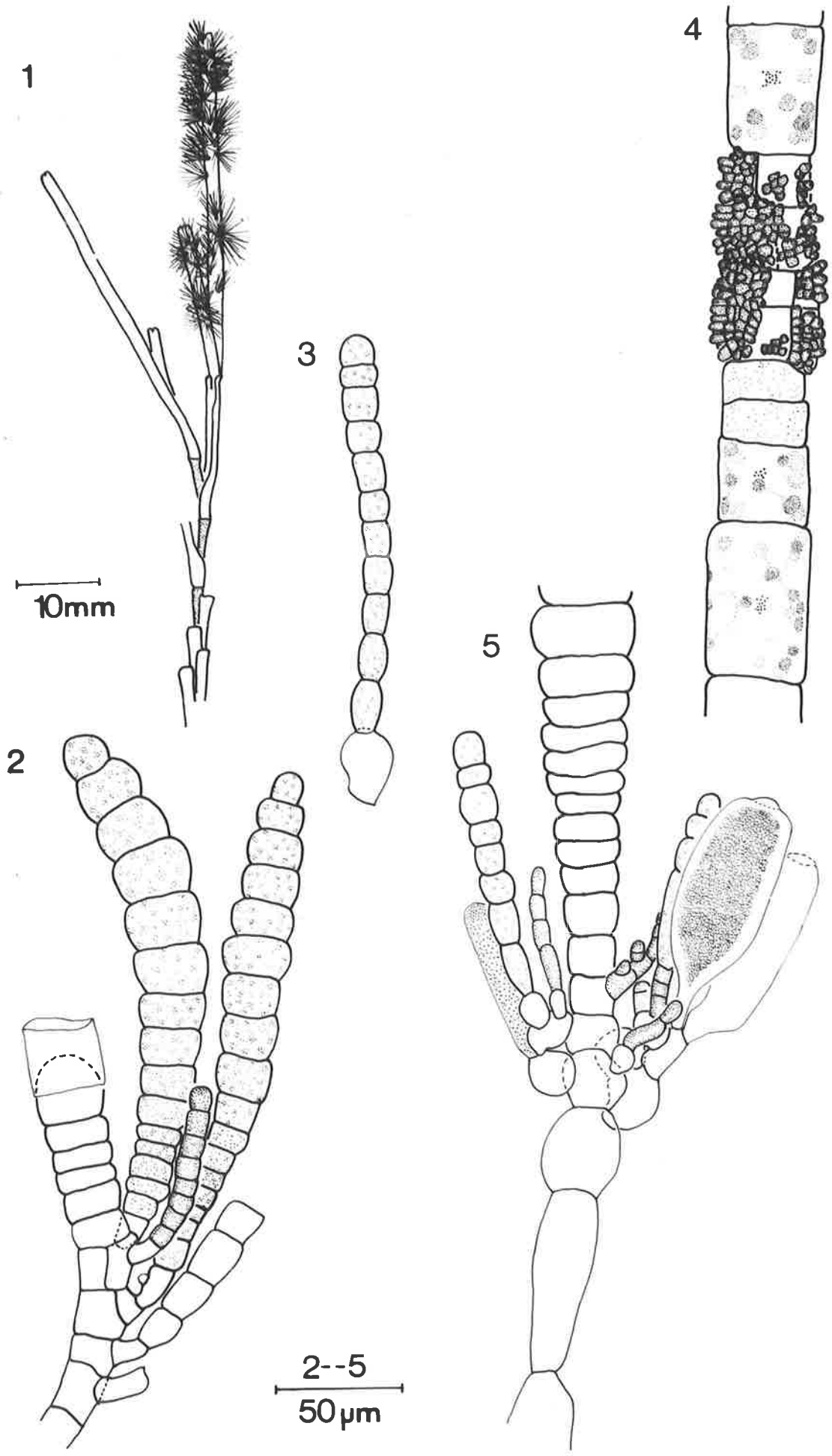

1
10mm
2
3
4
5
2--5
50 µm

Figure 6. *Portphillipia australis* (J.Ag.) Silva

1. Habit, on *Xiphophora chondrophylla* (after ADU, A34,809, Apollo Bay, Vic.)
2. Thallus fragment, boundary of medulla and cortex; (ADU, A49067, Point Lonsdale, Vic.)
3. Thallus fragment showing medullary filament and clampirons, as well as cortical and long assimilatory filaments; (ADU, A34,809).
4. Unilocular sporangia; (ADU, A49067).

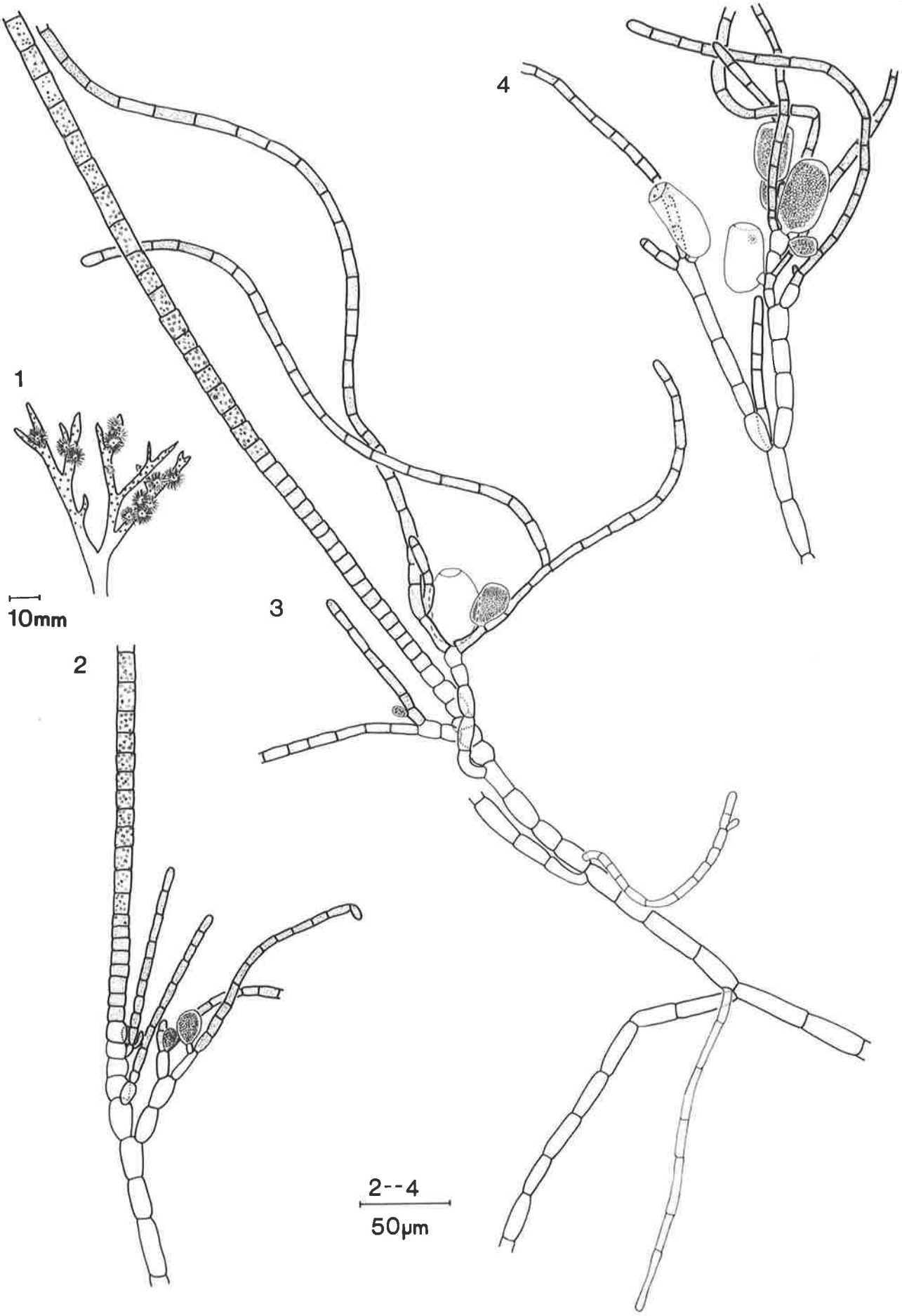

1
10mm
2
3
4
2--4
50µm

Figure 7. *Strepsithalia*

A. *Strepsithalia aemula* sp. nov. (ADU, A49564, Sou'West River, K.I., S. Aust.)

1. Thallus fragment showing hairs, cortical filaments as well as the curved nature of the basal system.
2. Unilocular sporangium.
3. Plurilocular sporangia.
4. Thallus fragment.
5. Thallus fragment showing an erect branch system with several cortical filaments.

B. *Strepsithalia liagorae* Sauvageau

1. Fragment of thallus, showing basal system and hair; (ADU, A47957, Apollo Bay, Vic.)
2. Fragment of thallus with cortical assimilatory filaments and empty unilocular sporangium; (ADU, A47957).
3. Thallus fragment with unilocular sporangia; (ADU, A49565, Point Sinclair, S. Aust.)

C. *Strepsithalia clavata* sp. nov. (ADU, A48890, Venus Bay, S. Aust.)

1a,b. Fragments of thallus with unilocular sporangia.
2a-d. Fragments of thallus with sporangiophores of plurilocular sporangia.
3. Cortical assimilatory filament with secondary plurilocular sporangia.

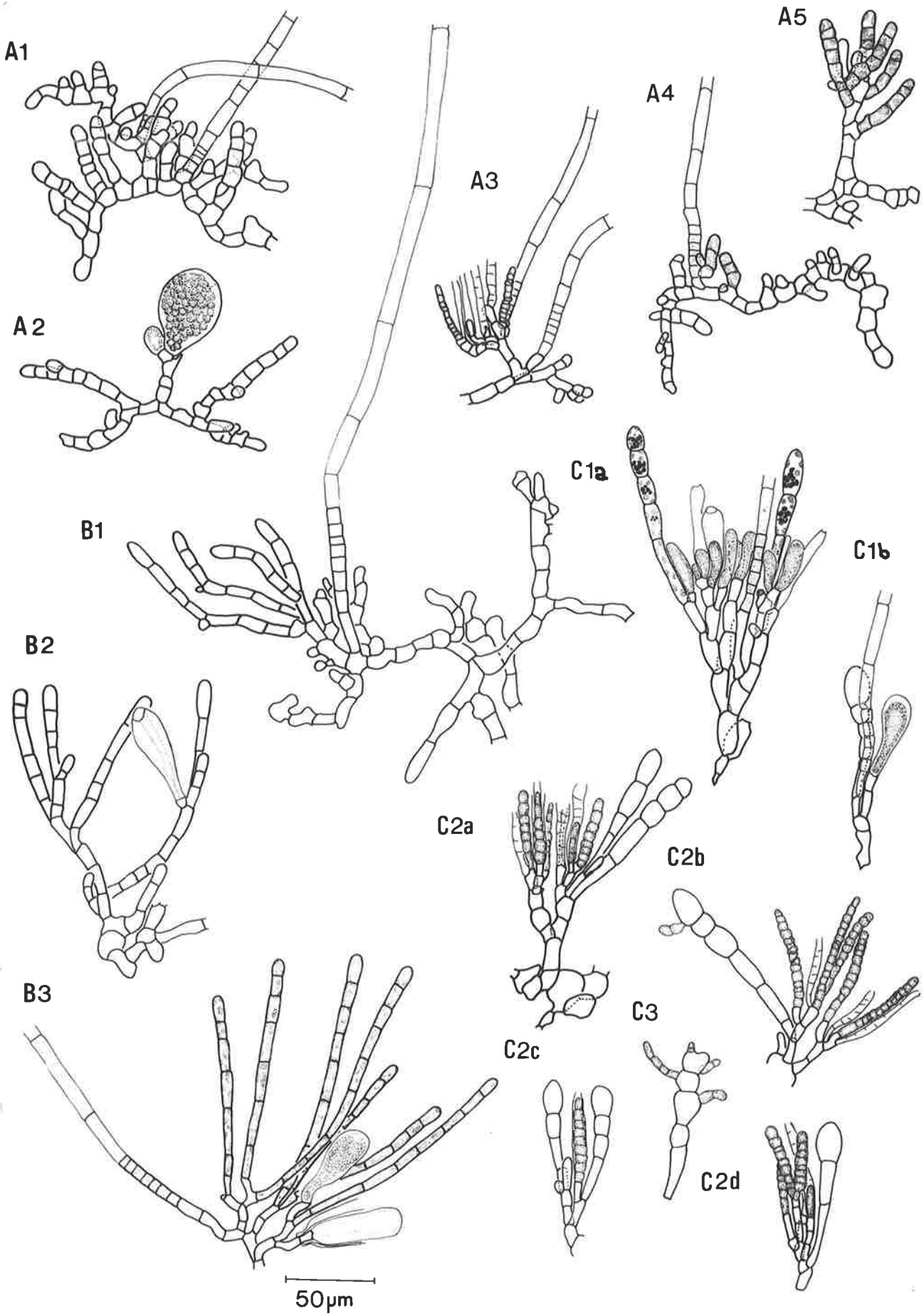

A1
A2
A3
A4
A5
B1
B2
B3
C1a
C1b
C2a
C2b
C2c
C2d
C3
50µm

Figure 8. *Myriactula*, 1

A. *Myriactula rivulariae* (Suhr) Feldm. var. *arabica*

1. Fragment of emergent thallus with unilocular sporangia; (ADU, A33619, Troubridge Light, S. Aust.)

B. *Myriactula rivulariae* var. *rivulariae*

1. Fragment of emergent thallus with unilocular sporangia; (ADU, A20836,

C. *Myriactula rivulariae* var. *chordae* (Aresch.) Rosenv. (ADU, A49777, Aldinga reef, S. Aust.)

1. Fragment of thallus with hair.
2. Fragment with juvenile cortical assimilators.
3. Fragment with unilocular sporangia, showing rhizoidal system in host (*Leathesia difformis*).

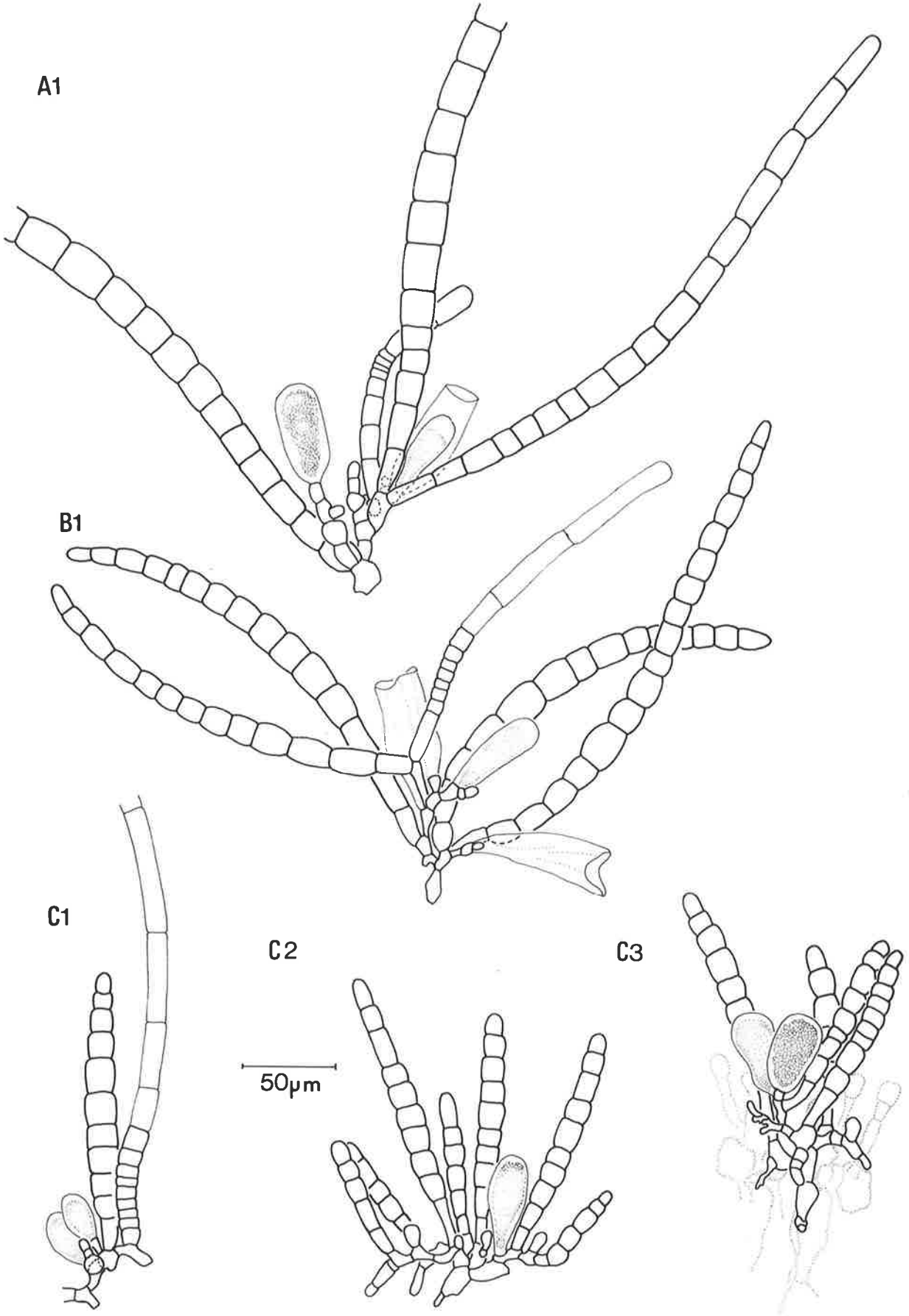

A1
B1
C1
C2
C3
50µm

Figure 9. *Myriactula*, 2

A. *Myriactula rivulariae* var. *arabica* (Kütz.) comb. nov.

1. Epicellular secondary plurilocular sporangia on cortical assimilatory filaments; (ADU, A48,241, Normanville,S.Aust.)
2. Emergent thallus fragment with primary plurilocular sporangia; (ADU, A48827, Normanville, S. Aust.)

B. *Myriactula haydenii* (Gatty) Levr. (ADU, A31873; Wanna, S.Aust.)

1. Thallus fragment drawn in situ, in host (*Scytosiphon lomentaria*).

2a & b. Emergent thallus fragments.

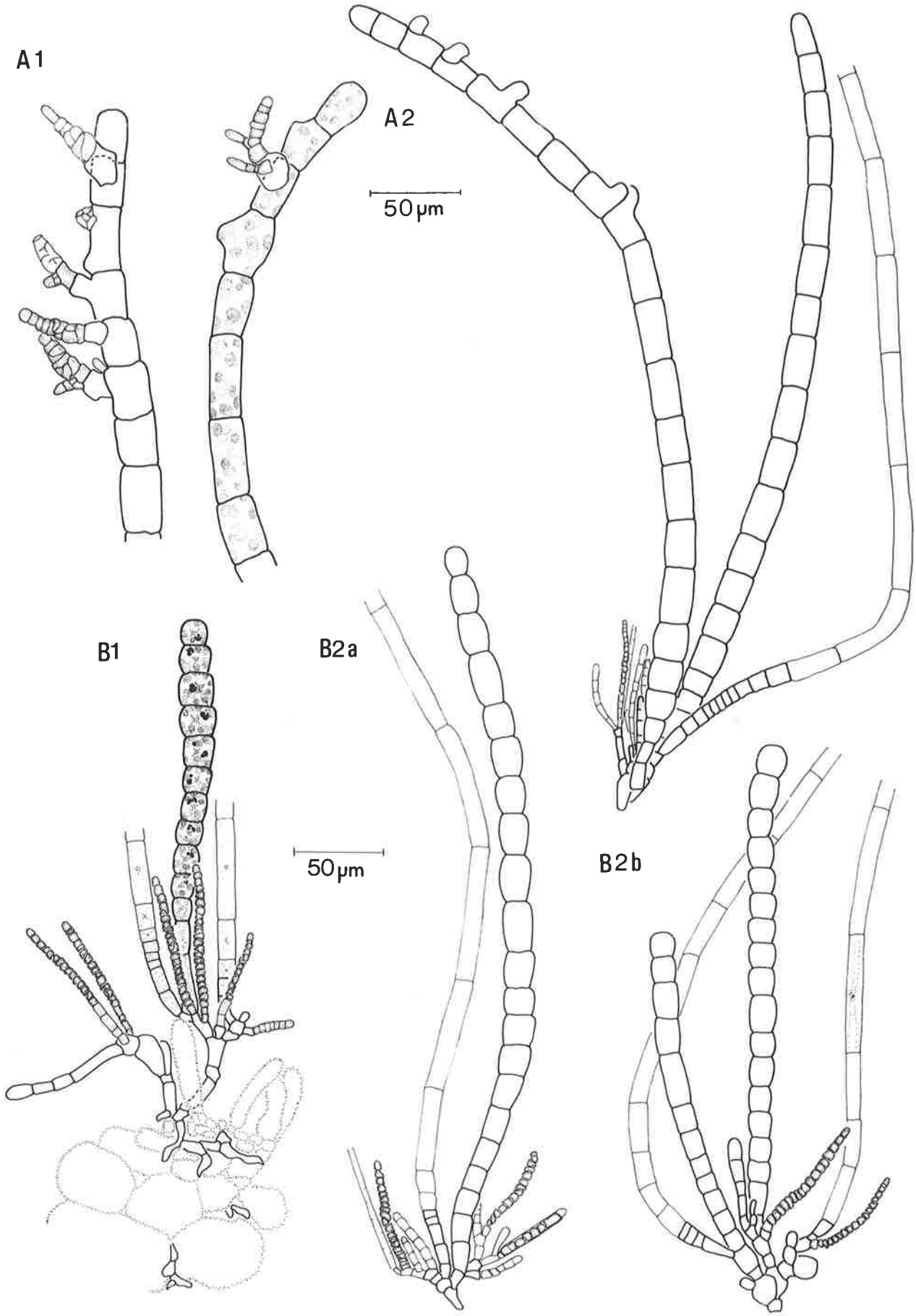

A1
A2
50µm
B1
B2a
50µm
B2b

Figure 10. *Corynophlaea cystophorae* J. Ag.

