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Board *of the* Botanic Gardens *and* State Herbarium



THE MARINE BENTHIC FLORA OF SOUTHERN AUSTRALIA

Part I

by

H.B.S. WOMERSLEY



Cover photograph: Thallus of Palmoclathrus stipitatus

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Handbook of the Flora & Fauna of South Australia, issued by the Handbooks Committee on behalf of the South Australian Government and published by favour of the Honourable the Premier (J. C. Bannon, M.P.)

THE MARINE BENTHIC FLORA OF

SOUTHERN AUSTRALIA

Part I

H.B.S. Womersley

Department of Botany, University of Adelaide South Australia

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FOREWORD

This important new work is a modern treatment of the green seaweeds and seagrasses of the southern coasts of Australia. As such it must make a major contribution to knowledge of the marine flora of the southern Hemisphere. It replaces earlier publications in this series on 'Seaweeds of South Australia' by A.H.S. Lucas and Florence Perrin.

Although seaweeds and seagrasses in Australia have limited commercial interest they are important in marine ecosystems, and even the most casual observer walking along the shore or fishing from jetties cannot fail to notice the variety of plant life attached to rocks, breakwaters and jetty piles or washed up on the beach. This book should be of significant value to students and a useful addition to the bookshelf of any seashore naturalist, apart from its obvious place as a standard work of reference in libraries.

Professor Womersley has a lifetime of experience in studying the marine flora, and as this is Part I of a three-part series, we can look forward to his further contribution in the books on brown and red seaweeds.

March 1984.

R & Albert

R. K. Abbott, Minister for Marine

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PREFACE

The need for a Marine Flora of southern Australia, suitable for use by both students with some background in marine plants and by marine researchers, has been evident for a long time. Rapid developments in phycology (the study of algae) made the earlier "Seaweeds of South Australia", Vol. 1 by A.H.S. Lucas, out-of-date within a few years of its publication in 1936. In particular, the classification of the Chlorophyta (green algae) and Phaeophyta (brown algae) has undergone radical changes, and many new species and genera have been added to the known flora. Nevertheless, Lucas' publication was of considerable value and helped to stimulate further interest in marine plants.

The present "Marine Flora" covers the benthic (i.e. attached) plants of the whole of southern Australia, including Tasmania. This has been shown to be a fairly uniform biogeographical region with most species found in suitable ecological habitats along the whole coast, but with smaller distinctive assemblages of species in the eastern (Tasmania and Victoria) region and on the south-west corner of Western Australia.

This Flora describes the known species of seagrasses and Chlorophyta, but almost certainly further taxa of microscopic Chlorophyta remain to be recorded. Deep water SCUBA collections may also discover unknown larger taxa. It is also evident that our knowledge of the reproduction and relationships of many taxa of Chlorophyta is far from adequate and there is ample opportunity for further detailed studies.

The introductory chapters are intended for senior students rather than research phycologists. They cover the nature of the algae, collection and preservation of them, historical aspects of studies on southern Australian algae, and brief accounts of their ecology and biogeography. The three main phyla of benthic algae are involved in these introductory chapters, but the rest of Part I covers only the seagrasses, the Chlorophyta and the single member of the Charophyta which occurs in marine situations. It is hoped that Part II on the Phaeophyta (brown algae) will follow within about two years, and the large group of the Rhodophyta after this.

This Flora is but a further stage in our knowledge of marine plants of the phyla concerned. Much remains to be done, especially in revisions of cosmopolitan genera such as *Ulva*, *Enteromorpha* and *Chaetomorpha*.

Note: Place names and their spelling follow the nomenclature authorities of each State.

ACKNOWLEDGEMENTS

Many phycologists, from students to researchers and SCUBA collectors, have contributed to the Flora, and the author expresses his gratitude to all of them, only some of whom can be mentioned below.

For many years support has been received from the Australian Research Grants Scheme (previously 'Committee') for research assistance, without which this work would be much further delayed. The assistance of Research Officer Mrs Enid Robertson B.Sc., and of Mrs Cheryl Price (1969 to 1980) and Miss Rosy Krahling (1980 to 1983) is gratefully acknowledged.

The chapter on the seagrasses has been contributed by Mrs Enid Roberston and that on the genus *Cladophora* is co-authored by Professor Chris van den Hoek of the University of Groningen, The Netherlands, who has an unrivalled knowledge of this genus on European, North Atlantic and other coasts of the world.

Australian phycologists who have kindly contributed material or commented on sections of this manuscript include Dr Elise Wollaston, Dr Elizabeth Gordon-Mills, Dr Stephen Skinner, Mr Steven Clarke and Mr Ralf Engler in Adelaide; Dr Gerry Kraft, Dr Sophie Ducker, Dr Margaret Clayton, Dr Bill Woelkerling and Mrs Doris Sinkora (who contributed abundant collections from Victoria) in Melbourne; Dr Robert King in Sydney; and Dr Murray Parsons and Dr Graeme MacRaild (especially on *Bryopsis* and *Derbesia*) in New Zealand. To all the above I am most grateful.

The work on seagrasses has been assisted in various ways by Dr John Jessop, Mr John Johnson and Mr Scoresby Shepherd in Adelaide; Dr Surrey Jacobs in Sydney; Mr Cameron McConchie in Melbourne; Dr John Kuo, Dr Margaret Brock and Mr Hugh Kirkman in Perth; Dr Ron Taylor of the University of New Brunswick, Canada and Dr Marion Cambridge (formerly of Perth) in the University of Groningen, The Netherlands. Their help is gratefully acknowledged.

During the progress of this Flora, collections have been consulted in or borrowed from many Australian Herbaria, and appreciation is expressed to the Directors of the National Herbaria of New South Wales (Sydney) and Victoria (Melbourne), the South Australian State Herbarium (Adelaide), the Tasmanian Herbarium (Hobart), the Western Australian Herbarium (Perth), and the Herbaria of the Departments of Botany in the University of Sydney, the University of New South Wales, the University of Melbourne, Monash University, La Trobe University, and the University of Western Australia. Specimens in numerous other herbaria have been consulted including the British Museum (N.H.), Paris, Leiden, Lund and the University of California (Berkeley).

Two SCUBA diving scientists in particular have contributed valuable collections, namely Mr Scoresby Shepherd (Department of Fisheries, South Australia) and Mrs Jan Watson (Melbourne). Other divers in the South Australian Department of Fisheries have also contributed. Dr Ron Southcott kindly supplied information on potentially dangerous animals in southern Australian waters.

Latin diagnoses (other than in *Cladophora*) were kindly supplied by Mr Scoresby Shepherd and Dr Bill Barker (*Lepilaena*).