1. Cortical assimilatory filaments (round celled), hair and unilocular sporangia; (ADU, A32188, Balgowan reef, S. Aust.)
2. Cortical assimilatory filaments (deltoid celled), sporangiophores with plurilocular sporangia; (ADU, A48582, Aldinga reef, S. Aust.)
3. Habit, on *Cystophora torulosa*; (ADU, A47858, Marengo, Vic.)
4. Cortical filament; (ADU, A31759, Apollo Bay, Vic.)
5. Cortical filaments; (ADU, A47271, Encounter Bay, S. Aust.)
6. Cortical filament; (ADU, A48851, Robe, S. Aust.)
7. Cortical filament; (ADU, A47858, Marengo, Vic.)
8. Medullary cells; (ADU, A31759).

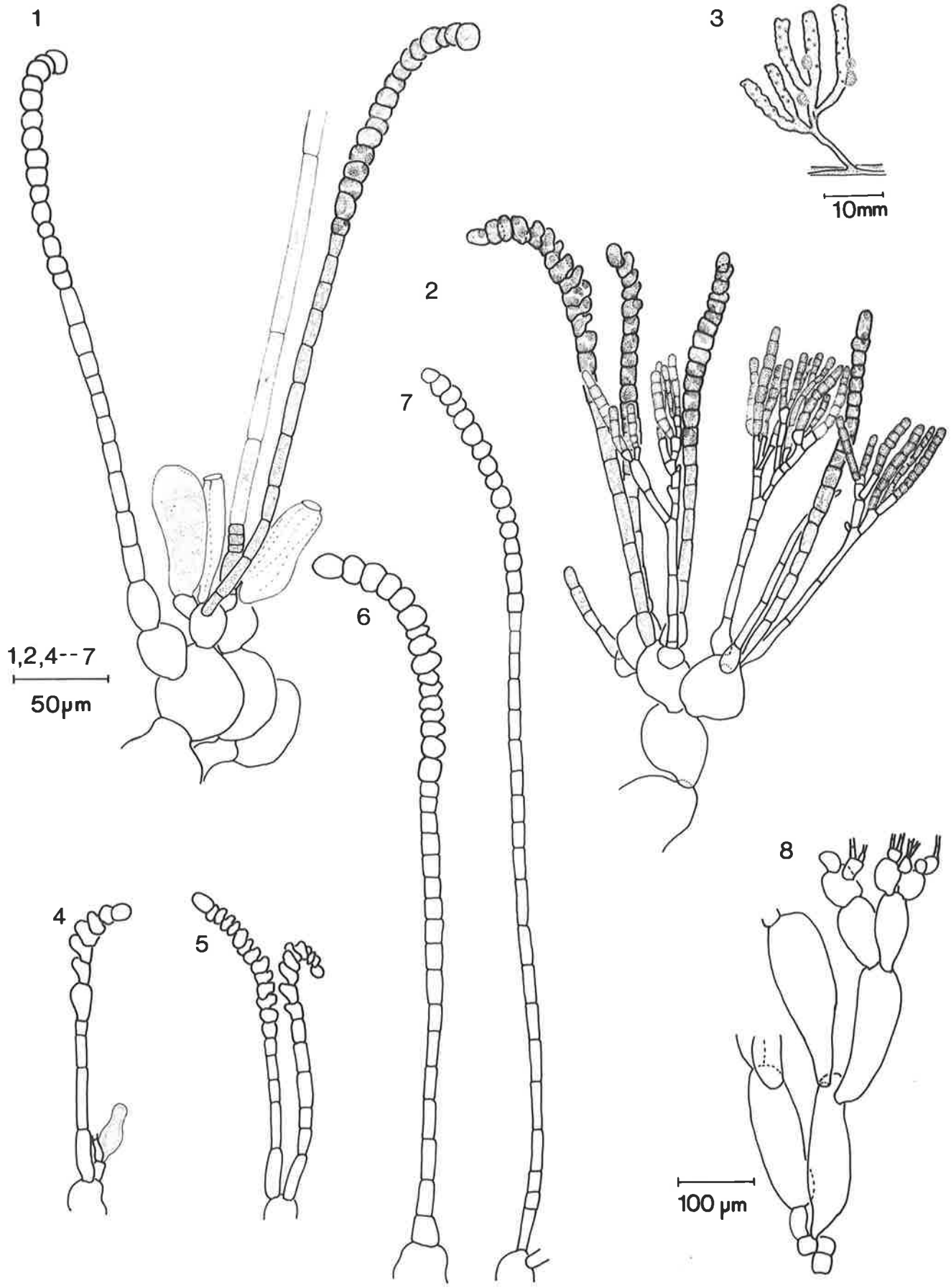

1
3
10mm
2
7
6
1,2,4--7
50µm
4
5
8
100 µm

Figure 11. *Corynophlaea* (cont'd)

A. *Corynophlaea filiformis* sp. nov. (ADU, A48582, Aldinga reef, S. Aust.)

1. Habit, on *Cystophora polycystidea*.
2. Cortical assimilatory filament.
3. Part of a sporangiophore, and subtending hair.
4. Part of sporangiophore.

B. *Corynophlaea cristata* sp. nov.

1. Upper cells of cortical assimilatory filaments with plurilocular sporangia; (ADU, A48886, Point Westall, S. Aust.).
2. Habit, on *Cystophora brownii;* (after ADU, A48630, Aldinga reef, S. Aust.).
3. Portion of thallus to show upper medulla and cortex, (ADU, A48886).
4. Medullary cells, showing tristichous branching; (ADU, A48630).

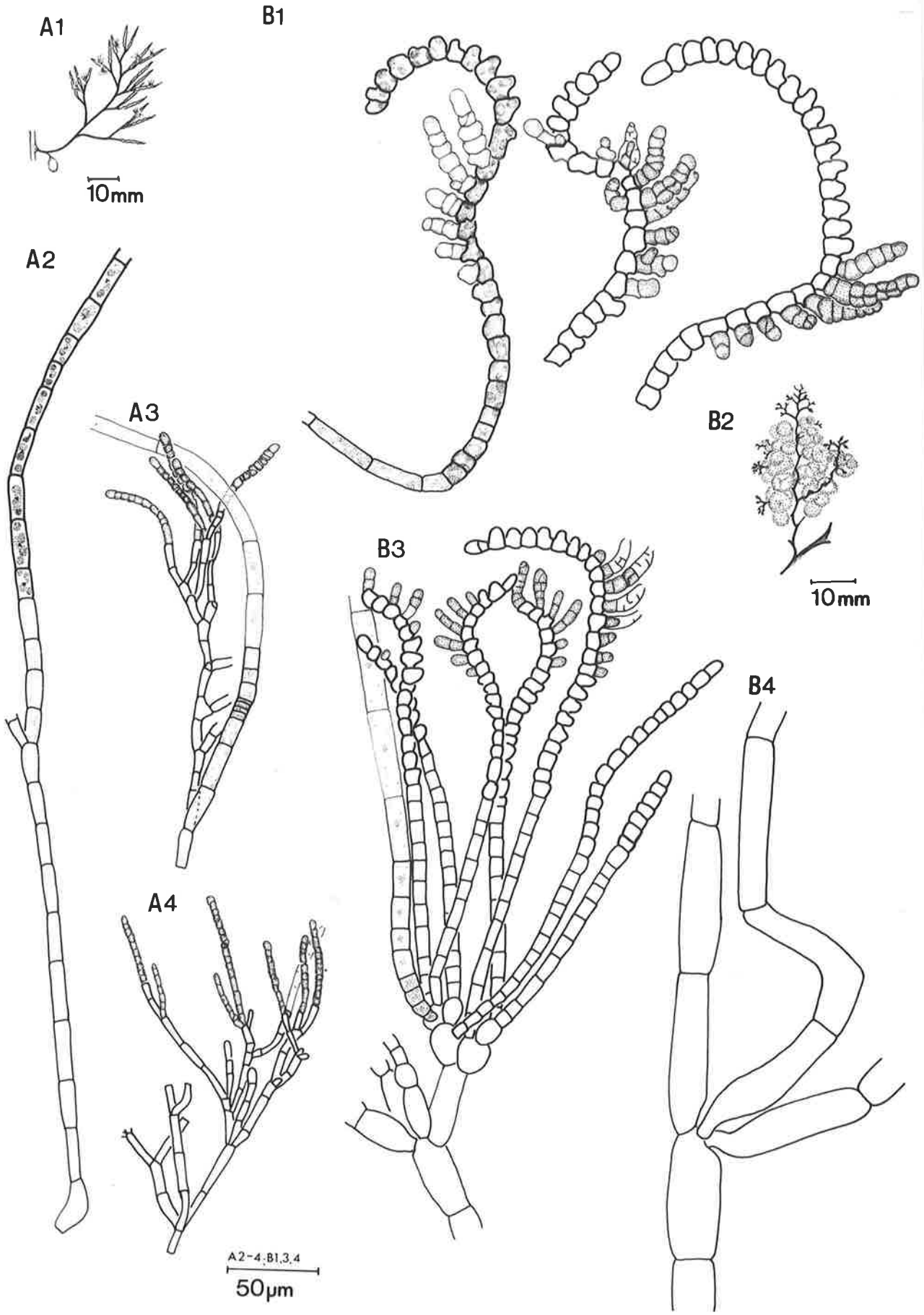

A1
10mm
B1
A2
A3
B2
10mm
B3
B4
A4
A2-4, B1, 3, 4
50μm

Figure 12. *Leathesia* and *Petrospongium*

A. *Leathesia difformis* (L.) Aresch.

1. Unilocular sporangia and long cortical filaments; (ADU, A47844, Normanville, S. Aust.).
2. Plurilocular sporangia and short cortical filaments; (ADU, A47962, Apollo Bay, Vic.).
3. Upper medulla, with intermediate cortical filaments; (ADU, A49174, Safety Cove, Tas.).
4. Plurilocular sporangium, hair and long cortical filaments; (ADU, A48889, Point Westall, S. Aust.).

5a. Habit, on coralline turf; (after ADU, A47960, Apollo Bay, Vic.).

5b. Habit, epiphytic on *Posidonia* sp.; (after ADU, A48627, Aldinga reef, S. Aust.).

B. *Leathesia intermedia* Chapm.

1. Habit, on *Caulerpa* sp. (after ADU, A47503, Robe, S.Aust.) (same scale as A5).
2. Unilocular sporangia, cortical assimilatory filaments, and hair; (ADU, A49180, Gordon, Tas.).
3. Plurilocular sporangia; (ADU, A47969, Robe, S. Aust.).
4. Medullary system; (ADU, A29943, Rocky Cape, Tas.).

C. *Petrospongium rugosum* (Okam.) S. & G.

1. Cortex, showing hair and branched cortical filaments; (ADU, A50231, Point Lonsdale, Vic.).
2. Unilocular sporangia, and buttress filament (ADU, A50231).
3. Habit; (after ADU, A50231).

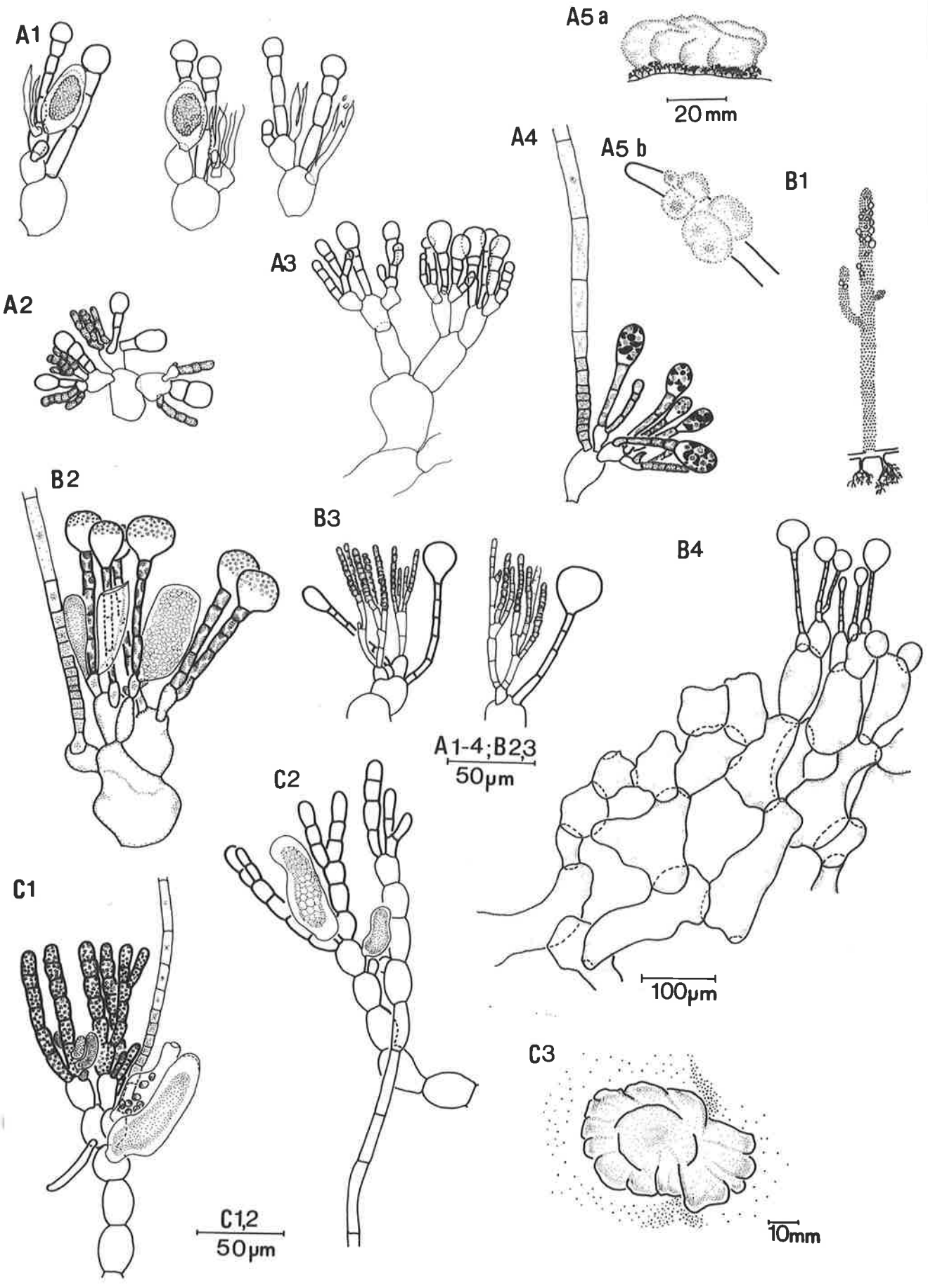

A1
A5 a
20 mm
A4
A5 b
B1
A3
A2
B2
B3
B4
A1-4;B2,3
50µm
C2
C1
100µm
C3
C1,2
50µm
10mm

Figure 13. *Flabellonema codii* gen et sp. nov., 1.

1. Habit, on utricle of *Codium mamillosum;* (ADU, A20906, Stanley Beach, K.I., S. Aust.).
2a. Branch, lateral; (ADU, A20906).
2b. Lateral plurilocular sporangium; (ADU, A20906).
2c. Branch, showing apical system; (ADU, A20906).
2d. Intercalary plurilocular sporangium; (ADU, A20906).
2e. Branches, with intercalary plurilocular sporangium; (ADU, A20906).
3. Terminal plurilocular sporangium; (ADU, A48123; Normanville, S. Aust.).

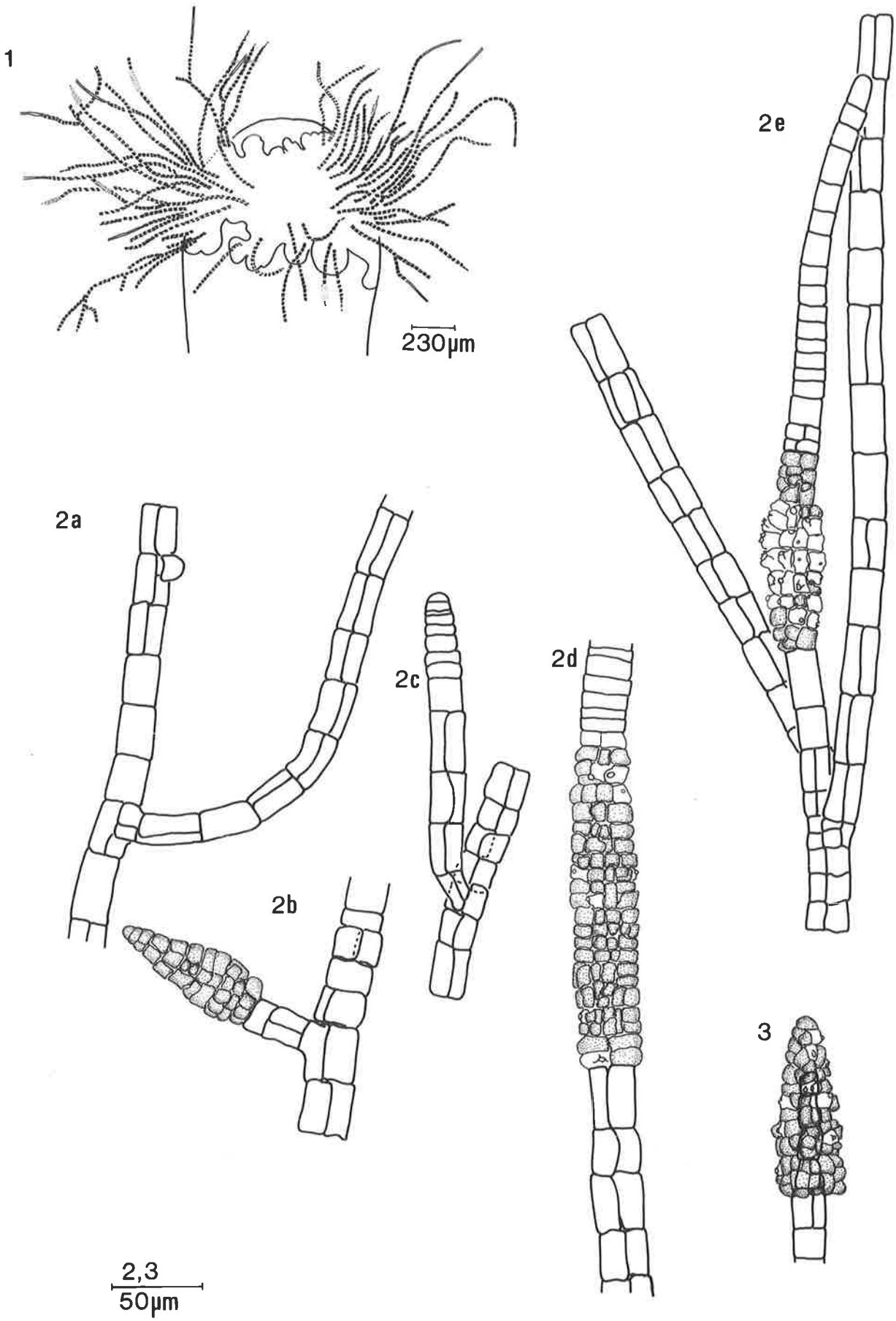

1
230µm
2e
2a
2c
2d
2b
3
2,3
50µm

Figure 14. *Flabellonema codii*, 2.

1, 1a. Hair filament, with one hair cell enlarged; (ADU, A20906).
2, 2a, b. Disc, with two erect axes, with axillary cells and disc cells, with axis initial, enlarged; (ADU, A48123).
3. New disc arising from stolon-like filament from older disc; (ADU, A20906).
4. Bases of erect axes; (ADU, A20906).

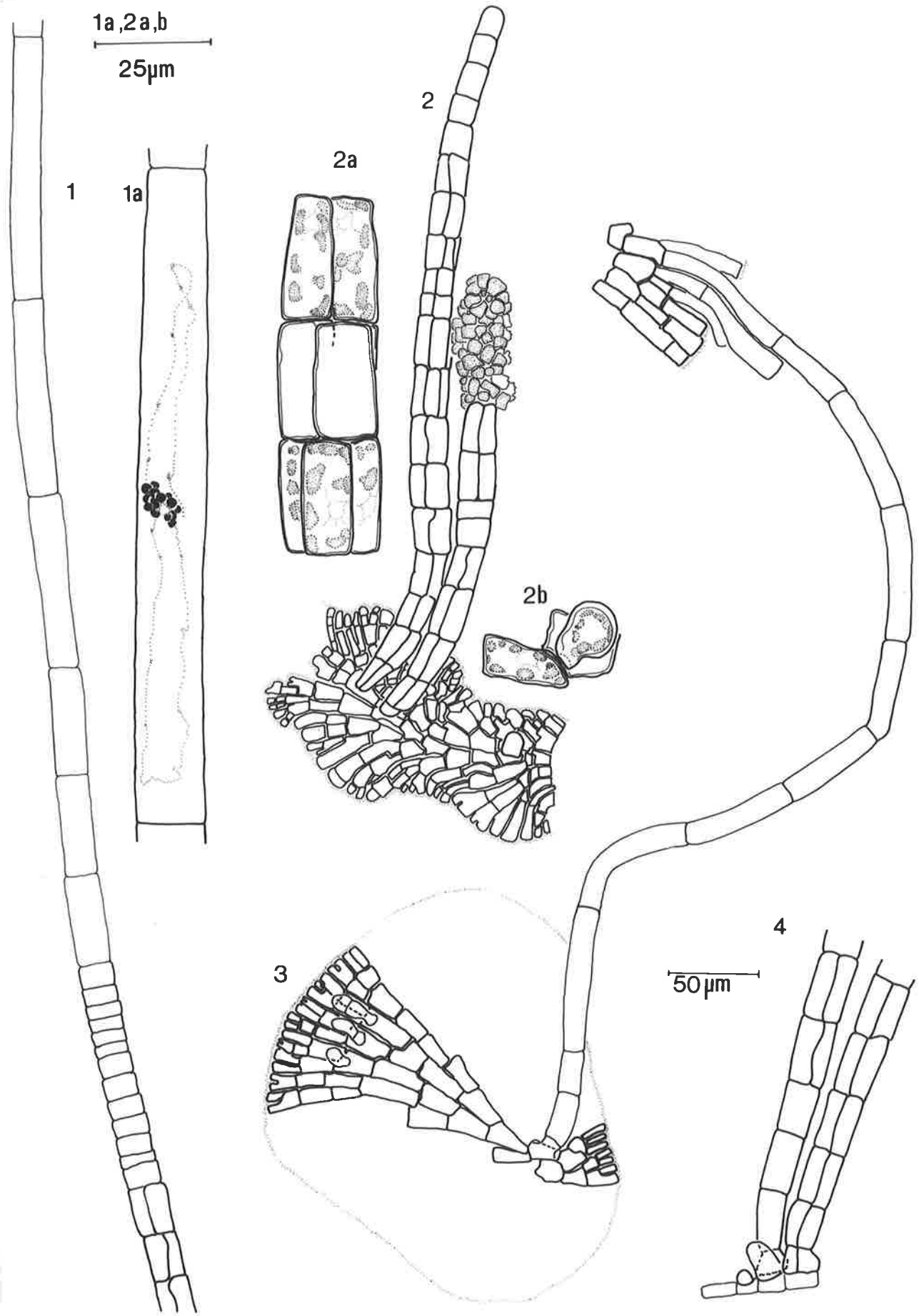

1a ,2 a ,b
25µm
1
1a
2
2a
2b
3
4
50 µm

Figure 15. *Giraudya sphacelarioides* Derbès et Solier

1. Erect axis showing meristem and basal rhizoides; (ADU, A48579, Aldinga reef, S. Aust.).
2, 2a. Erect axis with two tiers of cells enlarged; (ADU, A48579).
3. Base of erect axis and axial initial; (ADU, A48579).
4a, b. Transverse sections of erect axes; (ADU, A48226, Aldinga reef, S.Aust.).
5. Intercalary plurilocular sporangia; (ADU, A35104, Port Gawler, S. Aust.).
6. Intercalary plurilocular sporangium, immature, (ADU, A35104).
7. Lateral plurilocular sporangia in sori; (ADU, A29612, Aldinga reef, S. Aust.).
8. Basal, branched plurilocular sporangium; (ADU, A29612).

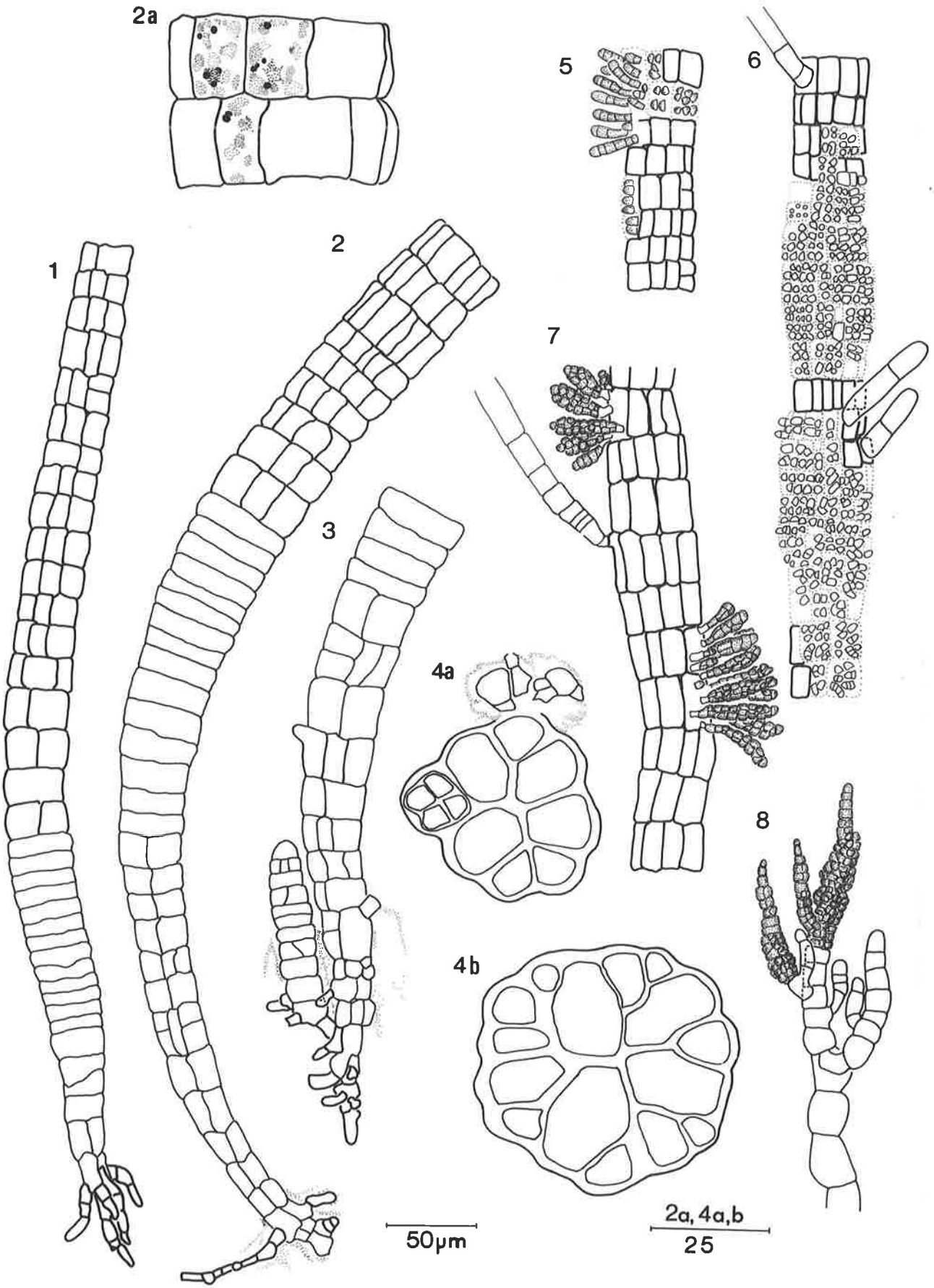

2a
1
2
3
4a
4b
5
6
7
8
50µm
2a, 4a,b
25

Figure 16. *Giraudya robusta* sp. nov., 1. (ADU, A20123, Pennington Bay, K.I., S.Aust.)

1. Unilocular sporangium and basal hair.
2. Basal plurilocular sporangium and base of erect axis.
3. Lateral plurilocular sporangia and solitary, subterminal hair.
4. Lateral branch with plurilocular sporangia.

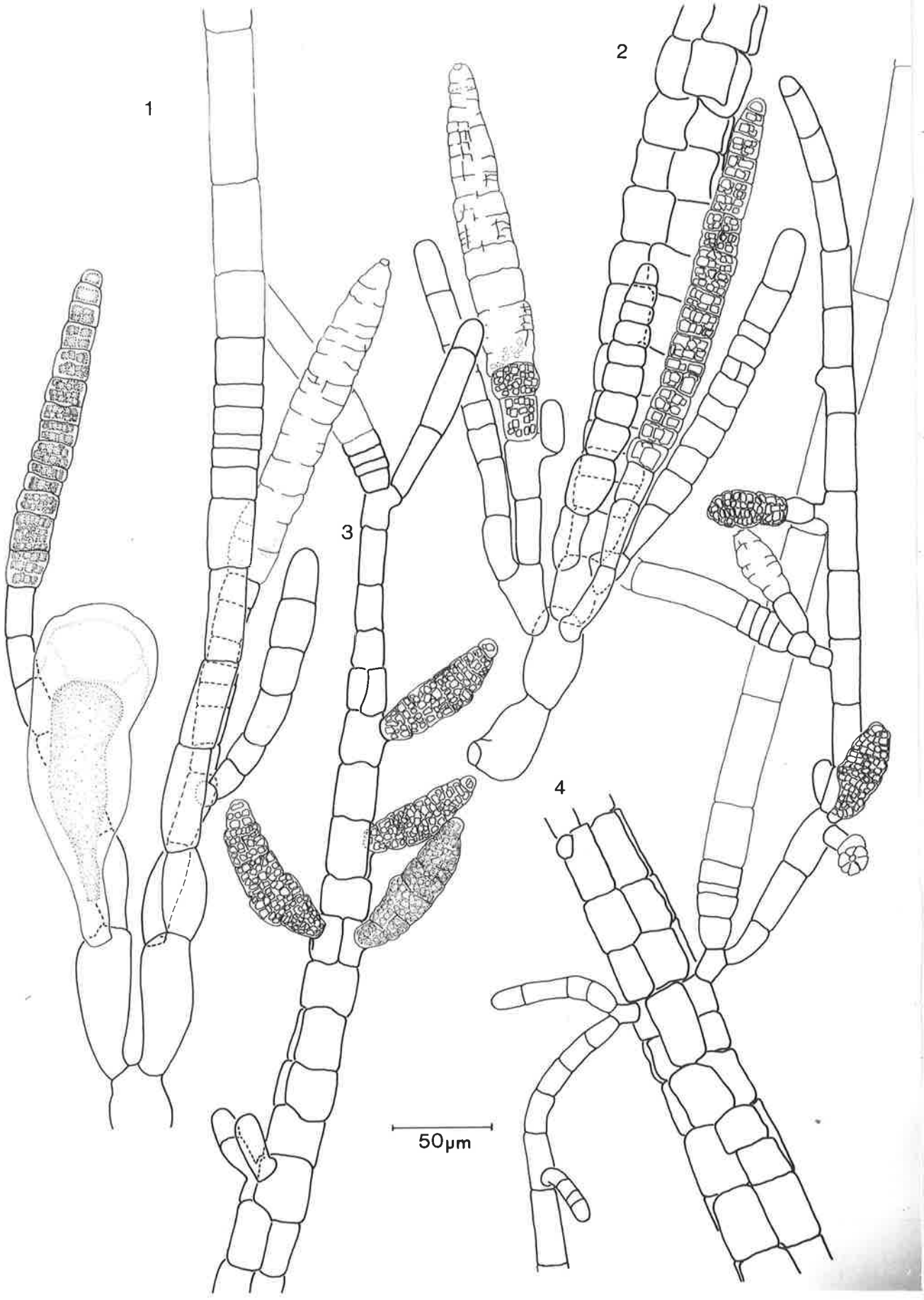

1
2
3
4
50µm

Figure 17. *Giraudya robusta* sp. nov., 2.

1. Tiers of axial cells; (ADU, A48243, Normanville, S. Aust.).
2. "Buoyancy" cells, showing anastomosis, at base of erect axes; (ADU, A48243).
3. Base of medulla; (ADU, A48911, Port Neil, S. Aust.)
4. Transverse section of tier of cells of erect axis; (ADU, A49412, Tipara reef, S. Aust.).
5. Rhizoids at base of erect axis; (ADU, A48243).
6. Base of erect axis, with basal bulb; (ADU, A48243).
7. Hair cell, enlarged; (ADU, A48243).

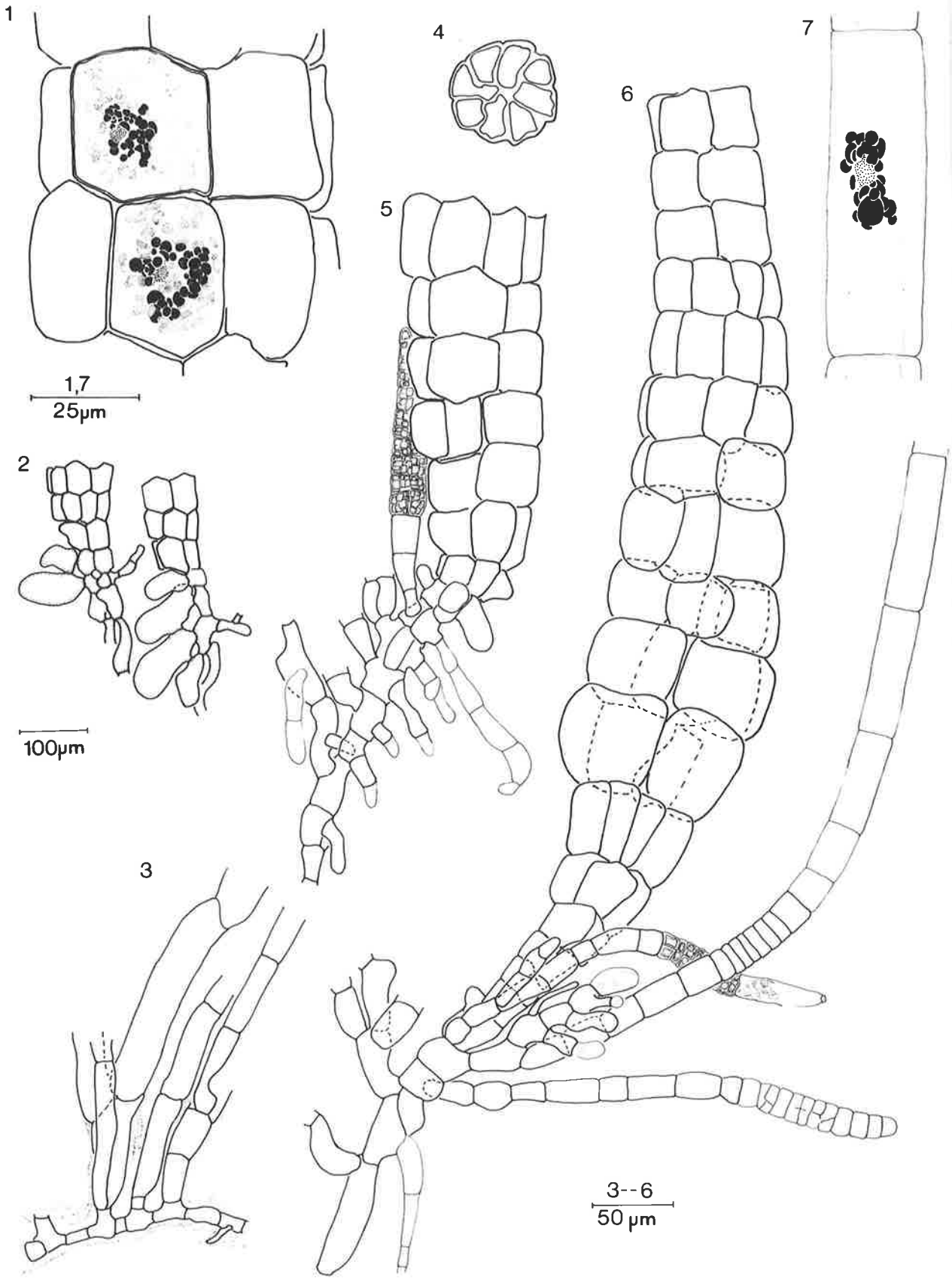

1
1,7
25µm
2
100µm
3
4
5
6
7
3--6
50 µm

Figure 18. Cultures, 1.

A. *Myrionema strangulans* Grev.

1. Tubular germlings, after two days; (ADU, A49513; ME-III).
2. Three-day plants; (ADU, A48259; ME-II).
3. Seven-day plants; (ME-II).
4. Juvenile pseudodiscoid thallus, after ten days; (ME-III).
5. Juvenile filamentous thallus, after ten days; (ME-III).

B. *Myrionema latipilosum* sp. nov. (ADU, A48142, ZT-I)

1. Amoeboid germlings, after two days.
2. Three-day plants, both amoeboid and tubular.
3. Seven-day plants, discoid, pseudodiscoid and filamentous.
4. Young disc, after eleven days.
5. Young filamentous plants, after eleven days.

C. *Elachista orbicularis* (Ohta) comb. nov.

1. Tubular germlings; (ADU, A47874; EN-III).
2. Three-day plants; (EN-III).
3. Four-day plants; (EN-III).
4. Five-day plants; (EN-III).
5. Seven-day plants; (EN-III).
6. Young plant with plurilocular sporangium, after thirty days; (EN-III).
7. Fragment of plant to show stolon-like behaviour of long assimilators in culture, after twenty days; (ADU, A49252, EA-IV).