The following kindly provided colour photographs, as acknowledged in the captions:— Mr M. McKelvey, Mr K. Branden, Mr J. E. Johnson, Dr M. Parsons, Mrs E. L. Robertson, Mr S. A. Shepherd, Dr E. M. Wollaston; other photographs are by H.B.S.W.

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Many of the photographs of herbarium specimens were taken by Photographic Services, Advisory Centre for University Education of the University of Adelaide and Figures 2-5 were kindly drawn by Mrs Sharon Proferes of the Department of Economic Geology, University of Adelaide. The manuscript was typed by Miss Carol Wilkins and Miss Cecelia Marcelline.

Permission to use certain illustrations from the Australian Journal of Botany (*Codium*), Phycologia (*Palmoclathrus*), and from "Marine Botany" (Longman Cheshire) is acknowledged by references in the appropriate places.

To all the above I extend my appreciation.

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H. B. S. Womersley.

NEW SPECIES AND COMBINATIONS

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1. INTRODUCTION

Since the early voyages of discovery to "Terra Australis", the marine flora of southern Australia has been known for its richness and the presence of many distinctive and unusual taxa. The earliest accounts resulted from the English and French expeditions of the late 18th and early 19th Centuries (which are discussed further in Chapter 3), and numerous descriptive accounts and lists were published during the latter half of the 19th Century. The early part of the present Century saw a partial hiatus in phycological studies, with A.H.S. Lucas being the only researcher. Since the 1940's, however, numerous thorough monographic and biological studies on southern Australian algae have been published.

Until 1936, the only readily available English language work on Australian marine algae was the magnificently illustrated "Phycologia Australica" of W.H. Harvey, published in five volumes from 1858 to 1863. In 1936 however, the first part of "The Seaweeds of South Australia" by A.H.S. Lucas, was published, covering the Chlorophyta (green algae) and Phaeophyta (brown algae), and including a brief account of the seagrasses. This was followed in 1947 by the second part, on the "Red Seaweeds" (Rhodophyta) by A.H.S. Lucas and F. Perrin. Both these accounts (the second in particular) were based largely on the publications of other authors (e.g. Lucas & Perrin was based mainly on the Latin descriptions of De Toni), and they were quickly out of date. They have, however, been the only publications on our marine flora available to the student or general reader.

The present Flora, of which only the first part on the seagrasses and Chlorophyta is presented here, is based on many years personal experience of the southern Australian benthic flora, and gives an account of the taxa now recognised on these coasts. Probably numerous additions (at least in the Chlorophyta) will be made during the next few years, especially of small epiphytic taxa, and the author will be glad to have new entities, or extended distributional ranges, brought to his attention.

The region (Fig. 1) covered in this Flora includes the whole southern coast of Australia, including Tasmania. The western limit is drawn at Cape Naturaliste and the eastern limit at the Victoria-New South Wales border. Southern Australian species which are known to occur northwards beyond the limits are so recorded, but only warmer water species which are known to penetrate to southern Australia, as defined above, are included in the Flora.

Localities mentioned below and in the Taxonomic Sections (Chapters 6 and 7) are shown on Figures 2-5, covering the coastlines of the southern States of Australia.

This southern Australian region is a natural biogeographic province, as discussed in Chapter 5. The great majority of southern Australian species are limited to this region, and very few species from the warmer western or eastern coasts of Australia penetrate to the southern coast.

Marine plants—of which the larger ones are commonly known as "seaweeds"—include several distinct groups. Most of them are relatively simple in structure, though their reproduction (especially in the red algae) is often highly complex. One major group belongs to the Angiosperms or flowering plants, and are known as "seagrasses". However, they are not true grasses (family Poaceae) and only a few superficially look like grasses. The southern Australian coasts are particularly rich in seagrasses. True seagrasses are adapted to, and only found in, normal marine conditions. On southern Australian coasts however, two genera (*Ruppia* and *Lepilaena*) which in many areas are brackish-water plants, do grow under true marine conditions often on the same tidal flats as seagrasses such as *Zostera* and *Heterozostera*. This Flora includes all such species growing in marine conditions.

Other Angiosperm groups which grow at least partly in the sea are mangroves and samphires. Only one species of mangrove occurs on southern Australian coasts, though several

genera and species occur in northern Australia. Our representative, Avicennia marina var. resinifera (Forster) v.d. Brink, occurs in the upper intertidal (but with the foliage never submerged) on sandy mud tidal flats in very calm situations (e.g. the South Australian Gulfs, Port Phillip and Western Port in Victoria). Its distribution in South Australia has been documented by Butler et al. (1977) and it is not further included in this Flora.

Samphires (several genera of salt tolerant Chenopodiaceae, especially *Sarcocornia, Sclerostegia* and *Halosarcia* (P.G. Wilson 1980)) are also common in sheltered localities at an upper intertidal to supratidal level. As with the mangroves, only the lower stems are occasionally covered by sea water, though occasional plants grow where totally immersed at high tides.

Both mangroves and samphires have a characteristic associated algal flora, growing on the lower stems (or pneumatophores of mangroves) and usually in shade. Mangrove and samphire communities, and their associated flora, are discussed by King (1981) and Beanland & Woelkerling (1982).

Occasionally other Angiosperms may be found in sheltered localities growing within, or at least rooted within, the intertidal zone. Some of these are discussed by King (1981), and they include the English hybrid grass *Spartina townsendii* Groves & Groves which was introduced to various localities in South Australia, Victoria and Tasmania in the early 1930's



Fig. 1. Map of Australia showing the biogeographical regions. This Flora covers the Flindersian Province (after Womersley 1981b, Fig. 11.1).

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Fig. 2. Locality map of Western Australia.



Fig. 3. Locality map of South Australia.



Fig. 4. Locality map of Victoria.

(Boston 1981) and is still existing (but not spreading) just north of Port Gawler in Gulf St Vincent, South Australia, and is also established at Corner Inlet in Victoria.

This Flora, then, includes only the typical marine plants which are totally submerged during high tides, or taxa of Chlorophyta (such as *Prasiola*) which grow at high intertidal levels and have marine affinities.

Although marine plants are commonly known as "seaweeds", they are not "weeds" in the sense applied to weeds on the land. They are growing in their natural habitat as "natives" and only a few cases of algae becoming "weeds" are known. One is the introduction of *Sargassum muticum* from Japan to southern England where it has spread in harbours along the coast (Boalch & Potts 1977). Introduction of any marine plant to a different part of the world is in general to be avoided, for its future growth and spread can never be accurately predicted.



Fig. 5. Locality map of Tasmania.