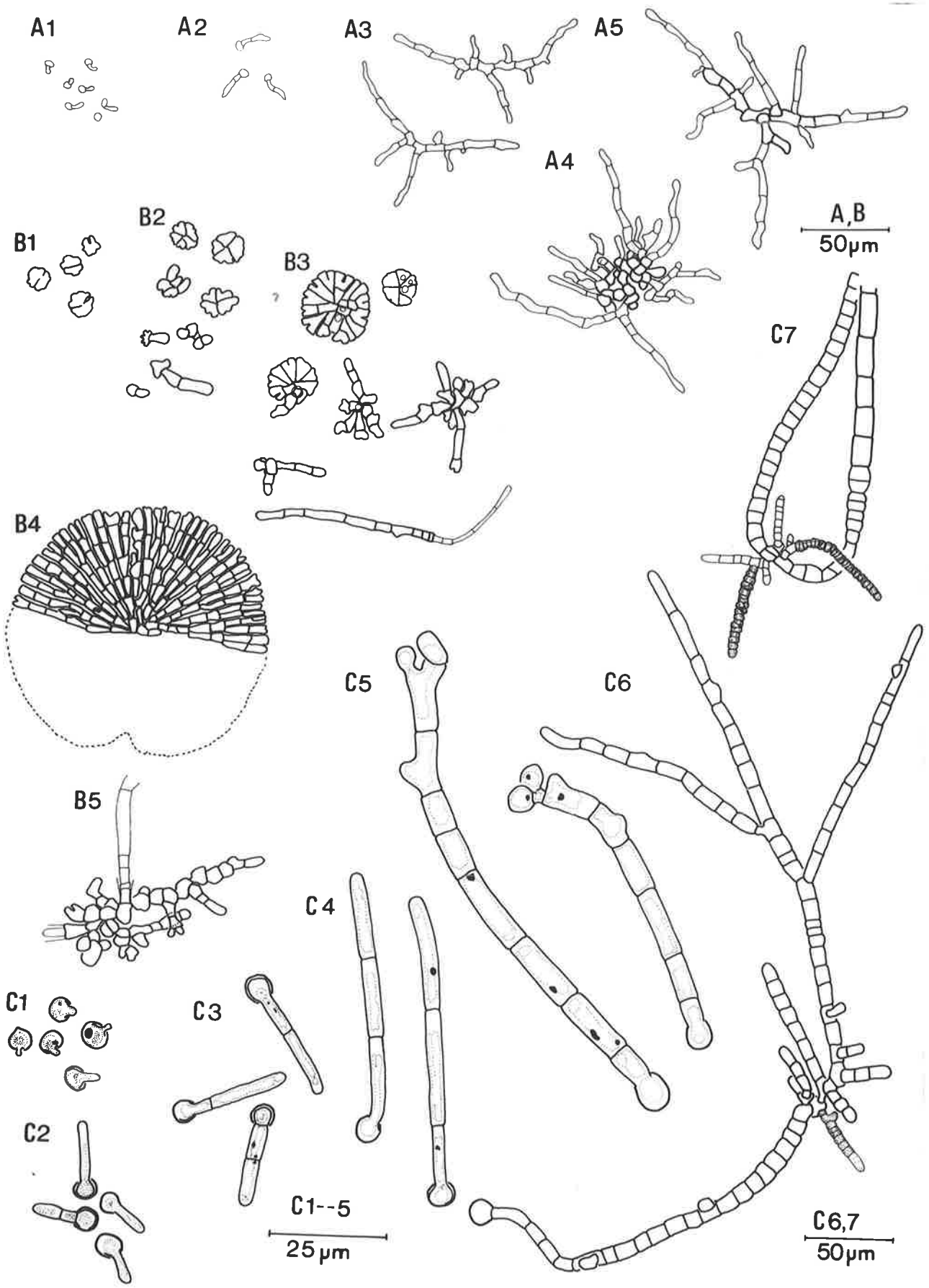

A1
A2
A3
A5
A4
A,B
50µm
B1
B2
B3
B4
B5
C7
C5
C6
C4
C1
C3
C2
C1--5
25µm
C6,7
50µm

Figure 19. Culture plants, 2.

A. *Giraudya sphacelarioides* Derbès et Solier

1. Tubular germlings; (GA-I)
2. Plants, after five days; (GA-I)
3. Fragment of plant with new erect axis, after 20 days; (ADU, A49782, GA-V).

B. *Giraudya robusta* sp. nov.

1. Tubular germlings, after three days; (ADU, A48859, GR-III).
2. Plant, after thirteen days; (GR-III).
3. Portion of plant with juvenile erect axis, after 5 months, no kinetin; (GR-III).
4. Portion of plant with older erect axis, after 5 months, no kinetin; (GR-III).

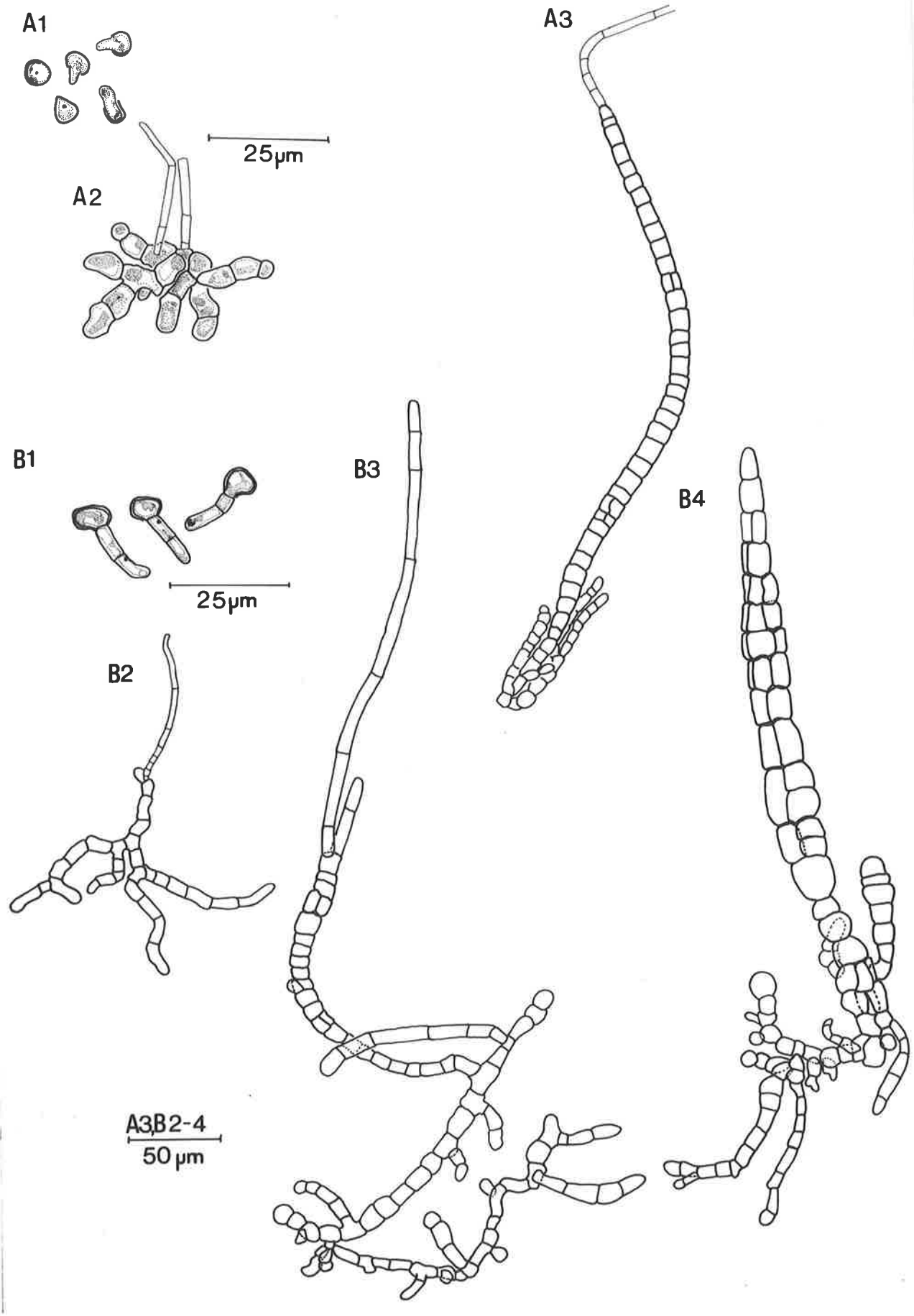

A1
25µm
A2
A3
B1
25µm
B2
B3
B4
A3,B2-4
50 µm

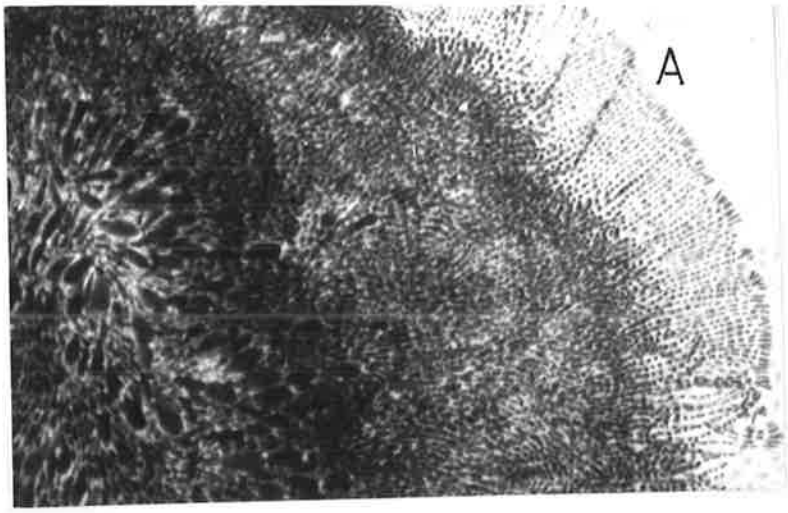
PLATE 1. Myrionemaceae

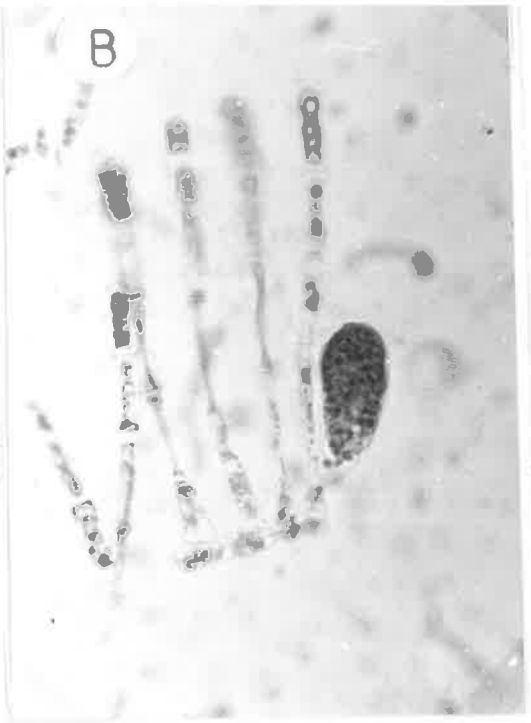
Myrionema strangulans Grev.

A. Segment of thallus, on *Ulva lactuca*. (Robe, S. Aust.; ADU, A29639).
B. Assimilatory filaments and unilocular sporangium. (Robe, S. Aust.; ADU, A47501).

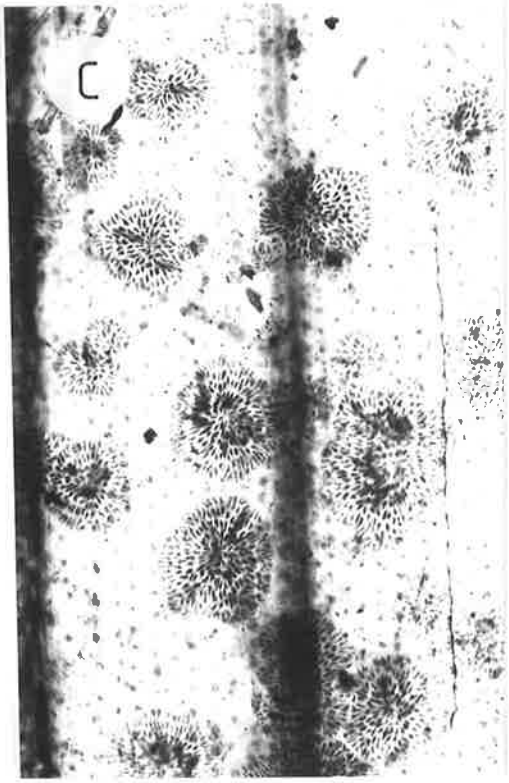
Myrionema latipilosum sp. nov.

C. Numerous thalli on blade of *Zostera* sp. (Onkaparinga Estuary, S. Aust.; ADU, A48142).
D. Hairs and erect filaments. (ADU, A48142).
E. Plurilocular sporangium and ascocyte. (ADU, A48142).
F. Unilocular sporangia and empty plurilocular sporangia. (ADU, A48141).

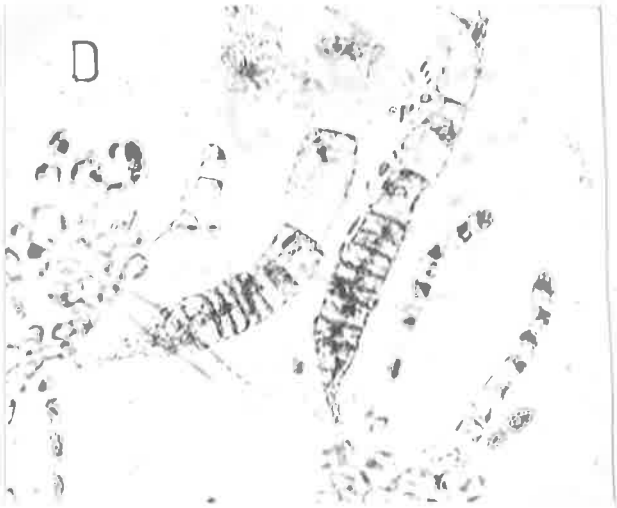


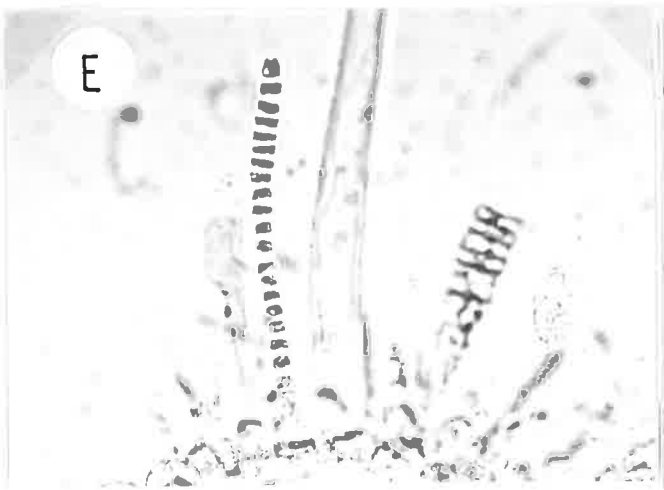


A,C
100 µm



B,D-F
50 µm





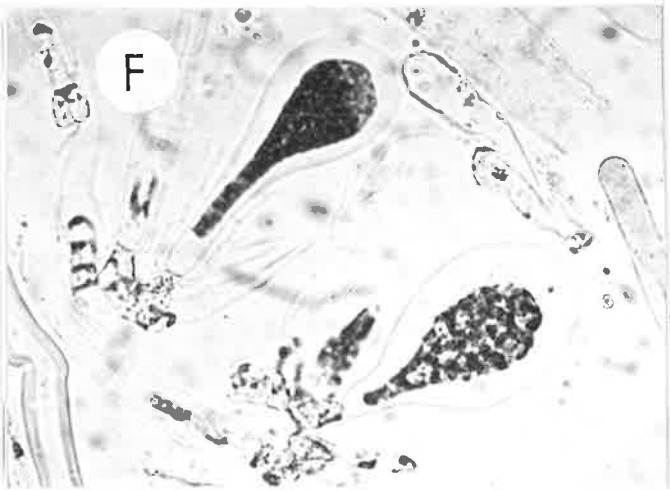


PLATE 2. Myrionemaceae (Cont'd)

Myrionema ramulans sp. nov.

A. Portion of thallus with mature assimilatory filaments and hairs. (Queenscliff, Vic.; ADU, A49058).
C. Immature assimilatory filaments and hair on long basal cells. (ADU, A49058).
B. Branched assimilatory filaments as sporangiophores for plurilocular sporangia (ADU, A49058).

Myrionema myriodesmae sp. nov.

D. Portion of thallus, with unilocular sporangia. (Seal Beach, Kangaroo I., S. Aust.; ADU, A28591).
E. Hair, showing long meristem, and short assimilatory filaments. (ADU, A28591).

Compsonema compactum sp. nov.

F. Single layered base and ascocysts. (Encounter Bay, S. Aust.; ADU, A47831).
G. Plurilocular sporangia, assimilatory filaments and hair initial. (ADU, A47831).
H. Peripheral filaments, with little pigment. (ADU, A47831).

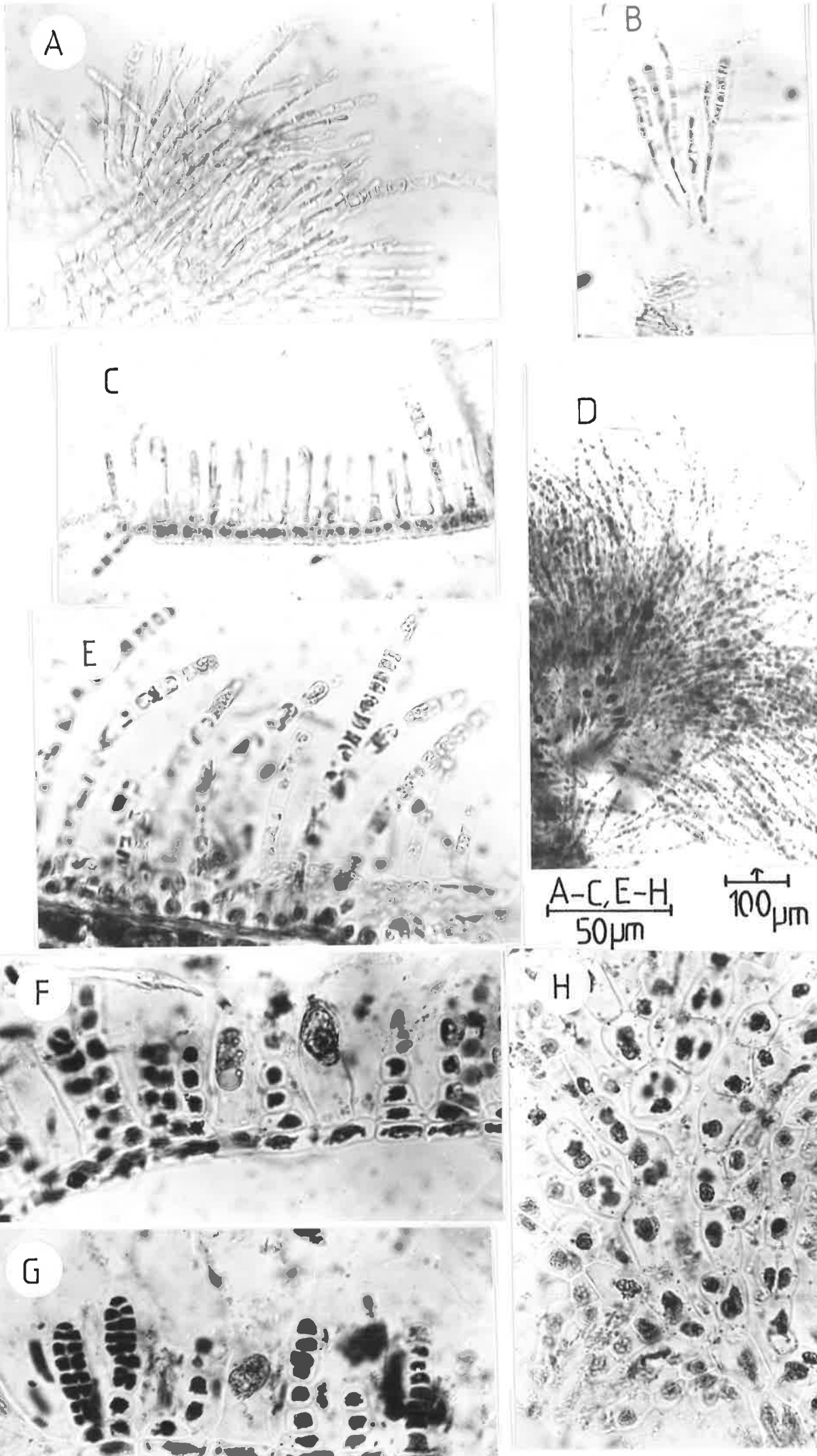

A
B
C
D
E
A-C, E-H,
50µm
100µm
F
H
G

Plate 3. Elachistaceae

Elachista orbicularis (Ohta) comb. nov.

A. Portion of thallus, Type fragment. (ADU, A49,377).
B. Portion of thallus. (ADU, A47215).

Elachista secundata sp. nov.

C. Portion of thallus. (ADU, A50331).
D. Cortex with balloon cells, squash. (MELU, 20520).

Halothrix ephemeralis sp. nov.