Apart from the seagrasses, all truly marine plants belong to the "algae", though this term covers several major groups ("phyla" or "divisions") and a great variety of forms. The benthic (attached) algae are dealt with in this Flora, and most are macro-algae in that they are readily seen. A few, however, are very small or microscopic and these are usually epiphytes on larger algae or seagrasses. The other major biological group of the algae is the phytoplankton—the minute, free floating, mostly unicellular plants of the photic (light) zone of the open seas. Many taxa of the same groups as in the phytoplankton (e.g. the diatoms) are common epiphytes on seagrasses or macro-algae, but these also are not included in this Flora.

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The benthic algae include three major groups and two of lesser importance (or at least less conspicuous). The three major groups (Phyla or Divisions) are the:

CHLOROPHYTA (green algae), characterised by their green colour due to their photosynthetic chlorophyll pigments (similar to those of land plants);

PHAEOPHYTA (brown algae), coloured light to dark brown due to additional brown pigments (especially fucoxanthin) which mask the green chlorophylls;

RHODOPHYTA (red algae), coloured various shades of red due to additional red protein pigments such as phycoerythrin, which however is easily destroyed by high light intensity so that red algae are not always bright red in colour.

The two lesser groups of benthic algae are the:

CYANOPHYTA (blue-green algae), which are often microscopic and inconspicuous, but some may be one to a few centimetres long and prominent intertidally. Their colour is due also to accessory blue-green photosynthetic pigments;

CHRYSOPHYTA, which include many of the phytoplankton (e.g. the diatoms), and also one genus of macroalgae (*Vaucheria*) which occurs as dark green mats of entangled, slender filaments on soft bottom substrates.

A further phylum, the CHAROPHYTA, is essentially a fresh-water group, but has one species which occurs in sheltered marine habitats such as the Coorong.

Of the above phyla, Part I of the Flora will cover only the seagrasses, the Chlorophyta, and the Charophyta. Part II will cover the Phaeophyta and Part III the Rhodophyta.

While the southern Australian marine algae and seagrasses are of considerable importance to botanists and marine biologists for their richness, high endemism, and relationships to floras elsewhere in the world, their possible utilisation and value as pollution indicators have also been studied.

Utilisation of the seagrass *Posidonia* in the South Australian Gulfs, for the very resistant fibre remaining in the mud substratum (1-3m deep) as siltation occurs, has been suggested and three companies had commenced operations in 1910 (Winterbottom 1917). These activities ceased during the 1914-18 war, and although mining of these fibre deposits has been advocated more recently, it has been found to be uneconomic. This is probably just as well, since seagrasses re-establish themselves only very slowly (areas off Port Broughton mined in 1911 were still barren in 1978) and they are important in the primary productivity of the Gulfs and also in providing habitats for various fish. Extensive mining of *Posidonia* fibres could severely damage the marine ecosystem of mined and nearby areas.

Marine algae are also utilised in a variety of ways, but this applies largely to the brown algae (for alginates) and the red algae (for agar and carrageenan). Alginates are widely used as stabilisers and thickeners in many foods such as ice-cream, cream and milk drinks, in cosmetics and in preparation of arc welding rods. The giant kelp *Macrocystis pyrifera* was harvested between 1965 and 1972 on the east coast of Tasmania for alginates, and since 1974 the "bull kelp" *Durvillaea potatorum* has been collected as drift weed on King Island in Bass Strait for the same purpose.

During and after the 1939-45 war, Australia's supplies of agar came largely from extensive beds of the red alga *Gracilaria* in Botany Bay and elsewhere on the N.S.W. coast. Agar is essential in bacteriology as a medium for growth of bacteria, and is widely used in canned foods, confectionery and condiments (Wood 1946). The beds of *Gracilaria* were gradually

destroyed by excessive harvesting, storms and pollution, and since the 1950's there has been no source of agar from Australian marine algae.

The value of seagrasses and marine algae as pollution indicators has been studied in several areas, especially in northern Spencer Gulf (Johnson 1981) and they have been surveyed in Westernport Bay, Victoria (Shapiro 1975). It is likely that such marine plants (as well as phytoplankton) will prove to be very useful indicators of a changed environment, since their variety is greatest under their normal conditions and they are reduced in number of species and frequency under abnormal (e.g. pollution) conditions when a few resistant species flourish and are good indicator species. The prevalence of *Ulva* and *Enteromorpha* adjacent to sewage effluent discharges is well known. It is, however, important that adequate baseline data is available on the flora prior to any environmental change, on its variety and richness, and on its seasonality and reproduction. Only if this is so can reasonable judgements be made on the overall biological effect of any changes, and thorough taxonomy is basic to such studies.

It is hoped that students with some botanical experience and others with marine biological interests will be able to use this Flora satisfactorily. Some preliminary knowledge however is necessary to use any flora, and where more basic information is needed reference should be made to recent texts such as Bold & Wynne (1978), or to Clayton & King (1981) for a more Australian viewpoint.

LAYOUT OF THE TAXONOMIC SECTION

Descriptions are given at each taxonomic level, followed by brief comments on their distinctiveness, numerical size for genera and above, and distribution. For each genus, the type species is named.

The most useful references only are given to the species of Chlorophyta; Womersley (1956) should be consulted for a more complete list of references.

Each generic and specific description is hopefully sufficiently comprehensive, along with the illustrations, for the taxa to be identified with some certainty. Key words are given in italics to aid in scanning the descriptions.

For each species, the type locality is cited, together with type data and herbarium (see abbreviations below) where the type is deposited. Following the summary of the known distribution (using essentially the western and eastern limits, with brief ecological notes), a list is given of "Selected specimens" or known specimens if there are only a few. These selected specimens are cited from west to east along the coast, with collection data and herbarium number where available. In some cases, the herbarium sheet data is abbreviated and the naming of zones is given as in Chapter 4 (e.g. "littoral" on herbarium specimens is changed to "eulittoral"). The selected specimens include those used in illustrations and in drawing up the descriptions. Brief comments on each species follow the citation of specimens.

Many species of southern Australian Chlorophyta have been included in the exsiccatae sets "Marine Algae of southern Australia" distributed by the author. These numbers are quoted in the "Selected specimens" for each species, and the sets have been sent to the following herbaria. ADU, AK, BA, BM, BO, CANA, CHR, CONC, HO, L, LD, LE, MEL, NSW, PC, PERTH, SPF, TCD, TNS, UBC, UC, US.

STANDARD HERBARIUM ABBREVIATIONS (Holmgren et al. 1981)

- AD State Herbarium, Botanic Gardens, North Terrace, Adelaide, South Australia 5000.
- ADU Department of Botany, University of Adelaide, Adelaide, South Australia 5001.
- AK Auckland Institute and Museum, Auckland, New Zealand.
- AKU Department of Botany, University of Auckland, Auckland, New Zealand.

BA	Herbarium, Departmento de Botanica, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Avda. Angel Gallardo 470, Casilla de Correo 10- Sucursal 5, Buenos Aires 1405, Argentina.
BM	British Museum (N.H.), Cromwell Road, London SW7 5BD, England.
BO	Herbarium Bogoriense, Jalan Raya Juanda 22-24, Bogor, Indonesia.
С	Botanical Museum and Herbarium, Gothersgade 130, DK-1123, Copenhagen K., Denmark.
CANA	Phycology Section, National Herbarium of Canada, National Museums of Canada, Ottawa, Ontario, Canada K1A OM8.
CANB	Herbarium Australiense, CSIRO, Canberra City, A.C.T. 2601, Australia.
CHR	Botany Division, DSIR, Private Bag, Christchurch, New Zealand.
CN	Laboratoire d'Algologie fondamentale et appliquée, 39 Rue Desmoneux, 14000- Caen, France.
CONC	Departmento de Botánica, Instituto de Biología, Casilla 1367, Conceptión, Chile.
FI	Herbarium Universitatis Florentinae, Museo Botanico, Via Giorgio La Pira 4, I-50121, Firenze, Italy.
FLAS	Herbarium, Department of Botany, University of Florida, Gainesville, Florida, U.S.A. 32611.
НО	Tasmanian Herbarium, C/- Department of Botany, University of Tasmania, Box 252C, G.P.O., Hobart, Tasmania 7001, Australia.
К	The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, England.
KIEL	Botanisches Institut der Universität Kiel, D-2300 Kiel, Federal Republic of Ger- many.
L	Rijksherbarium, Schelpenkade 6, 2313 ZT Leiden, Netherlands.
LD	Botanical Museum, Ö. Vallgatan 18, S-223 61 Lund, Sweden.
LE	Herbarium, Botanical Institute of the Academy of Sciences, 197022, Prof. Popov Str. 2, Leningrad, P-22, U.S.S.R.
LINN	The Herbarium, The Linnaean Society of London, Burlington House, Piccadilly, London WIV OLQ, England.
LIV	Herbarium, The Hartley Botanical Laboratories, Liverpool 3, England.
LTB	Department of Botany, La Trobe University, Bundoora, Victoria 3083, Australia.
MEL	National Herbarium of Victoria, Royal Botanic Gardens, South Yarra, Victoria 3141, Australia.
MELU	Department of Botany, University of Melbourne, Parkville, Victoria 3052, Australia.
MONU	Department of Botany, Monash University, Clayton, Victoria 3168, Australia.
MPU	Institut de Botanique, 163 Rue Auguste Broussonnet, 34000 Montpellier, France.
NSW	National Herbarium, Royal Botanic Gardens, Sydney, N.S.W. 2000, Australia.
OXF	Department of Botany, University of Oxford, Oxford OX1 3RA, England.
Р	Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, 16 Rue de Buffon, 75005 Paris, France.
PC	Muséum National d'Histoire Naturelle, Laboratoire de Cryptogamie, 12 Rue de Buffon, 75005 Paris, France.
PERTH	Western Australia Herbarium, Department of Agriculture, George St., South Perth, Western Australia 6151, Australia.
RO	Erbario dell'Instituto Botanico dell'Universita di Roma, Citta Universitaria, 00100 Roma, Italy.

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22	INTRODUCTION
S	The Herbarium. Naturhistoriska riksmuseet, Roslagsvägen 106, S-10405 Stockholm, Sweden.
SPF	Departamento de Botânica, Instituto de Biociências, Universidade de São Paulo, Caixa Postal 11461, 01000 São Paulo, Brazil.
SYD	John Ray Herbarium, School of Biological Sciences, University of Sydney, Sydney, New South Wales 2006, Australia.
TCD	School of Botany, Trinity College, Dublin 2, Eire.
TNS	National Science Museum, Department of Botany, Hyakunin-cho 3-23-I, Shinjuku-ku, Tokyo, Japan.
UBC	Department of Botany, University of British Columbia, Vancouver, B.C., V6T IW5, Canada.
UC	The Herbarium, Department of Botany, University of California, Berkeley, California 94720, U.S.A.
UNSW	Department of Botany, University of New South Wales, P.O. Box 1, Kensington, New South Wales 2033, Australia.
US	U.S. National Herbarium, Department of Botany, Smithsonian Institution, Washington D.C., 20560, U.S.A.
UPS	The Herbarium, University of Uppsala, S-751 21 Uppsala, Sweden.
UPSV	Herbarium, Växtbiologiska Institutionen, S-751 22 Uppsala, Sweden.
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2. COLLECTION AND PRESERVATION OF MARINE PLANTS

Extensive and well prepared collections are the basis of all studies of marine organisms, and this is not difficult for the benthic plants. The importance of good collections for taxonomic studies is evident, but it is equally important that representative collections—often referred to as voucher specimens—be kept of each species recorded in ecological surveys. Without such specimens, there is little possibility of later checking on the basis of names used in publications and reports. Likewise, voucher specimens should always be kept of plants used in physiological, biochemical or genetical studies. Such specimens should be numbered, their purpose indicated along with the usual field data (see below), and they should be deposited in a recognised herbarium perferably in the State where the studies took place.

The importance of accurate labelling of specimens with field data cannot be overemphasised. This should be done when the specimens are mounted on herbarium sheets, and it is simplest to incorporate the data on the sheet, in black waterproof (Indian) ink, before the specimen is floated out. In cases where this cannot be done, a temporary numbering system can often be used to eliminate the possibility of error. If typed or written labels are later glued to the sheet, this must be done with care and the labels properly and fully glued down. Labels on small specimen sheets should never be cut off and repositioned on larger sheets.

Specimens should always be incorporated in a recognised herbarium, and only duplicates kept as a private herbarium. There is no security for specimens in private herbaria, though these are usually presented to an established herbarium at some later stage. Type specimens should be lodged in one, or preferably more, recognised herbaria when they are described.

All herbarium collections should be numbered. Collectors often use their own field numbers, but on incorporation in a herbarium each specimen is numbered in the system in use by that herbarium. In most cases this is a system of consecutive numbering of each specimen as incorporated, and gives the total size of the herbarium. However, the main purpose of numbering is simply to give an easy and clear reference to each specimen, so that later researchers can be sure they are studying a particular specimen referred to in a publication. Other numbering systems have been used, such as the Rijksherbarium Leiden system of year (e.g. 937), day of the year (e.g. 122) and number for that day (e.g. 21), resulting in a specimen number 937, 122...21, but such a system is more cumbersome than consecutive numbering.