E. Portion of thallus, with unilocular sporangia. (ADU, A32664).
F. Habit, with plurilocular sporangia. (ADU, A32664).

Portphillipia australia (J.Ag.) Silva

G. Upper medulla and cortex. (ADU, A49067).
H. Unilocular sporangia. (ADU, A49067).

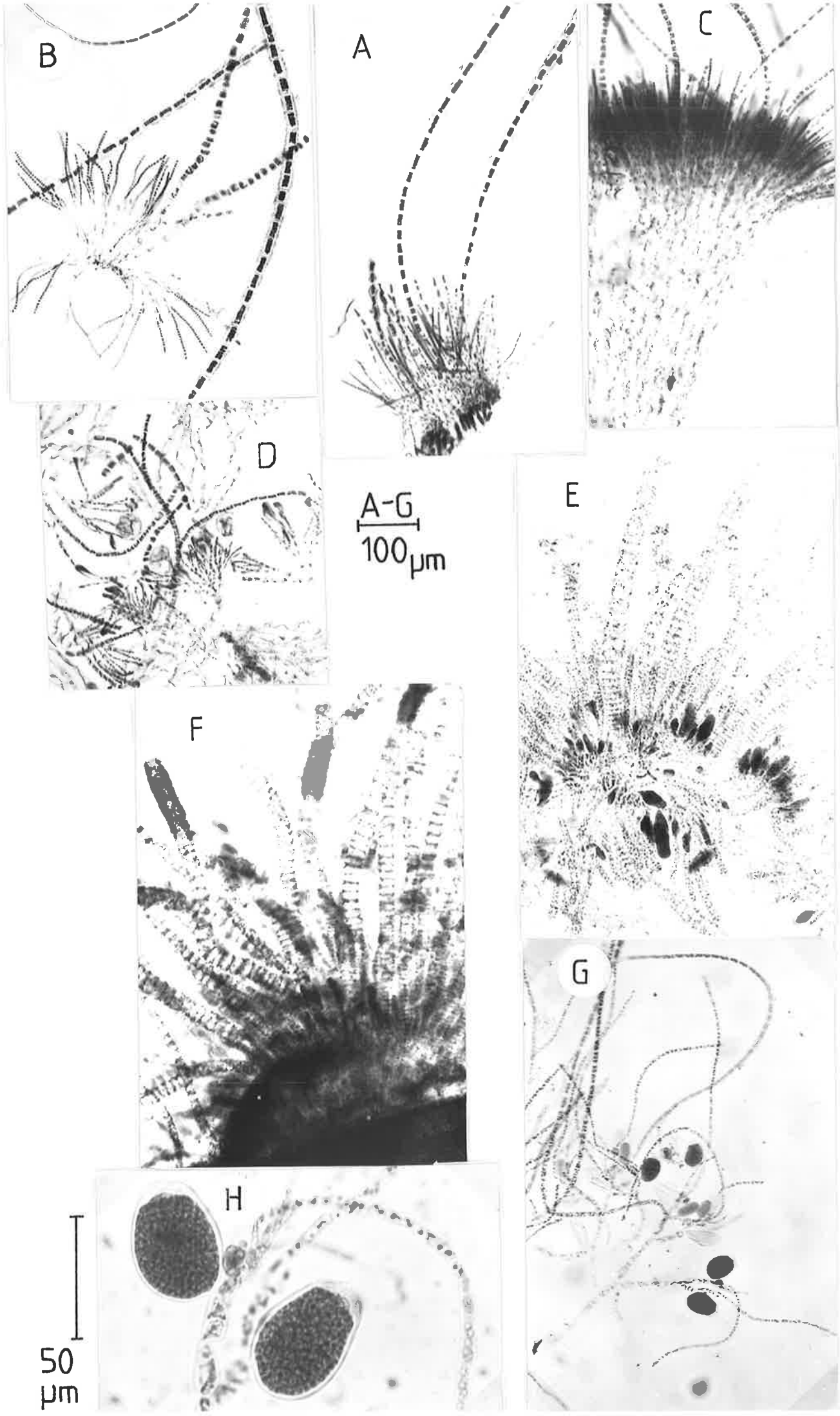

B
A
C
D
A-G
100 µm
E
F
G
H
50
µm

Plate 4. Corynophlaeaceae - *Strepsithalia*

Strepsithalia aemula sp. nov.

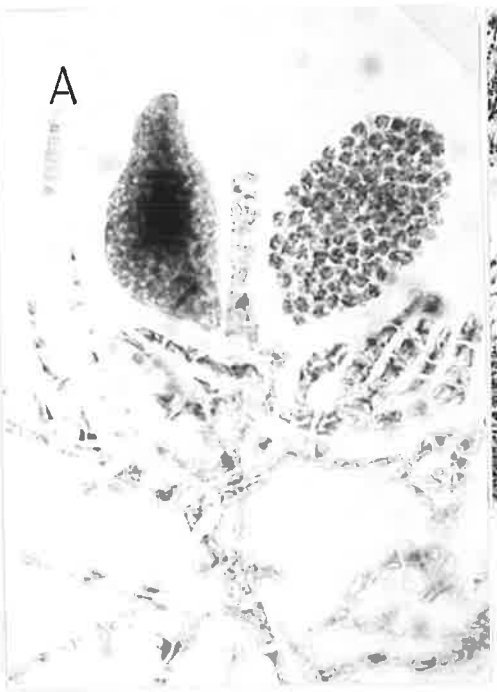
A. Unilocular sporangium and curved basal filaments. (ADU, A49564).

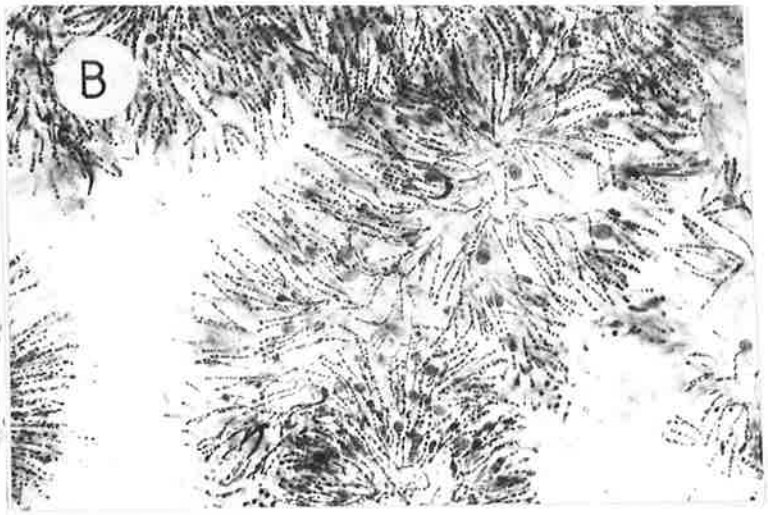
Strepsithalia liagorae Sauvageau

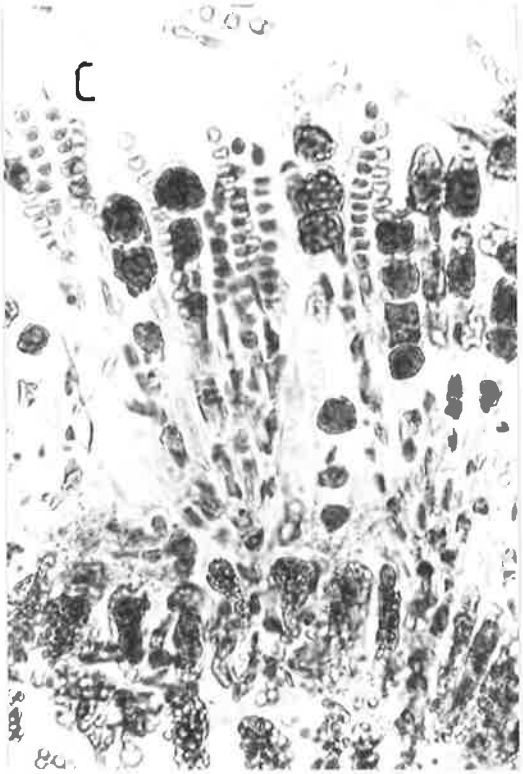
B. Habit, squash. (ADU, A47959).

Strepsithalia clavata sp. nov.

C. Habit. (ADU, A48890).
D. Plurilocular sporangia. (ADU, A48890).
E. Unilocular sporangia. (ADU, A48890).







A,C,E
50 µm

B,D
100 µm

Plate 5. Corynophlaeaceae - *Myriactula*

Myriactula rivulariae var. *rivulariae* (Suhr) Feldm.

A. Habit. (ADU, A20836).

M. rivulariae var. *chordae* (Aresch.) Rosenv.

B. Habit. (ADU, A49777).

M. rivulariae var. *arabica* (Kütz.) comb. nov.

C. Habit, with unilocular sporangia. (ADU, A33619).
D. Habit, with plurilocular sporangia. (ADU, A48241).
E. Culture, after 1 month. (ADU, A48827).

Myriactula haydenii (Gatty) Levr.

F. Habit. (ADU, A31873).
G. Secondary epicellular plurilocular sporangia on cortical filaments, with emergent part of thallus. (ADU, A31873).

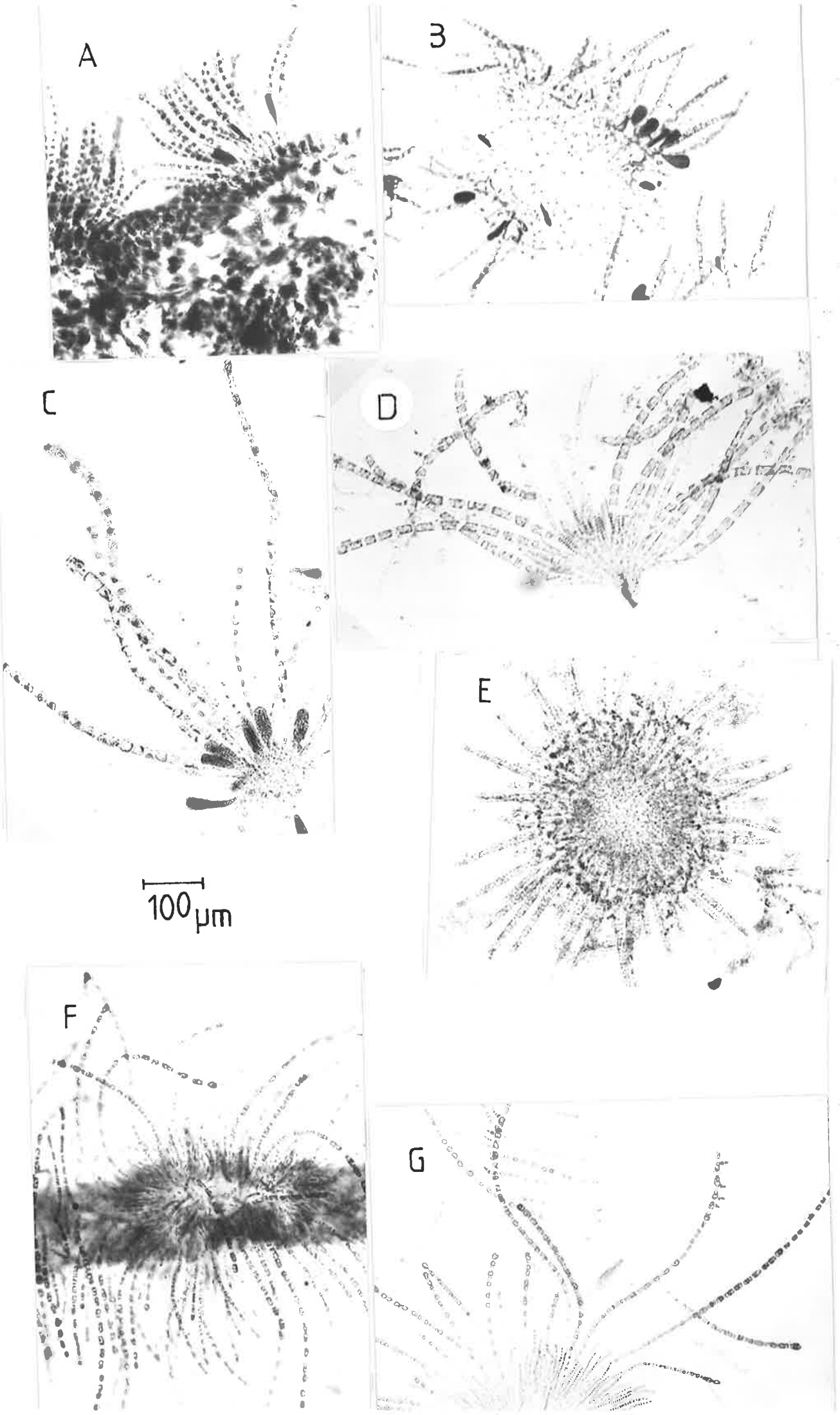

A
B
C
D
E
F
G
100 µm

Plate 6. Corynophlaeaceae - *Corynophlaea*

Corynophlaea filiformis sp. nov.

A. Habit, squash. (ADU, A48582).

Corynophlaea cristata sp. nov.

B. Medulla and cortex. (ADU, A48886).
C. Crest of plurilocular sporangia on upper cells of cortical filament. (ADU, A48886).

Corynophlaea cystophorae J. Ag.

D. Medulla and cortex with sporangiophores of plurilocular sporangia. (ADU, A48830).
E. Cortex, with unilocular sporangium, and rounded cells in cortical filaments. (ADU, A47858).
F. Unilocular sporangium, and deltoid cells in cortical filaments. (ADU, A47499).

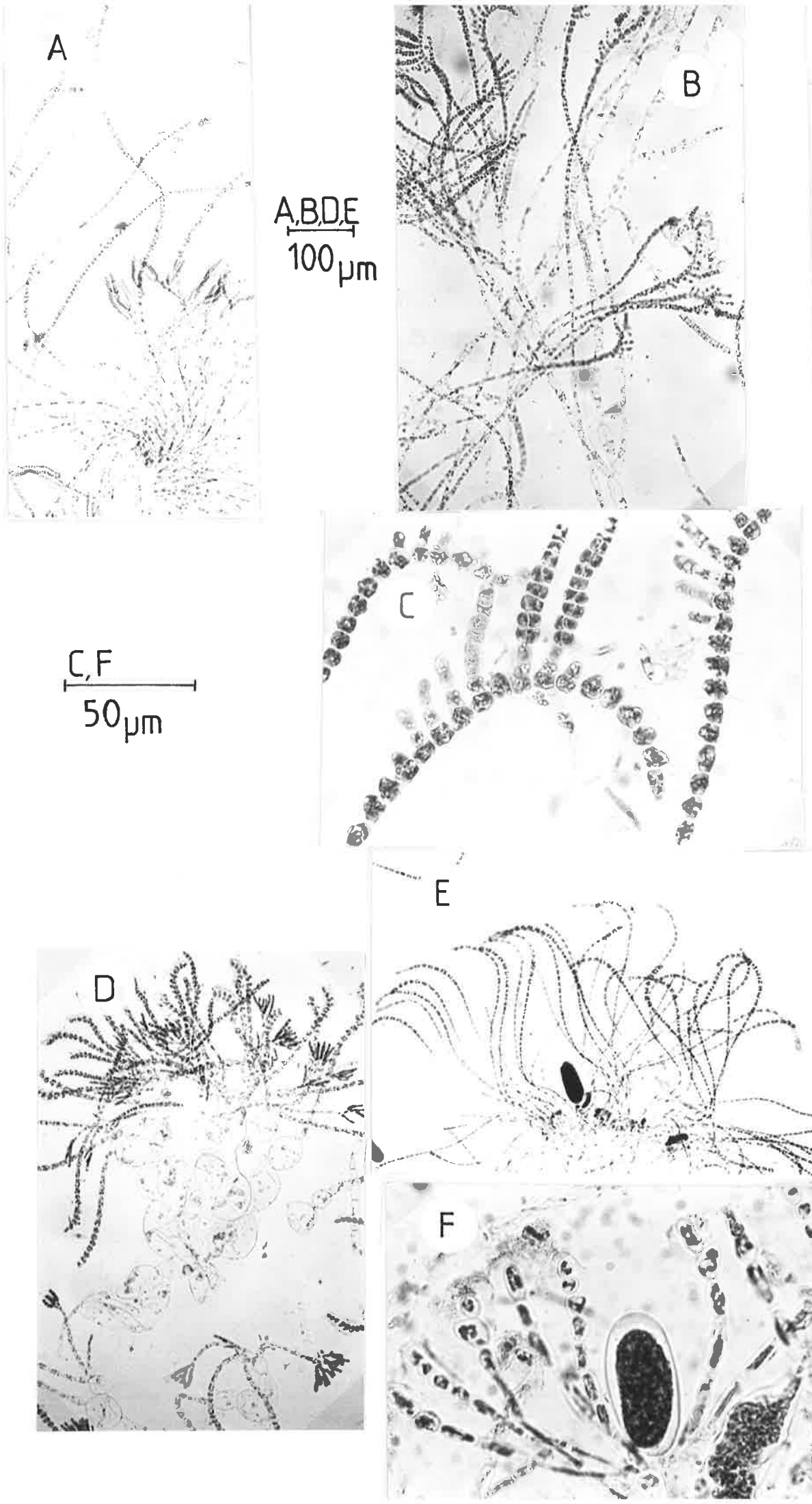

A
B
A,B,D,E
100 µm
C
C,F
50 µm
E
D
F

Plate 7. Corynophlaeaceae - *Leathesia, Petrospongium.*

Leathesia difformis (L.) Aresch.

A. Medulla, showing anastomosing cruciate cells; (ADU, A47960).

Leathesia intermedia Chapm.

B. Medulla, showing anastomosing irregular subglobose cells; (ADU, A37814).
C. Cortical filaments and unilocular sporangia; (ADU, A49063).

Leathesia sphaerocephala Yamada

D. Cortical filaments, for comparison with "C"; (ADU, A49425).

Petrospongium rugosum (Okam.) S. & G.

E. Cortical habit, squash; (ADU, A50231).
F. Unilocular sporangium and bifid cortical filaments; (ADU, A50231).

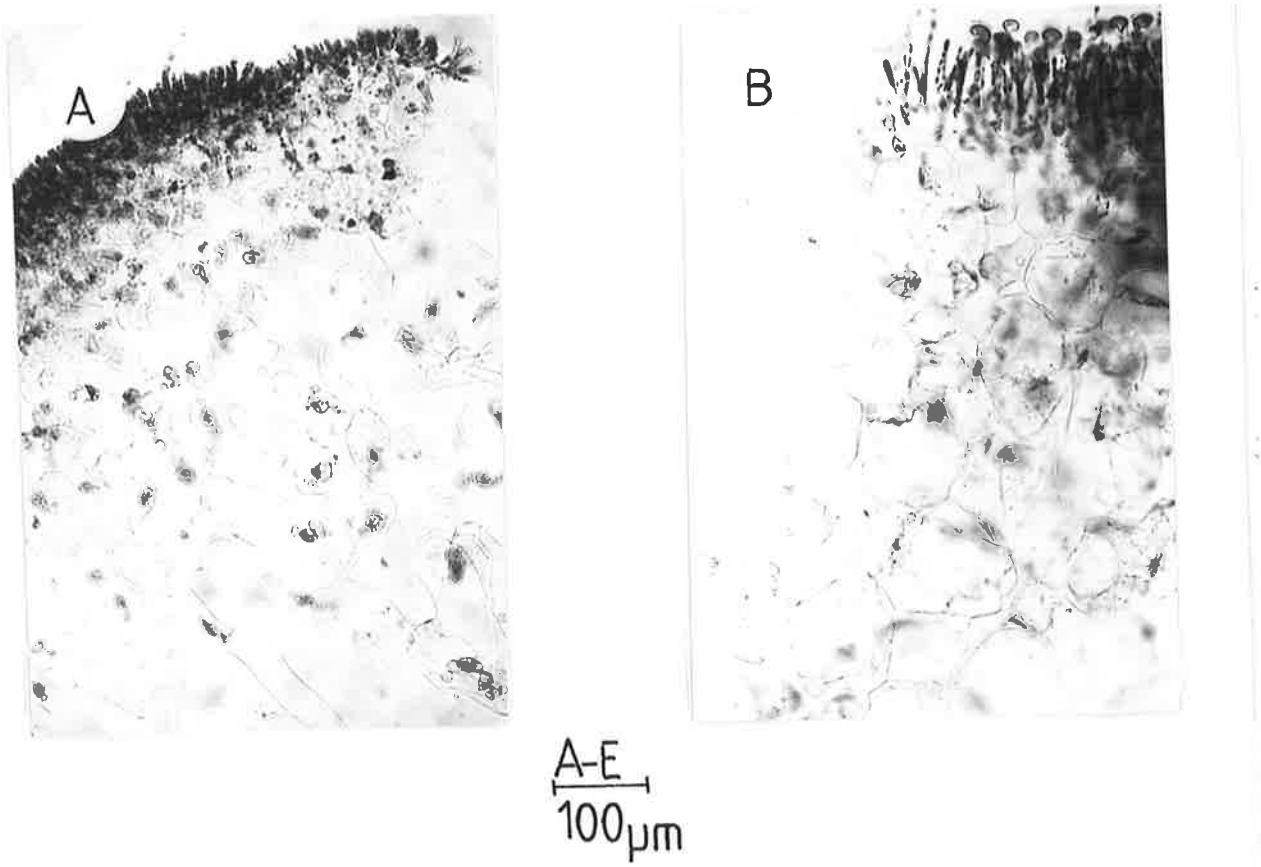

A
B
A-E
100µm
C
D
E
F
50µm

Plate 8. Giraudyaceae - *Flabellonema* gen nov.

Flabellonema codii sp. nov.

A. Habit; (ADU, A20906).
B. Basal system, showing fanlike pattern. (ADU, A20906).
C. Margin of disc showing dichotomous marginal meristem, and stolon-like filament; (ADU, A20906).
D. Axial initials; (ADU, A20906).
E. Lateral branches from an erect axis; (ADU, A20906).
F. Intercalary plurilocular sporangium; (ADU, A20906).

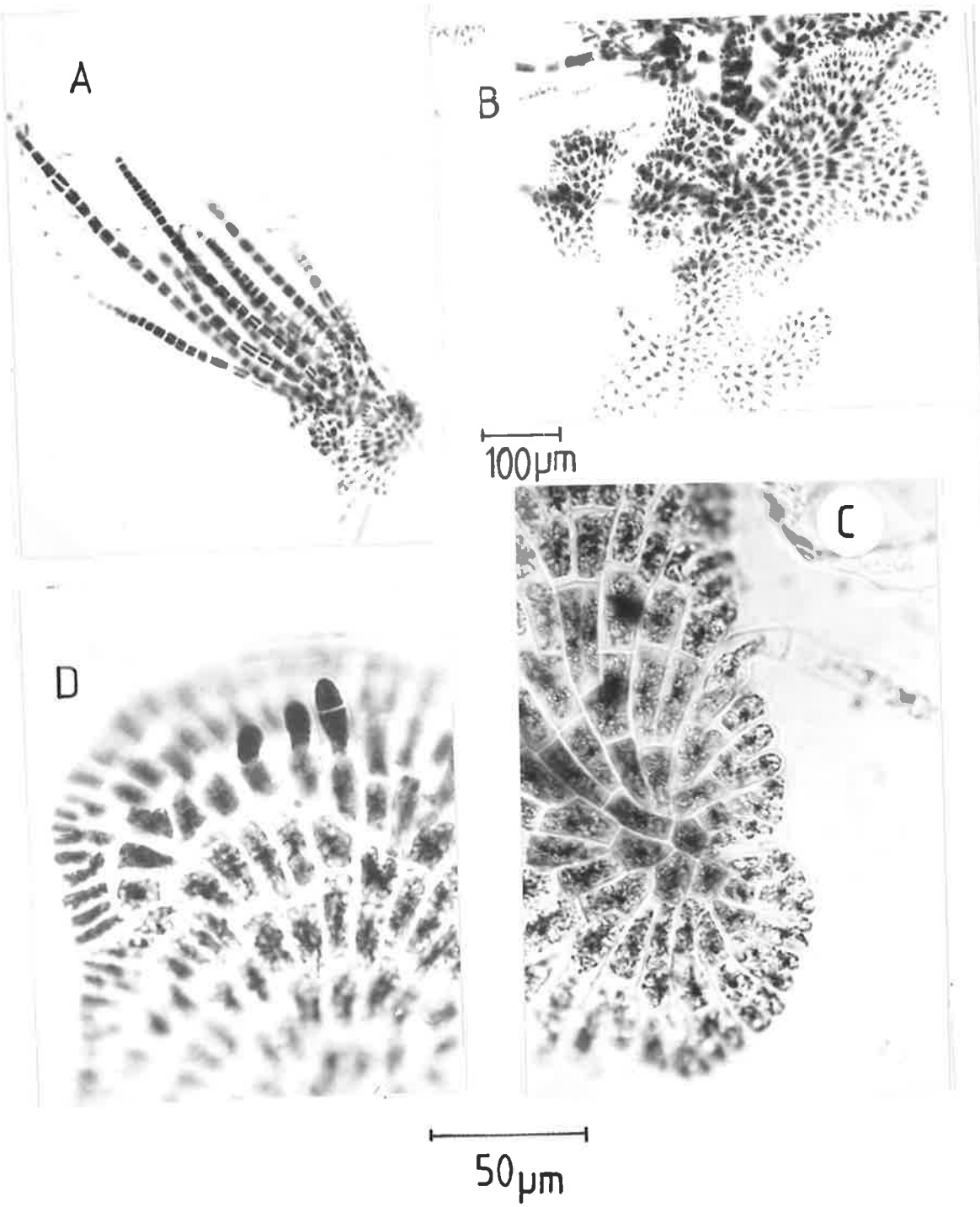
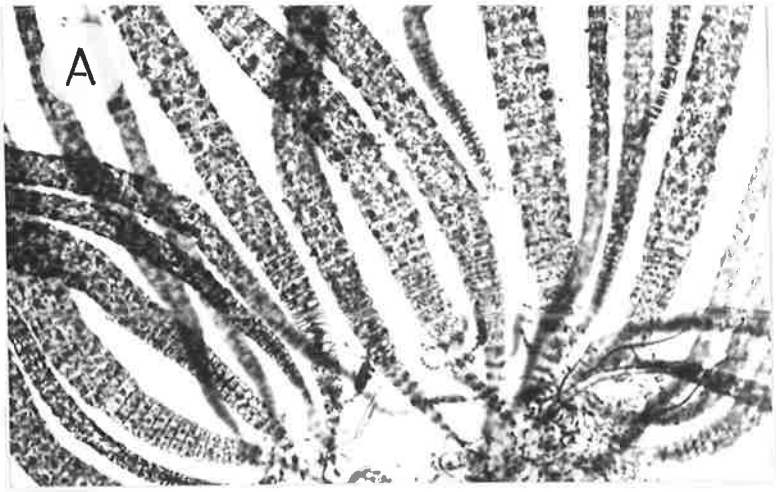
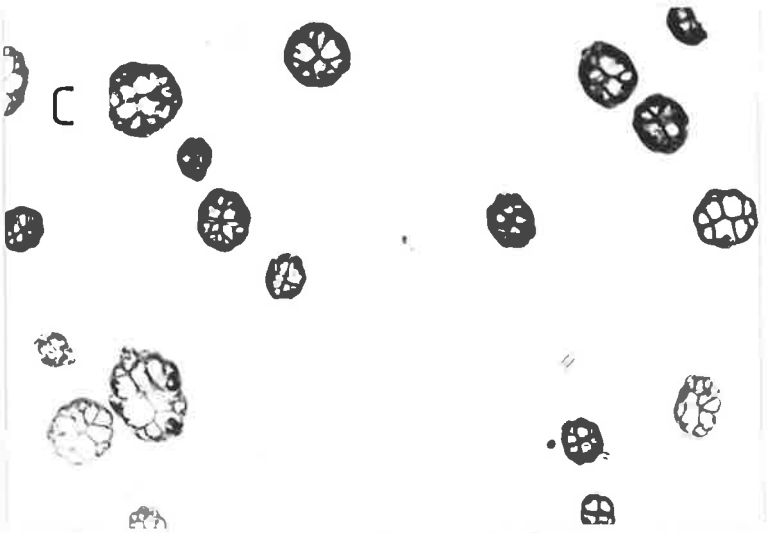

A
B
100µm
C
D
50µm
E
F

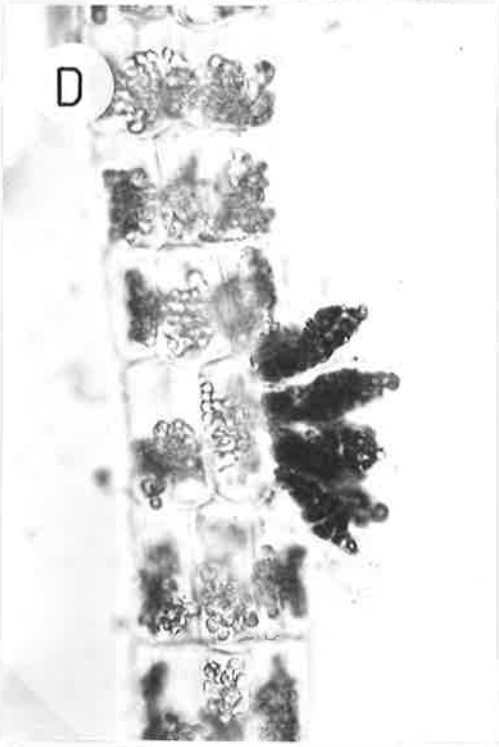
Plate 9. Giraudyaceae - *Giraudya, 1.*

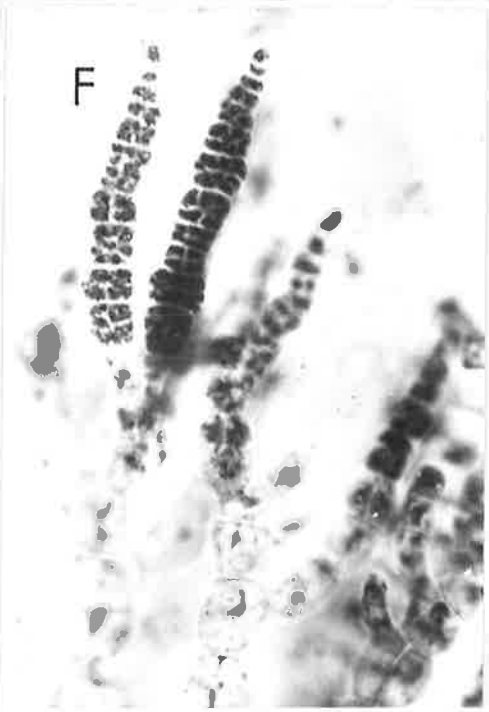
Giraudya sphacelarioides Derbès et Solier

A. Erect axes with basal meristem; (ADU, A49557).
B. Medulla, with basal plurilocular sporangia; (ADU, A41226).
C. Transverse sections of erect axes; (ADU, A48226).
D. Sorus of lateral multiseriate plurilocular sporangia; (ADU, A49557).
E. Part of intercalary plurilocular sporangial region; (ADU, A48579).
F. Branched basal plurilocular sporangia; (ADU, A29617).









A-C
100 µm

D-F
50 µm

Plate 10. Giraudyaceae - *Giraudya*, 2.

Giraudya robusta sp. nov.

A. Bases of erect axes; (ADU, A20123).
B. "Buoyancy" cells and medullary filaments; (ADU, A20123).
C. Unilocular sporangium; (ADU, A20123).
D. Basal plurilocular sporangia on medullary filaments; (ADU, A20123).
E. Lateral plurilocular sporangia; (ADU, A20123).
F. Plurilocular sporangia on sub-terminal branches; (ADU, A20123).
G. Juvenile plant, from the field; (ADU, A48269).

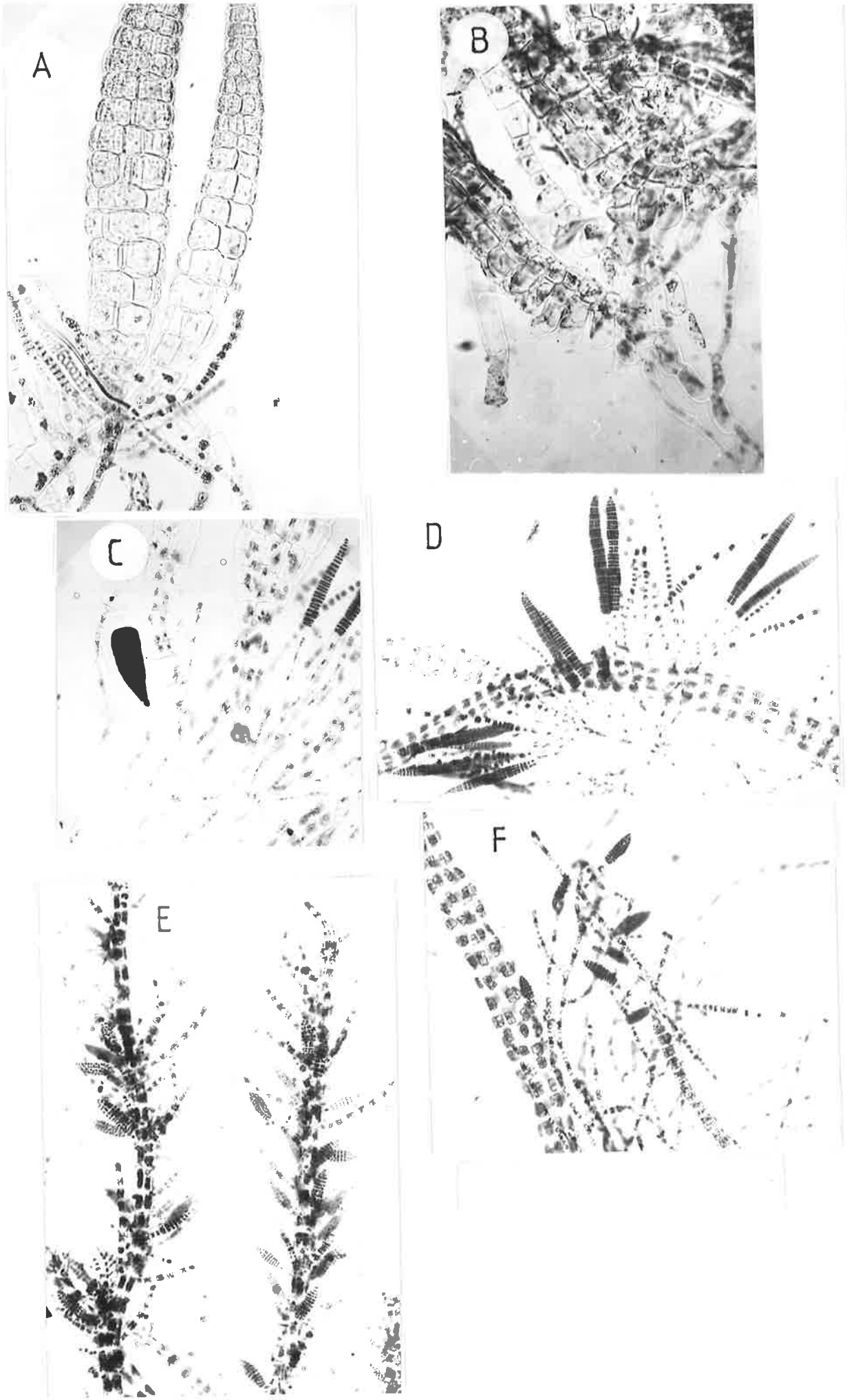

A
B
C
D
E
F
100µm

Plate 11. Culture studies, 1 - *Myrionema strangulans* (ME-III)

A. Amoeboid germlings, after two days;
B. Pseudodiscoid plant with unilocular sporangia;
C. Unilocular sporangium, phase contrast; (photo V. Sarafis)
D. Unilocular sporangia, squash;
E. Filamentous plant, after ten days;
F. Filamentous plant, mature;
G. Intercalary plurilocular sporangia in filamentous plant.

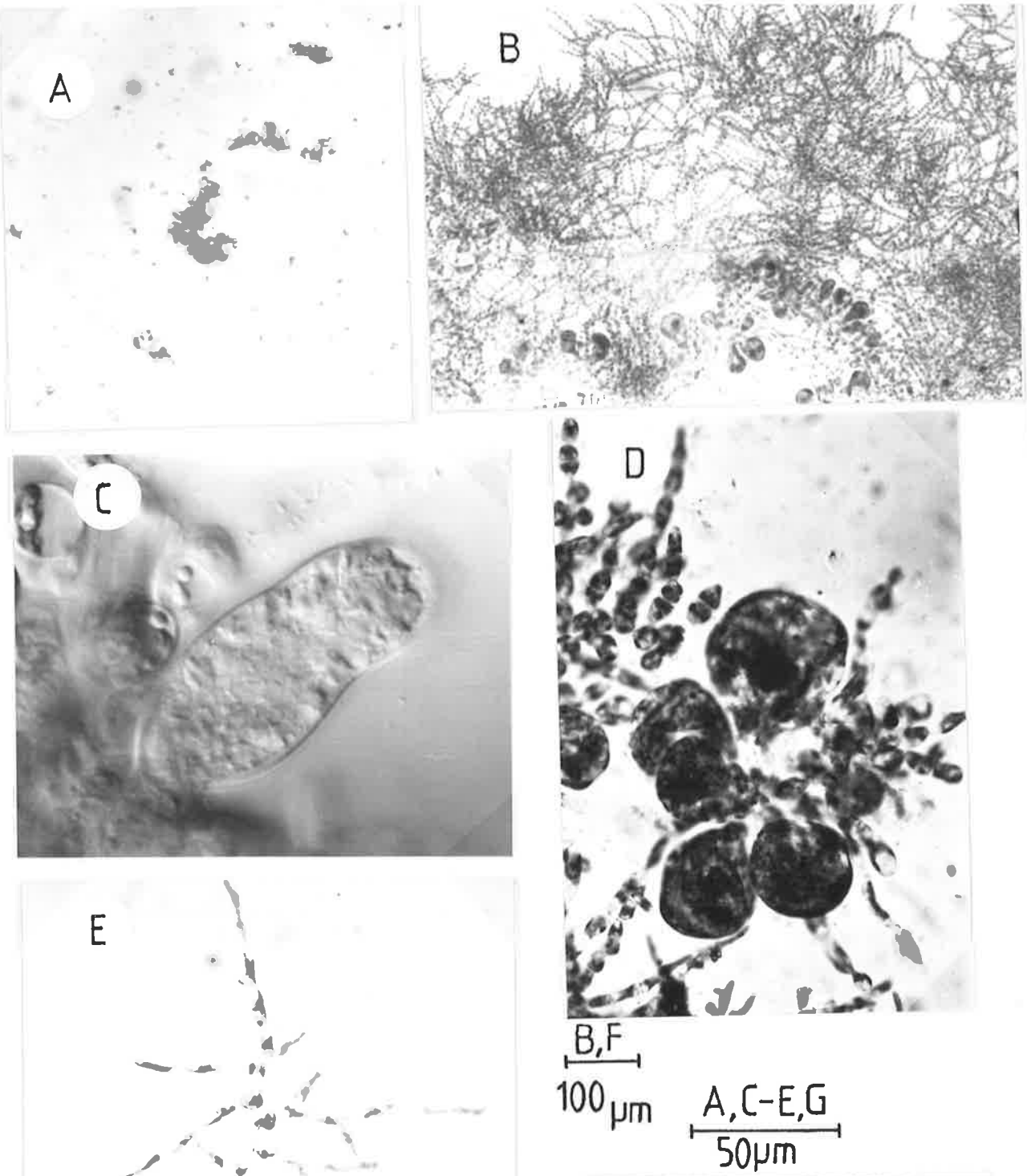

A
B
C
D
E
F
G
B,F
100 µm
A,C-E,G
50µm

Plate 12. Culture studies, 2 - *Myrionema latipilosum* (ZT-1)

A. Zooids and amoeboid germling, second generation.
B. Discoid plants, after fourteen days.
C. Pseudodiscoid plant, after fourteen days.
D. Filamentous plant, after fourteen days.
E. Sterile filamentous plant, at maturity.
F. Plurilocular sporangia on pseudodiscoid plant, at maturity.
G. Filamentous plant (pseudodiscoid), second generation.
H. Discoid plant and stolonlike multiplication of pseudodiscoid plant, second generation.
I. Unilocular sporangium, post-mature first generation plant.