HABITATS OF MARINE PLANTS

The coasts of southern Australia have a great range of habitats, from very rough water (or high wave energy) coasts facing the southern ocean to sheltered and often almost land locked bays and inlets where the water conditions are usually a flat calm. The intertidal and subtidal ecology of benthic plants is discussed further in Chapter 4, and here we are concerned with collecting of plants in marine habitats.

Collecting in the intertidal region is done mainly at low tide, though in calm water situations specimens can often be seen more clearly when covered by water, and use of a face mask and snorkel or glass bottom bucket at half tide can be effective. On most coasts, however, the low tide period as given by tide tables (available from Departments of Marine and Harbours in each State, and usually from fishing supply shops) must be utilised, with collecting starting an hour or two before low tide and extending as far as suitable after low water. While tide tables usually give accurate predictions, other environmental factors can greatly influence low tide periods, especially on southern Australian open coasts where the maximum tide range is little over one metre. In particular, the state of the sea and the wind direction are important. The best conditions usually occur in summer, when the sea is calmer, offshore winds are more prevalent, and the lowest tides usually occur during the day (in winter they are often during the night). Also, mean sea level is some 12-15 cm lower in summer months than in mid winter months.

Care must always be exercised when collecting intertidally, especially on rough-water coasts subject to heavy surf from the south to south-west. Always work in pairs at least, and never separate far from each other. On rock platforms, step only where you can see the substrate or you may finish in a deep rock pool, and stand firm when that heavier wave is approaching you. Most of our open coast is also subject to the occasional much heavier "king" or seiche waves, which should always be kept in mind. On steeply sloping rock subject to heavy surf, great care must be exercised and in some circumstances the collector may need to be secured by a rope to assistants at a safer level. Always watch for slippery patches of blue-green or other algae in the mid intertidal region.

Southern Australian waters do not have many dangerous animals for which one has to be alert. One exception is the blue-ring octopus which is sometimes seen in pools or shallow subtidal areas where it can readily hide, e.g. in old cans. In general, do not feel in nooks and crannies where you cannot see, unless your hands are covered. In deeper water (10-30m), a stinging hydroid *Thecocarpus divaricatus* may occur in shaded habitats, and the sponge *Neofibularia mordens* causes a severe rash and contact with the skin or eyes (even via gloves) should be avoided. Batches of the surface floating Portuguese man-of-war, *Physalia physalis*, are occasionally blown ashore, and these and several smaller species of jellyfish can inflict painful weals.

The richest areas for marine plants are undoubtedly subtidal regions where water movement is moderate to very great. As discussed in Chapter 4, water movement is greatest just subtidally and decreases with depth, the rate of decrease depending on the degree of wave action at the surface. Whereas years ago the subtidal flora was known either from drift specimens after storms, by dredging, or by helmet diving, our knowledge has advanced greatly with the advent of SCUBA and the freedom this gives to the diver. Ecological knowledge of subtidal regions is almost entirely dependent on the work of SCUBA divers, and mastery of this technique is essential for such studies. Divers, however, should always be properly trained and certificated, and should always work in pairs.

Perhaps the most difficult region from which to collect is the immediate subtidal on rough-water coasts, where the surge of waves both creates dangers and restricts the time to observe and collect specimens.

In the subtidal generally, a great variety of habitats is available for plants. Most algae grow on rock in well lit situations, but some are restricted to low light areas either in caverns or under overhangs, or occur only in greater depths. Many are encrusting forms (coralline algae or others) and must be detached with the rock. Most of the seagrasses and some algae (e.g. some species of *Caulerpa*) do occur on soft bottoms of sand or sandy mud, usually where water movement is slight.

Many algae occur as epiphytes, either on large algae or on seagrasses (especially on *Posidonia* and *Amphibolis*), and in many cases are seasonal in their growth or occurrence. Such epiphytes are usually relatively small in size (less than 5 cm long) and not easy to differentiate in the field. Bulk collections are then necessary, to be sorted and separated in the laboratory.

While the subtidal flora is best investigated by SCUBA, the value of drift collections should not be overlooked. Certain bays along the coast, where swirling currents deposit material from offshore reefs, are noteworthy for drift material. If this can be collected when fresh, it often gives an abundance of good material, especially if the plants are floating in shallow, clear water.

COLLECTION AND PRESERVATION

FIELD AND COLLECTING EQUIPMENT

The relatively mild climate on most southern Australian coasts means that heavy field clothing is not usually necessary. In winter, warm and wind proof jackets are helpful, but in other seasons shorts and canvas shoes are usually adequate. Rubber soled shoes are suitable, but rope soled ones are better if available. Except for calm water conditions, knee length or longer rubber boots are not usually necessary or suitable, and can be dangerous if the wearer is knocked over and the boots filled with water.

Field collecting equipment includes implements to remove the plants, containers to hold them, a suitable means of preservation, labels, and containers for transport to the laboratory.

Collecting

Many algae and some seagrasses can be removed by hand (often with judicious use of the fingernails), but a stout knife may be necessary. A garden fork or spade is useful in seagrass beds, and a rake can be handy for material in deeper pools. Some thick encrusting algae can be removed with a knife or small paint scraper, but many (especially the crustose coralline algae) must be collected along with the substrate. This can only be done by use of a heavy instrument such as a geologist's hammer or a cold chisel.

For the non-diver, subtidal seagrass and algal beds in calm to moderate water movement can be sampled (at least down to several metres) by use of a light dredge. A suitable type is in the form of a double-sided rake with long prongs, dragged by a suitable length of rope. While some algae on rock may be missed by dredging, a wide variety is usually obtained with many smaller types entangled amongst larger ones.

Field Containers

Plastic containers have greatly eased marine collecting, compared with the heavy glass jars of limited size which were used 20 or more years ago. Their light weight, range of sizes, ease of use, and airtight nature makes plastic a great improvement.

For intertidal collecting, buckets and bags of various sizes are used, and for subtidal collecting plastic bags (usually perforated) or mesh bags clipped to the diver's belt are generally used. It is important that several sizes of bags, with numerous smaller bags, are available to the collector to hold collections of individual species separated in the field. Small clip-top bags are ideal for smaller algae, though small plastic vials can also be used.

Material must not be crowded in bags when collected, since increased temperature from continued respiration can result in disintegration of delicate species. Certain species (such as sarcomenioid red algae) disintegrate particularly readily, and the brown alga *Desmarestia* (rarely found on south-east Australian coasts) rapidly becomes acid as it dies and should be isolated from other collections.

If material can be studied within a few hours of collection, it can be kept cold with ice. Otherwise, it must be preserved for later detailed study.

Preservation

Field preservation is almost entirely done with commercial formalin, unless the material has to be fixed for cytological purposes. Formalin is about 40% by volume formaldehyde, and is diluted about 1/10 with seawater, giving a solution of 10% formalin or 4% formaldehyde. The concentration is not critical and half the above will usually give good preservation. Unfortunately formalin tends to become acid, and should be neutralised by addition of borax to the stock supply.

Formalin can be taken into the field in 2 or 5-litre plastic containers, but is conveniently dispensed from squeeze bottles such as household detergent containers (provided they scal properly after use). Some people are allergic to formaldehyde, and it is always a strong irritant and should not be inhaled. Hands should be well washed after using it and rubber gloves may be advisable for sorting; avoid any possible contact with the eyes. Formaldehyde and hydrogen chloride can form bischloromethyl ether above certain low levels, and this compound is potentially carcinogenic. However, this reaction occurs only in acid conditions and sea water is alkaline and well buffered so formation of the ether is not likely in formalin preservation of marine algae.

Algae or seagrasses are best soaked in the formalin solution in a bucket for an hour to overnight, but if they are bulked in plastic bags, a good squirt of neat formalin and thorough shaking of the bag will usually be adequate. After soaking in the solution, the plants are placed "drip wet" in a plastic bag, labelled, tied up with a strong rubber band and placed in the dark.

Labelling

Unless specimens are properly and accurately labelled, they are of little value. Labels must be of strong, resistant paper such as herbarium paper or wet strength "laundry tag" paper. Preferably the label is placed within the plastic bag or jar so as to be visible from the outside; labels tied to the top of the bag, or written on the bag, are often damaged. A dark lead pencil is suitable, but make sure the writing is clear.

Information on the label should be that to be placed later on the herbarium sheet (see below).

Containers for transport

Years ago, preserved algae were returned to the laboratory in glass jars or scaled metal drums. Present containers are almost universally plastic barrels (black or at least dark and opaque) of about 20 litre capacity, with screw lids (preferably of full width) which seal completely. They are usually available from fishing or camping shops, being used extensively for gear that has to be kept dry.

It is vital that preserved algae be kept in the dark until studied and mounted as herbarium sheets. If exposed to the light, most will lose their colour within a day or so.

SELECTION OF SPECIMENS

Many specimens in herbaria are of little value since they are incomplete, poorly developed, or lack reproductive structures, and on many also the data is of little value since it is too general for locality and gives no ecological information.

Ideally, specimens selected for the herbarium should be complete and fertile. The latter involves a knowledge of reproductive periods and while some algae are fertile throughout the year, others are fertile only in particular seasons (usually spring and early summer). Seagrasses are usually strongly seasonal in their fertility, flowering in September to December and bearing seeds in December to February.

Seagrasses possess a horizontal or apically upturned rhizome in the sandy mud substrate (or on rock for *Amphibolis*), anchored by roots, and with erect leaves from the rhizomes. Specimens should include two or more nodes of the rhizome with roots and leaves, and preferably the growing tip of the rhizome. Well developed plants should be selected, special attention being given to the leaves and their tips which should be complete and not grazed or broken off. Flowering and fruiting specimens are most important, and many seagrasses are dioecious. Most species of macro-algae are 2 to 50 cm long, so the whole specimen can be mounted with little difficulty. Well grown specimens with the basal holdfast intact and upper fertile parts present should be selected. The best season for growth and fertility of many algae is spring and early summer, but others grow best in winter. Several specimens of each species should be collected to show the range in form and also to cover all reproductive stages. Many brown algae have distinct gametophytes and sporophytes, or the sexual plants may be dioecious, and in the Rhodophyta most species have distinct tetrasporangial, male and female plants. All these must be examined for a complete study of the species.

Species of *Sargassum* produce fertile fronds annually and these appear quite different from the basal sterile leaves. Specific determinations can only be made if the basal leaves and the upper fertile fronds are present, so there is little value in collecting either part by itself.

Very small species, less than one to a few centimetres high, are usually collected associated with others or as epiphytes. Such taxa are very numerous on southern Australian shores.

Large species, such as the kelps or larger fucalean algae (Phaeophyta) can only be represented in part as herbarium sheets, but it is important that whole plants be collected, from holdfasts to upper juvenile regions and fertile parts. Preservation of such specimens is further discussed below.

While it is important that good, fertile specimens be selected for identification and preservation, this is not always possible in ecological surveys or monitoring studies. The limitation of short term studies of this nature must be recognised, but identification can be assisted if more mature specimens are searched for, perhaps outside the survey area, and are preserved as well as the voucher specimens from the survey.

PREPARATION OF THE COLLECTIONS

While in the past, collections were often dealt with in the field or nearby and herbarium sheets prepared, it is now general practice to return the formalinised material to the laboratory where it can be examined in more detail. Fertile material can then be selected for liquid preservation, and critical (usually little known) species can be more easily recognised.

It is best if bags can be undone and material washed out and sorted under a fume hood (or at least in a well ventilated room), to avoid the irritant effects of the formalin fumes. Most algae can be washed out in fresh water, but some delicate forms should be rinsed in sea water since they may disintegrate or cells may burst in fresh water. On the other hand, larger specimens should not be mounted direct from salt water as this results in hygroscopic salt in the paper or on the specimen. White plastic or enamel trays are suitable for sorting.

While herbarium sheets can be made from fresh material, they must be dried quickly to prevent mould. In general, it is better to formalinise all material (including seagrasses) before mounting.

Specimens should be examined microscopically when sorted and before mounting as herbarium sheets. Then good, fertile specimens can be selected and parts put aside for liquid preservation, and if suitable, permanent microscope slides can also be made.

Herbarium collections

Herbarium paper should be of good quality (e.g White Systems board 135, GSM 250). Two sizes should be used, with the large size about 1 cm less in dimensions than standard herbarium folders (which in ADU, are 445 mm by 280 mm) and the other half this size. Smaller sheets, if used, are best mounted in turn on larger sheets.

Small delicate species are often best spread carefully on pieces of mica and air dried. These are then housed in a suitable size of folded envelope, securely glued to a herbarium sheet bearing the data.

Sheet Data. The name (if known) and collection data are best inscribed, carefully and neatly, in waterproof (Indian) ink on the bottom right of each sheet before the specimen is mounted, and the herbarium number added then or later in the top left corner. Otherwise, some other numbering system (referring to field notes) must be used until the data can be added to the dried sheet.