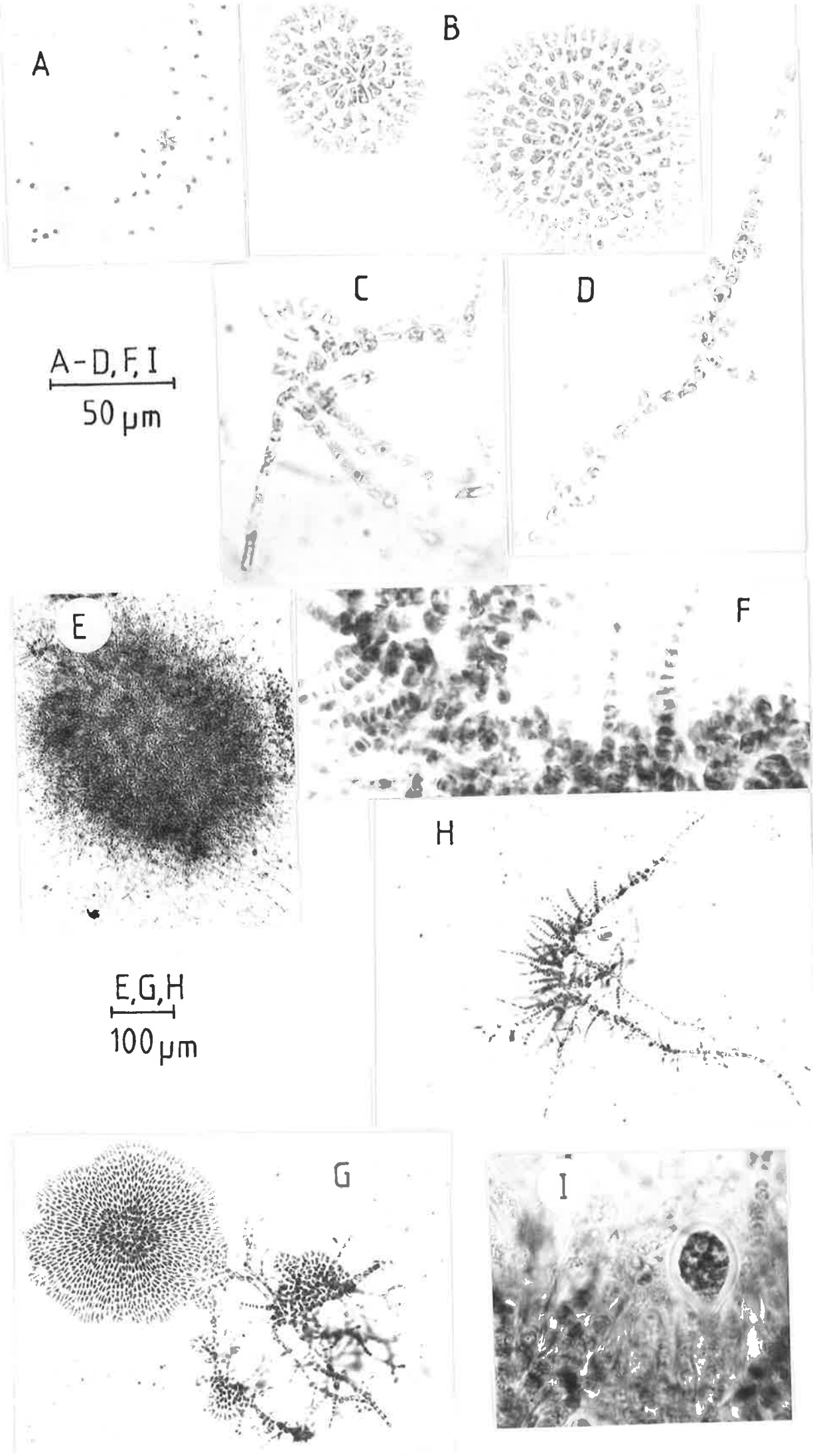

A
B
C
D
A-D, F, I
50 µm
E
F
H
E, G, H
100 µm
G
I

Plate 13. Culture studies, 3. - *Elachista orbicularis* (EA-V)

A. Plants, after 20 days;
B. Plants, tussock forming, after 28 days;
C, D. Stolonlike multiplication of plants, after 34 days.
E. Mature cultured plant, showing all normal features except on organized medulla.

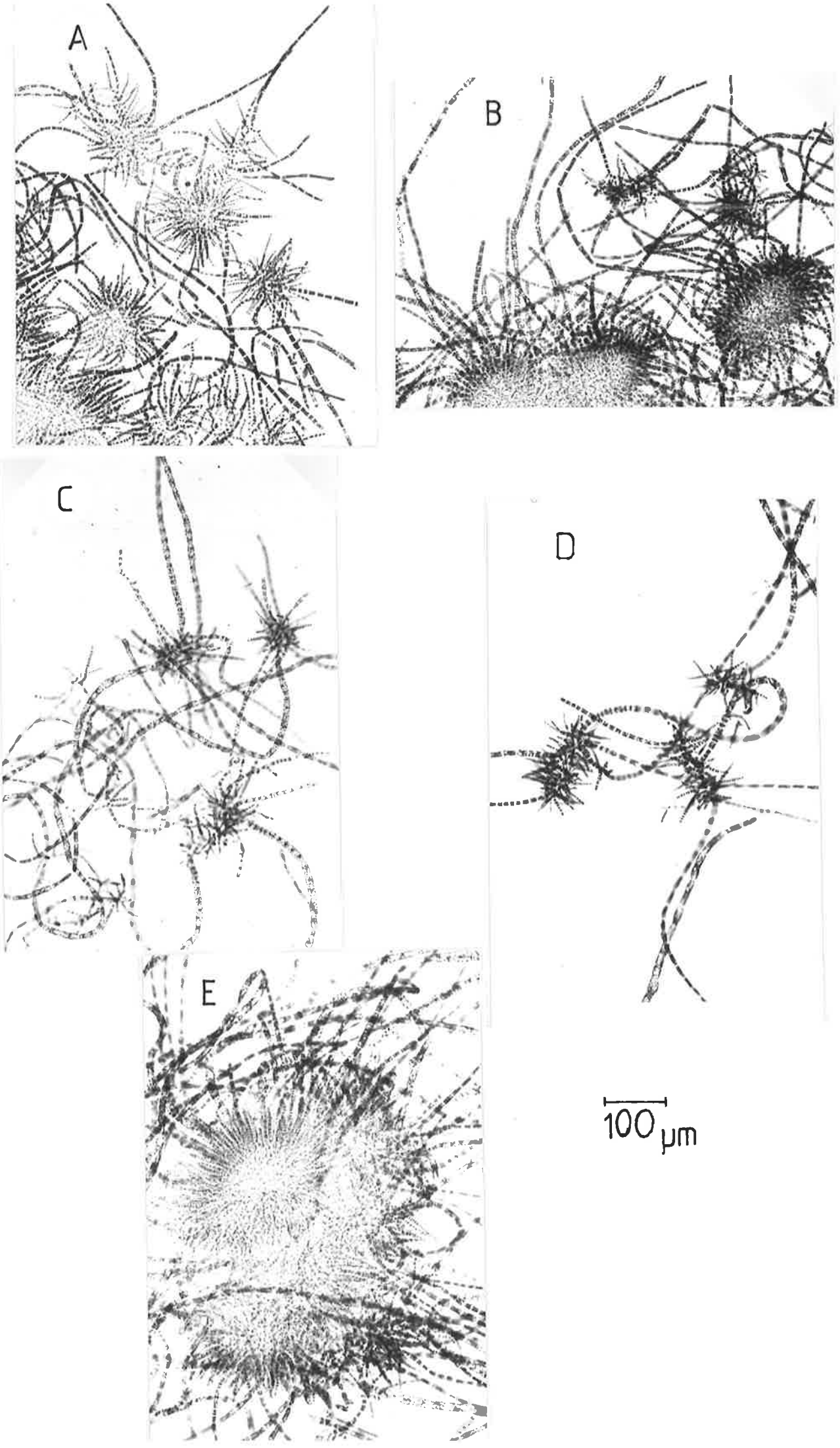

A
B
C
D
E
100 µm

Plate 14. Culture studies, 4. *Halothrix*, *Strepsithalia* and *Corynophlaea*.

Halothrix ephemeralis (HA-I)

A. Plantlets, from unilocular sporangia, after ten days.
B. Sterile tuft, after 30 days.

Strepsithalia liagorae (SA-I)

C. Very young plantlets, after seven days.
D. Plantlets after 11 days.
E. Filamentous plants, sterile, after 18 days.

Corynophlaea cystophorae (CA-III)

F. Dimorphism of plantlets, after 15 days.
G. Filamentous plantlets from F.
H. Biseriate filamentous plantlets from F.

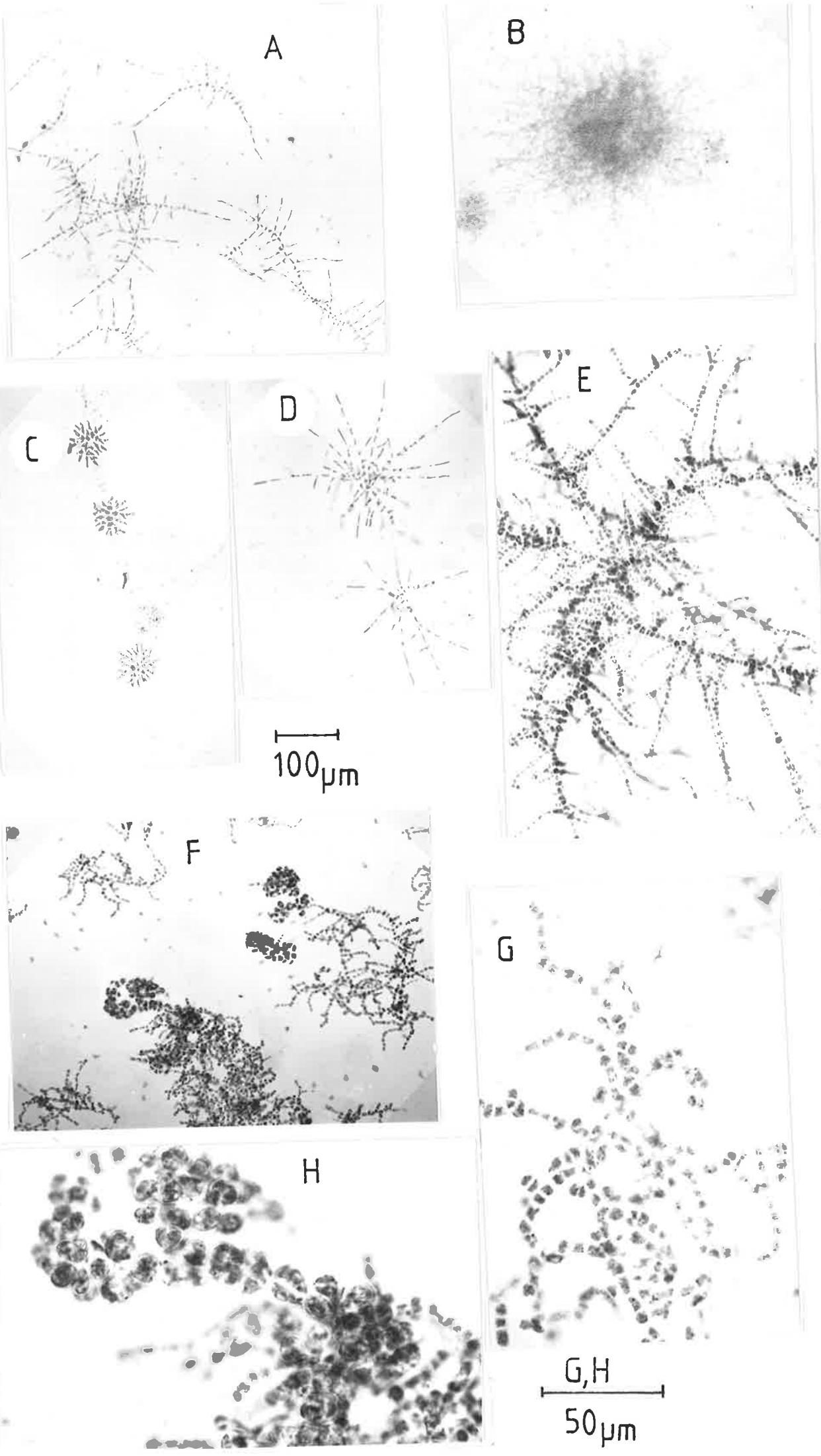

A
B
C
D
E
100µm
F
G
H
G,H
50µm

Plate 15. Culture studies, 5a. *Giraudya sphacelarioides*, GA-V.

A. Amoeboid germlings, after two days;
B. Discoid and filamentous plantlets, after 7 days;
C. New erect axis from filamentous plant, after 20 days;
D. Discoid plant, after 20 days;
E. Second generation filamentous plant.
F. Second generation discoid plant, with stolon-like multiplication;
G. Young erect axes from discoid plants;
H. Multiseriate plurilocular sporangia in lateral sori.

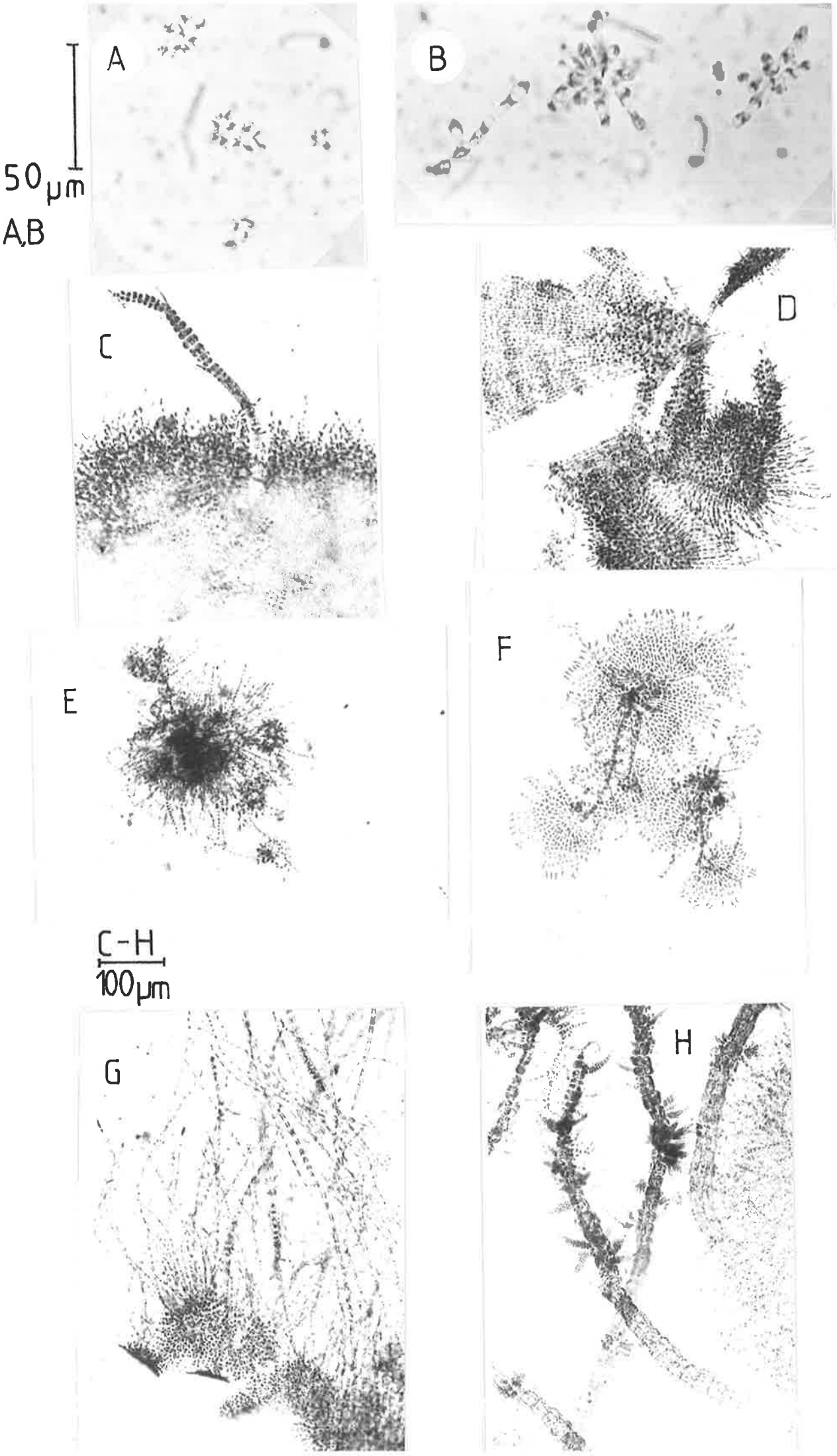

A
B
50 µm
A,B
C
D
E
F
C-H
100µm
G
H

Plate 16. Culture studies, 5b. - *Giraudya phacelarioides* GA-V cont'd.

A. Intercalary plurilocular sporangial masses;
B, C. Habit of mature second generation plants;
D. - F. Plants from "*Ascocyclus*" parent plants.
D. Plant treated with IAA only,
E. Plant treated with Kinetin, IAA and GA_3.
F. Plant without hormones.

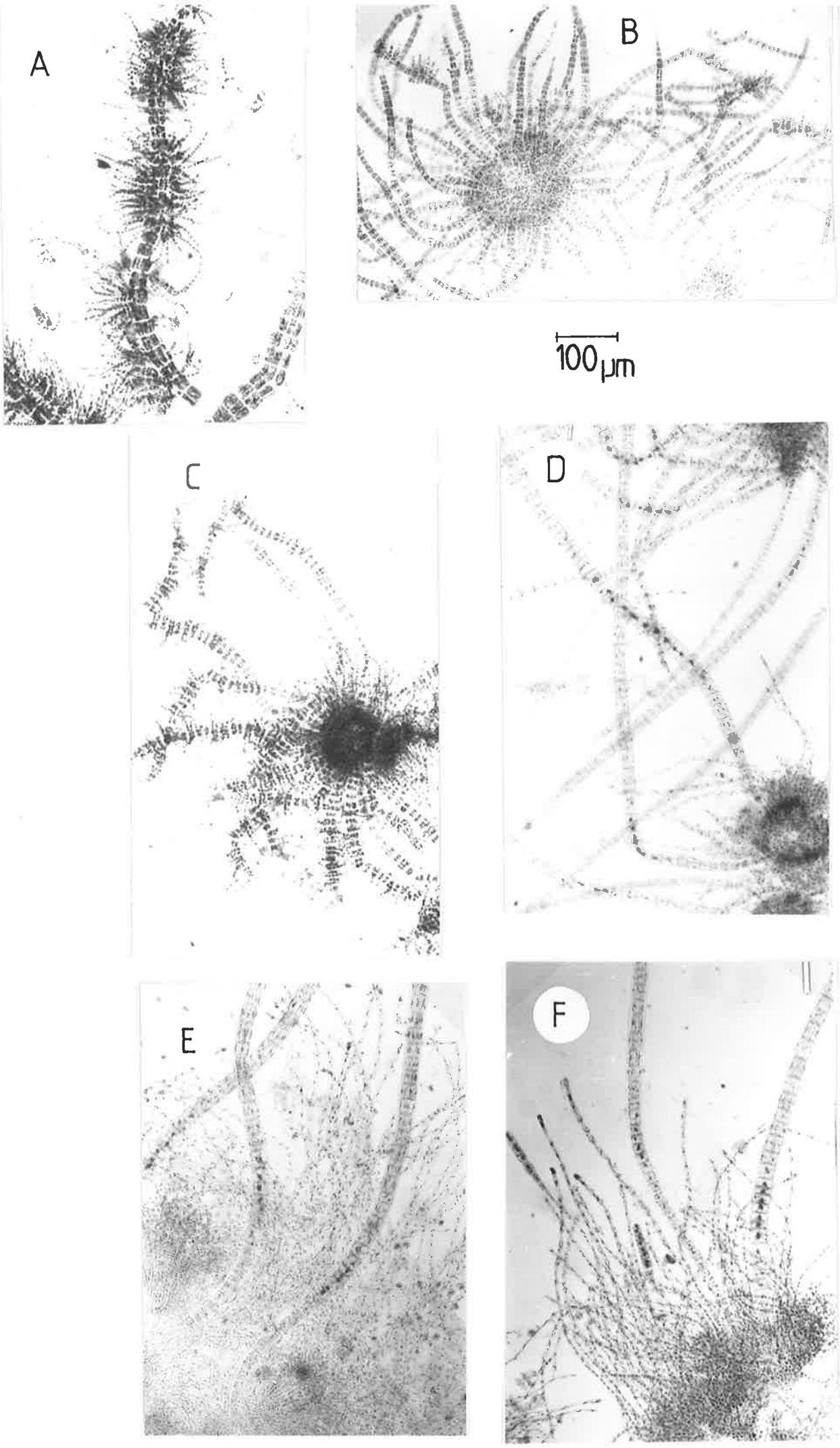
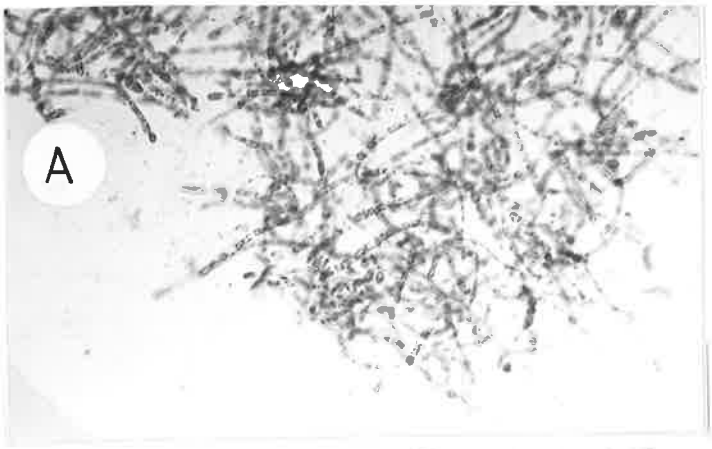
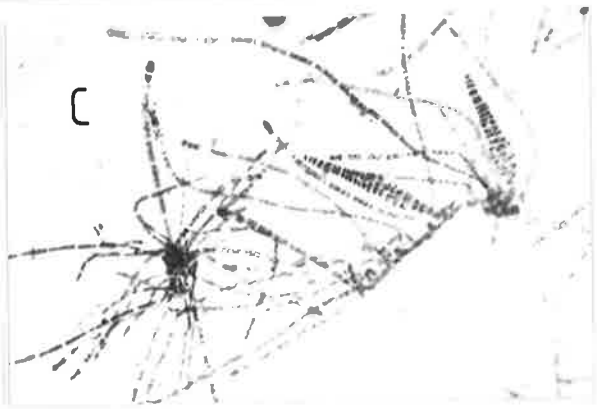
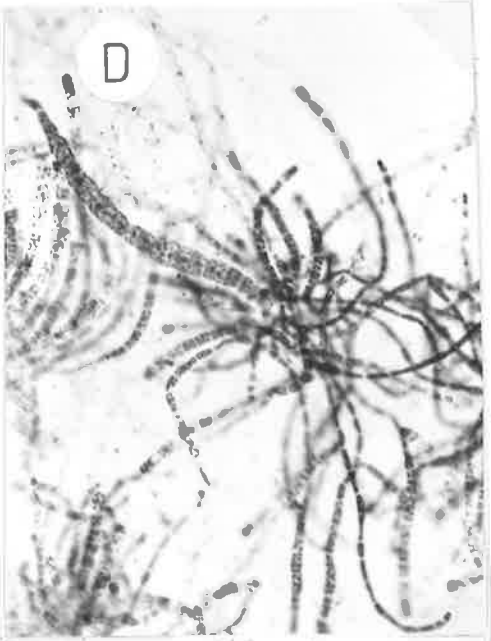

A
B
100 µm
C
D
E
F

Plate 17. Culture studies, 6. - *Giraudya robusta*, GR-IV.