Data recorded with each specimen should include

- (a) the locality, in enough detail for others to return to it or nearby; in a less well known locality, a better known reference point or the latitude and longitude are useful;
- (b) ecological notes, including the zone (if intertidal—see Chapter 4) or depth, the degree of water movement, and whether shaded or not;
- (c) the date, given as day of the month (arabic), month (roman or abbreviated) and year in full;
- (d) the collector's name, and field number if used.

Mounting should be done with care, to display the typical branching pattern of a mature and preferably reproductive plant. Bushy plants need to be carefully pruned, and often a smaller piece of the same plant can be added to show details of branching.

Mounting is done by "floating out" the plant, immersed in water, onto a sheet of herbarium paper also immersed. Larger robust plants (e.g. larger brown algae and some seagrasses), however, can usually be displayed without the need for floating out, and crustose forms are dried separately for box storage. While almost any container can be used for floating out, with a sheet of wood or metal to support the paper and specimen, a bath with a sloping bottom is ideal. Such a bath is shown in Fig. 6 and permits the hands to be used to draw the paper up the slope and to display the specimen as this is done. After draining off excess water, the mounted specimen is dried (see below).



Fig. 6. "Floating out" bath for preparation of herbarium specimens.

Many species (especially red algae) adhere well to the paper by their own mucilage. Others do not adhere and have to be glued down when dry by means of spots of good quality mucilage or plastic glue between the thallus and paper. Larger brown algae usually stain the paper brown and also do not adhere. These are best dried between newspaper and glued when dry to herbarium paper; however, care must be exercised in correctly labelling such specimens. Paper clips, staples or anything metal should not be used for attaching specimens to sheets, nor should cellulose tape since it is not permanent and may mark the paper or specimen.

Some algae, especially the large brown algae of the Fucales, become rather brittle on drying. This can be avoided by treatment in glycerine (see below) before drying.

Crustose algae, whether browns such as *Ralfsia* or reds such as *Cruoria*, *Hildenbrandia* or the coralline algae, are dried on their natural substrate, preferably in the dark (to minimise fading) and kept in boxes of suitable size, along with their labels.

Articulate coralline algae present a special problem, since if simply dried they become very brittle and readily separate at the joints. This can be largely prevented by soaking them in a 30-50% glycerine solution (with phenol or formalin to prevent bacterial growth) for a week in the dark, before drying.

Large brown algae such as the kelps and some fucoids also present a problem since they are too large for a single herbarium sheet. In such cases, pertinent parts can be mounted, showing in particular the base, mature thallus, growth regions and reproductive regions, and a photograph of the whole plant can be incorporated.

A better method for preserving such large plants, if space permits or teaching needs are involved, is to soak the plant for a week in a 30-50% glycerine solution (with a preservative such as phenol) and then hang them up to dry in a warm, shaded place for a week or so. This results in a pliable specimen suitable for examination.

Drying of herbarium sheets is done by placing the wet (but drained of surplus water) sheet and specimen on newspaper, covering with a piece of calico or butter muslin and then further newspaper; several folded sheets of newspaper should be used in each case. For some delicate (but not mucilaginous) algae, a sheet of waxed paper is better than calico as a cover, and is more easily removed when the specimen is dry. A stack of herbarium sheets (with specimens) and newspaper is built up and placed in a plant press under moderate pressure.

The newspaper must be changed at frequent intervals, at first at 2-3 hourly intervals, then morning and night until the specimens are quite dry. The calico is not changed and can be carefully stripped off the specimens when dry. Drying can be hastened, and specimens kept flat, by use of strong cardboard corrugates between batches of specimens and newspaper, and placing the press in a warm place with air passing through the corrugates. A simple drier is used in many laboratories. This consists of an enclosed rack with heat from electric globes or strip heaters below, and in which presses are placed on edge so that warm air passes through the corrugates. Specimens should not be left in the drier too long since some become unduly brittle. Allow the specimens to cool before removal from a warm press.

Liquid preserved collections

While it is remarkable how much information can be obtained by re-soaking dried specimens, it is essential that selected material of growth and reproductive stages be kept in liquid for future research investigations. Although formalin is by far the easiest, cheapest and generally most satisfactory field preservative, it is not good for long-term storage of algae, since it tends to become acid and the specimens gradually disintegrate. This is lessened however by neutralising with borax. After return to the laboratory, selected material (e.g. growth apices, reproductive stages of algae, flowering and fruiting material of seagrasses) of each species required for future research should be placed in 70% ethyl alcohol with 5%

glycerine to prevent complete (and accidental) drying out. Although some delicate species shrink in alcohol, they recover when returned to water and are then suitable for detailed study.

This "wet stack" material is best kept in glass or plastic tubes or vials, with tight fitting corks or caps. Tubes 10 centimetres long and 2.5 centimetres in diameter are usually satisfactory, and these can be housed in holes in wooden blocks in cabinets, classified as in the herbarium. Larger containers may be needed for large species or bulky crustose coralline algae, but uniform-size tubes in racks should be used as far as possible.

Each tube should contain a label with data identical to that on the herbarium sheet, and the herbarium sheet number can conveniently be placed on the cork in ink or on the vial cap in paint or on a self adhesive label. Wet stack collections should be checked annually for the level of the liquid.

Microscope slide collections

Either when first sorted and examined, or later from the wet stack collections, permanent microscope slides should be made of selected reproductive and other critical stages. Such slides should bear the name of the alga, important collection data, the number of the herbarium sheet with which it is associated, and a slide number. The slides are best kept in 100-slide vertical boxes in the sequence in which they are made and the number is written on the top of the corresponding herbarium sheet, so indicating that a permanent slide exists. A card index to the genera and the species represented by slides is valuable.

By far the best general mounting medium for marine algae is corn syrup (Karo), obtained from the U.S.A. where is is a food additive and sweetener. Gourmet food shops in Australian capital cities often stock it, and chemists stock liquid glucose which can be used in a similar way. The medium is used in several dilutions and must have 2-3% phenol added to stop fungal and bacterial growth.

Various stains are available, but the most generally useful one, which stains protoplasm (depending on its density), is aniline blue. The following schedule can be used, either in watch glasses or on slides, removing and adding the solutions by means of fine pipettes.

- 1. Stain in 1% aqueous aniline blue for 5-10 minutes.
- 2. Acidify with 1-2 drops of dilute (1N) hydrochloric acid, for a few seconds.
- 3. Wash with water.
- 4. Add a few drops of 20% Karo, for 2-10 minutes.
- 5. Replace with 50% Karo, for 2-10 minutes.
- 6. Replace with 80% Karo, for 2-10 minutes.
- 7. Mount under a coverslip in 80% Karo.