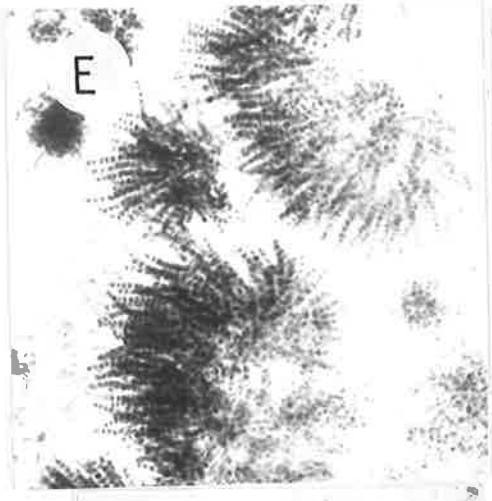
A. Loosely filamentous plantlets;
B. Tuft filamentous plantlets, with sporangia;
C. Older loosely filamentous plantlets, with sporangia;
D. New erect axis, from loosely filamentous plants;
E. Second generation tufted plants;
F. New erect filaments and axes from tuft plant;
G. Basal and lateral plurilocular sporangia;
H. "*Ascocyclus*" plants;
I. Fertile "*Ascocyclus*" plants with erect axial initial.

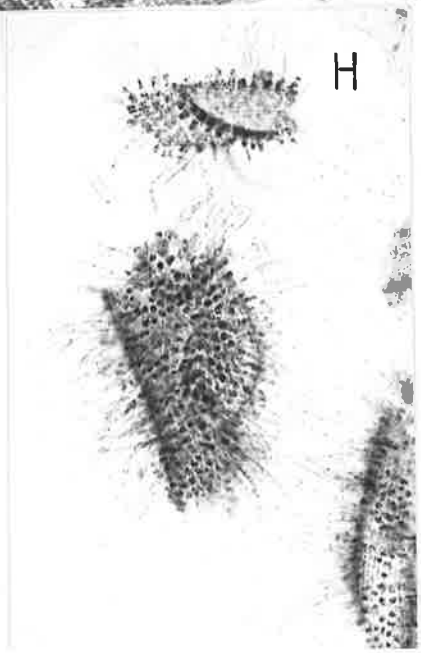






100 µm





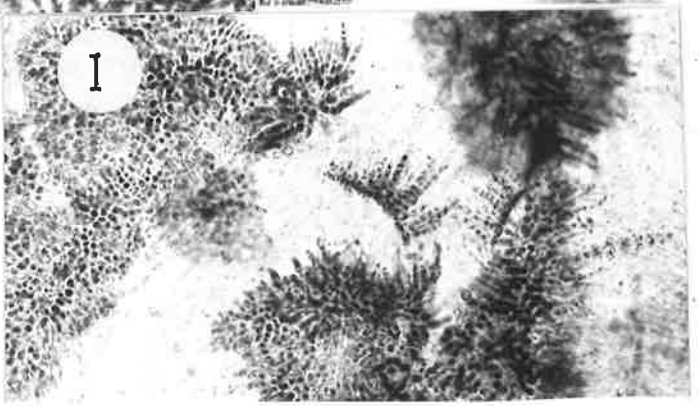


Plate 18. Comparative morphology.

Sphacelaria biradiata (Safety Cove, Tas.; ADU, A50767).

A. Branching structure, for comparison with *Flabellonema*.

Myriotrichia claviformis (Trevone, Cornwall, U.K.; ADU, A28309).

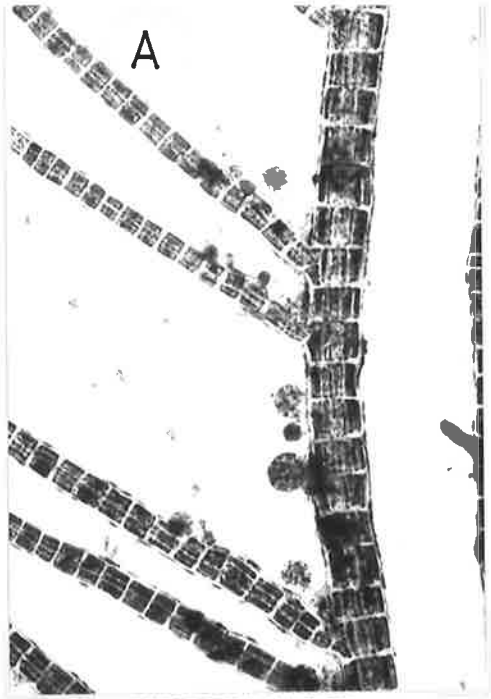
B. Upper axis and branch, for comparison with *Flabellonema* and *Giraudya*.

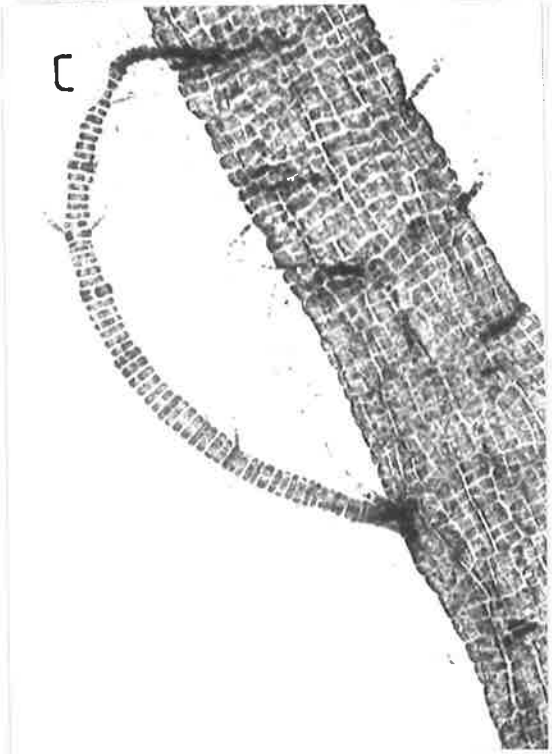
Stictyosiphon sp. (West Lakes, S. Aust.; ADU, A49759).

C. Young lateral branch, showing tiers of cells.
D. Tip of branch showing hairs.

Asperococcus sp. (Cap Le Grand, W. Aust.; ADU, A50252).

E,1,2 Basal system of young thallus showing basal disc, rhizoids of holdfast and young stem.





A,C,E
100 µm

B,D
50 µm

Plate 19. Specimen Sheets, 1.

Myrionema strangulans Grev.

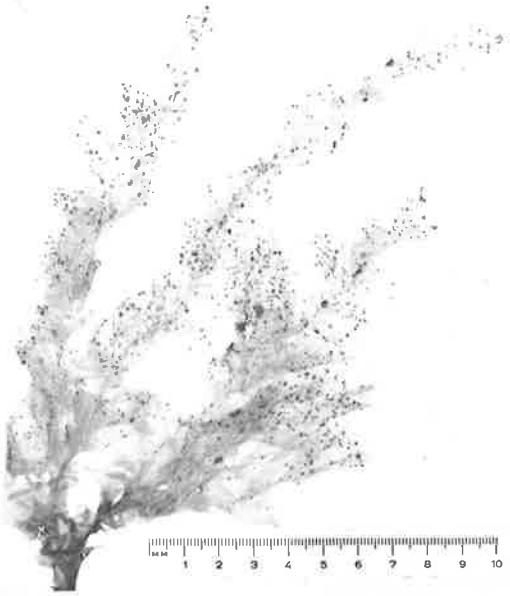
A. On *Ulva lactuca*, Nora Creina, S. Aust.; ADU, A47502.
B. On *Enteromorpha* sp.; Encounter Bay, S. Aust.; ADU, A48260 .

Elachista orbicularis (Ohta) comb nov.

C. On *Ecklonia radiata*, Encounter Bay, S. Aust.; ADU, A50236.

A47502

A



Myrionema strangulans Grev.
Nora Creina, S. Aust.
upper litt pools in reef of stacks at south head of main Bay; on Ulva sp.
30-X-1976.
coll. S. SKINNER.

A48260

B

Myrionema strangulans Grev.
Encounter Bay, S Aust.
on Enteromorpha sp. & E. compressa epiphytal,
28-IX-1978
coll & det S. SKINNER

C

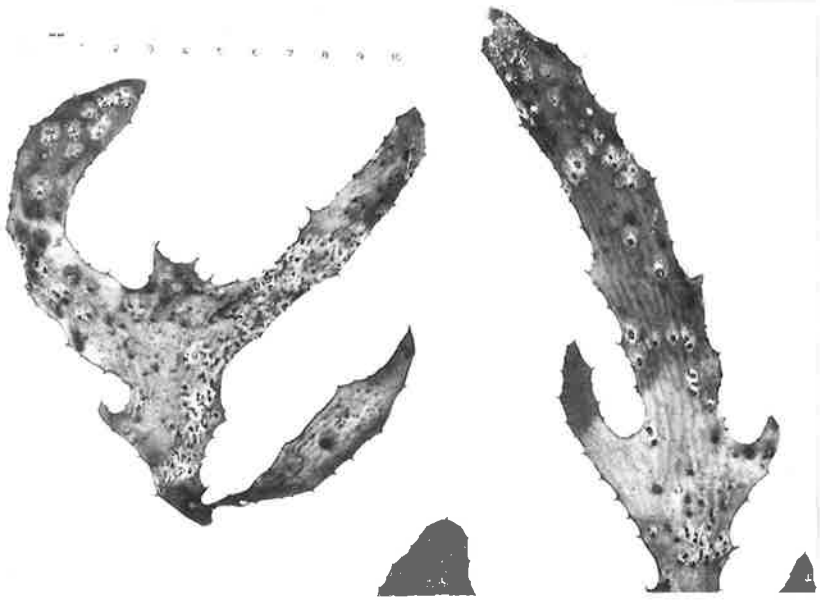


Plate 20. Specimen Sheets, 2.

Elachista secundata sp. nov.

A. On *Sargassum* sp., Queenscliff, Vic.; ADU, A50331.

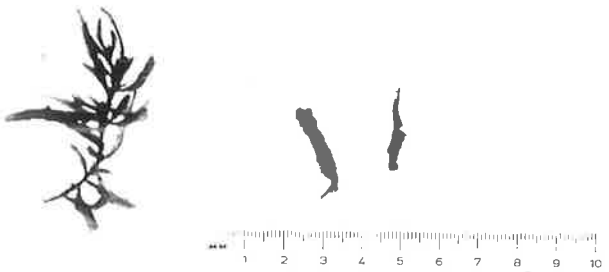
Halothrix ephemeralis sp. nov.

B. TYPE, on *Heterozostera tasmanica*, Aldinga reef, S. Aust.; ADU, A32664.

Portphillipia australia (J.Ag.) Silva

C. On *Xiphophora chondrophylla*, Apollo Bay, Vic.; ADU, A34809.

A



Elachista secundata sp.no
on Sargassum sp
Queenscliff, Victoria.

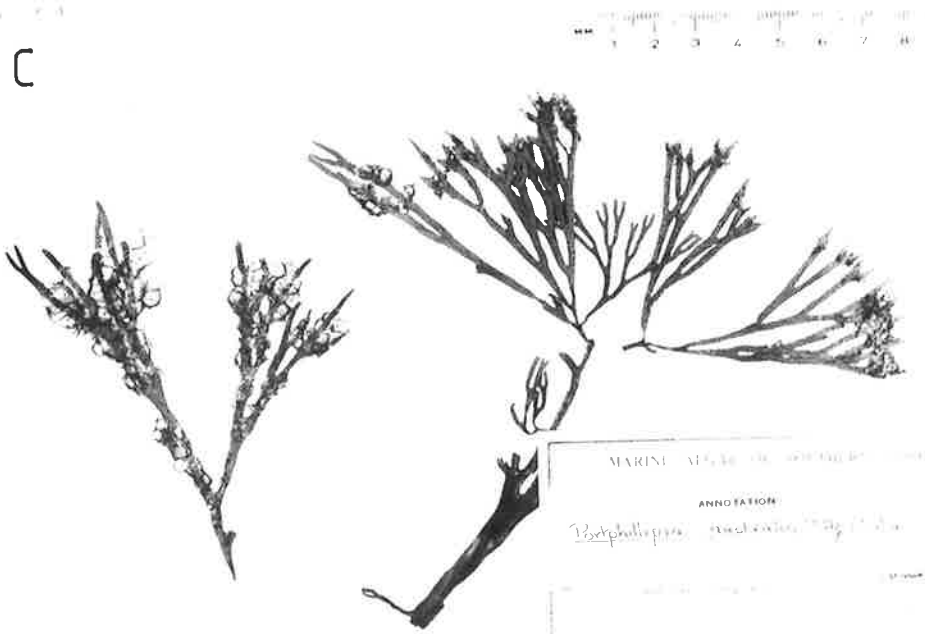
16·IX·1969
coll. M.N. Clayton
det. S. Skinner.

TYPE

B

ANNOTATION
Halothrix ephemeralis sp nov
on Heterozostera tasmanica

C



MARINE

ANNOTATION

Plate 21. Specimen Sheets, 3.

Corynophlaea cystophorae J. Ag.

A. On *Cystophora polycystidea*, Aldinga reef, S. Aust.; ADU, A48580.

Corynophlaea cristata sp. nov.

B. TYPE, on *Cystophora brownii*, Point Westall, S. Aust.; ADU, A48886.

Leathesia difformis (L.) Aresch.

C. Epilithic on coralline turf, Safety Cove, Tas.; ADU, A49174.

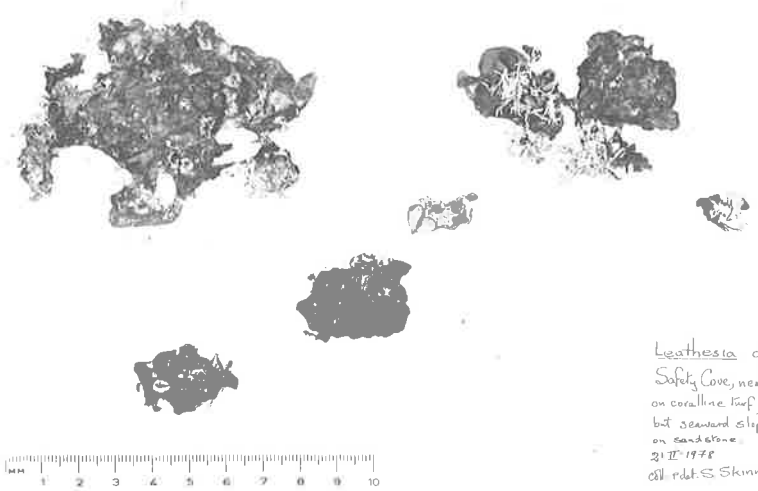
A

Corynophlaea cystophorae
Aldinga reef, S Aust.
on Cystophora sp, upper sublittoral rocks
14-x-1977
coll & det S. Skinner.

A48886

B

C



Leathesia difformis (L.) Aresch.
Safety Cove, near Port Arthur, Tasmania
on coralline turf, forming a carpet on the shi
but seaward slope of pools in the mid eulittor
on sandstone
21.II.1978
Coll. & det. S. Skinner.

Plate 22. Specimen Sheets, 4.

L. difformis, cont'd.

A. Epiphytic on *Posidonia* sp., Aldinga reef, S. Aust.; ADU, A48627.

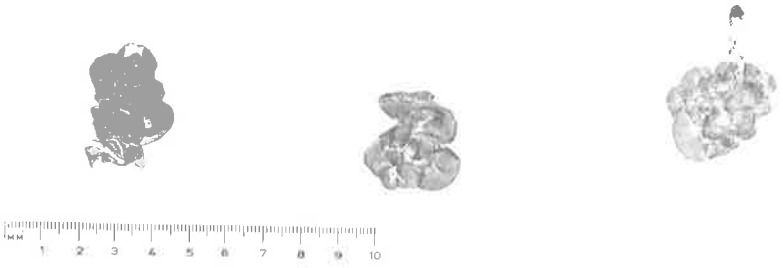
L. intermedia Chapm.

B. On *Caulerpa brownii*, Robe, S. Aust.; ADU, A50212.

Petrospongium rugosum (Okam.) S.& G.

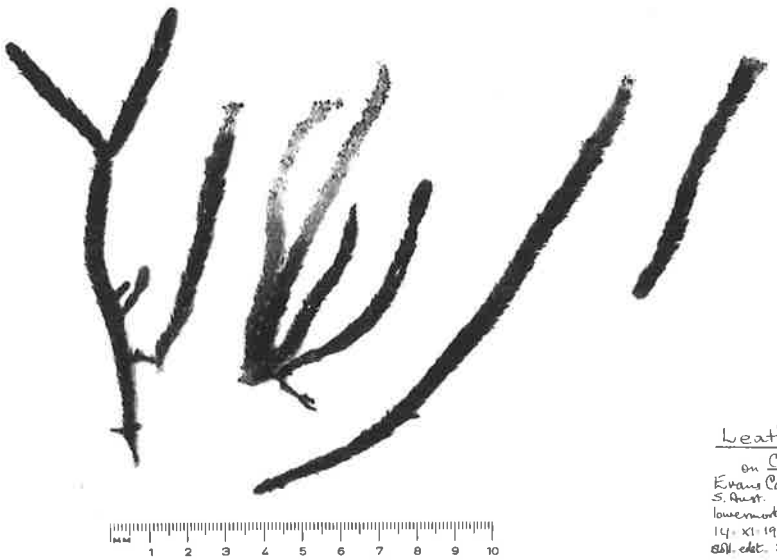
C. Point Roadknight, Vic.; ADU, A49080.

A



Leathesia difformis (L) Areschoug
Hildings roof, S Aust.
mid eulitt post, on Posidonia, south end
of reef.
26 x 1977
coll & det S Skinner

B



Leathesia intermedia C
on Caulerpa brownii
Evans Cave, Cape Lannes, Robe,
S. Aust.
lower mort eulittoral
14 XI 1971.
Coll. det. S Skinner.

C

Petrospongium rugosum (Okam.) S. F
Point Roadknight, Victoria
on rock in breaker area of lower eulitt,
emergent at high tide.
6 I 1978
coll. & det. S. Skinner.

Plate 23. Specimen Sheets, 5.

Flabellonema codii gen. et sp. nov.

A. TYPE, on *Codium mamillosum*, Stanley Beach, K.I., S. Aust.; ADU, A20906.

Giraudya sphacelarioides Derbès et Solier

B. On *Posidonia* sp., Aldinga reef, S. Aust.; ADU, A48226.

Giraudya robusta sp. nov.

C. TYPE, on *Posidonia* sp., Pennington Bay, K.I., S. Aust.; ADU, A20123.

A

Slide 500

A 20, 106

TYPE

Flabellonema codii gen. et sp. n.
on Codium mamillosum Harv.

B

Giraudya
Aldinga reef, S. A.
lower eulitt. pool, on
16. VIII. 1977
Coll. S. SKINNER

20,123

C TYPE