Either selected material or sections can be stained as above. If the former, small stained apices or reproductive parts should be dissected and spread carefully before the coverglass is added, and (while observing under a stereomicroscope) enough pressure applied to the coverglass to separate ("squash") the material so as to show the structure or reproductive stages. A small lead weight on the coverslip during drying may be useful, but an adequate amount of Karo must be present to prevent undue spreading of the material. Mounts in 80% Karo harden gradually over some weeks and are permanent. Slides made 40 or more years ago are usually quite satisfactory.

Sections of the algal material can be cut on a slide by means of a new razor or scalpel blade, using the finger or another slide as a guide, or the material can be held in carrot tissue. Experience permits quite thin sections to be cut, especially if done under a stereomicroscope, but for thinner and more even sections a freezing microtome is used. If sections of dried herbarium specimens are required, they are nearly always best cut freehand (as above) from the dried material, then lifted and soaked up for staining and mounting.

Herbarium material when delicate is often best prepared as slides by soaking off with a drop of detergent and mounting directly into a solution of acidified 1% aniline blue in 20% Karo. Such material usually disintegrates and is lost if processed through the several Karo percentages above, but in this solution the material gradually takes up the stain and the 20% Karo gradually concentrates and dries. More Karo may have to be added at the side of the coverslip. However, slides made in this way often show a dark emulsification of the medium after some years.

Herbarium organisation

The dried herbarium sheets must always be the core of the collections, with wet stack material and permanent slides both referred to herbarium sheets. The "life" of dried algae is indefinite, and specimens prepared nearly 200 years ago are still adequate for study. They should, however, be kept in a relatively dry environment and in the dark.

Herbarium sheets are placed in folders of similiar paper, either singly or in groups of specimens, and the folders grouped within larger, usually overlapping folders of appropriate size; these may be for genera, or groups of species within large genera. Within a genus, the species are always arranged alphabetically. Above this level, they may either be arranged in classified order in families, orders, phyla etc., or in alphabetical order for genera within phyla. The first arrangement is preferable for a teaching herbarium and for ease of locating related genera or families, but requires a card index for genera and a numbered shelf system. The second arrangement is easier for location of a particular genus.

As stated above, all herbarium sheets or boxes should be numbered, and specimens of one species with identical collection data should have the same number.

Bulky specimens should be housed in boxes of suitable sizes, with the label and number on the outside as well as inside the box.

The folders and boxes are housed in a system of shelves, either on a pigeon-hole system (simply slid onto the shelf) or in larger boxes which in turn fit onto the shelves. Numbering or naming of the shelves or larger boxes for the group housed there is important to help prevent return to the wrong shelf. In planning a herbarium, adequate room must be left for incorporation of further collections.

Culture of living material

For investigations of reproduction and life histories of the algae, it is essential that material be cultured under a range of conditions. Constant environment cabinets and various, specified, culture solutions are needed. Reference can be made to the first volume of "Handbook of Phycological Methods" (Stein 1973) for such details.

3. THE HISTORY OF STUDIES OF SOUTHERN AUSTRALIAN MARINE ALGAE

The history of phycology in Australia has been reviewed previously by Womersley (1959) and Ducker (1981a) and will be briefly outlined here to give perspective to our present knowledge of the southern Australian marine algae. A more detailed world review for the period 1853 to 1953 was given by Papenfuss (1955), and Dawson (1966, pp. 288-301) also discussed the history of marine phycology, especially in North America.

For southern Australia, our phycological history can conveniently be divided into three periods.

- 1. The early collections by naturalists on English and French expeditions of discovery along the Australian coast, and their study by English, French and Swedish phycologists.
- 2. Collections by resident Australian naturalists, and by W.H. Harvey from Dublin who resided and travelled in Australia for 18 months in 1854-1855. Apart from Harvey's, these collections were studied by J.G. Agardh (Sweden) and other European (especially German) phycologists.
- 3. The present century (starting from about 1890), with two periods of collection and study by Australian phycologists;
 - a. by gifted amateurs, notably J.B. Wilson and A.H.S. Lucas,
 - b. by phycologists in University positions.

COLLECTIONS FROM EARLY EXPEDITIONS (1791 to about 1850).

Most of the expeditions concerned with the discovery and mapping of the Australian coastline carried botanists (or scientists who devoted some time to the plants) but they were more concerned with life on the land. Only a few algae were collected on early expeditions, and these were the more conspicuous taxa.

The earliest record of an Australian marine alga is the description and illustration of a brown alga [recognisable as Cystoseira (Cystophyllum) trinodis] from Shark Bay, by Dampier (1703, p. 109, pl. 2 fig. 2), and the first formal description was by Velley (1800) of Conferva umbilicata [= Microdictyon umbilicatum] from New South Wales. The first expedition to collect marine algae in southern Australia was that of Vancouver in 1791, with Menzies as botanist. This expedition landed only at King Georges Sound, later passing south of Tasmania to New Zealand. Turner (1808-1819) later described three species of Fucus (now Hormosira banksii, Scytothalia dorycarpa and Sargassum linearifolium) from King Georges Sound.

Although the Menzies specimens were the first collected in southern Australia, Labillardiere (1807) described eight species of brown algae and one red alga from Tasmania, collected by the French expedition (1791-4) under D'Entrecasteaux which visited the Recherche Archipelago in Western Australia and southern Tasmania ("Cape van Diemen"), where the main landing place was in Recherche Bay. He also described the first southern Australian seagrass, *Amphibolis antarctica* (as *Ruppia*). The algae described include the giant brown, *Durvillaea potatorum*. This expedition was followed in 1802 by the French expedition of Baudin which covered much of southern Australia, and on which algae were collected by Peron, Leschenault and Lesueur. The collections were deposited in the Paris Museum but not described as a whole, though many were later described by C.A. Agardh, Mertens (see Ducker 1981c), Lamouroux and Lamarck. Unfortunately the locality given was usually "Novae Hollandiae" and it is now seemingly impossible to specify the type localities of many of these species. Later French expeditions (see Ducker 1979) apparently collected few algae on southern coasts, though they did on the more tropical coasts of Australia.

A most extensive and important voyage around Australia was that of Matthew Flinders in the "Investigator" 1801-1803, with Robert Brown as botanist. Brown returned with some 3 900 species of Australian land plants and some 31 species of algae. The marine algae were described by Dawson Turner (1808-1819) in his classical "Fuci", and came largely from the Kent Islands in Bass Strait, with some from Port Dalrymple in Tasmania, from King Georges Sound, or simply from the "south-coast" of New Holland.

The second Dumont D'Urville expedition (1837-40), with the "Astrolabe" and "Zélée", made two visits to Hobart in Tasmania, from 11 Dec. 1839 to 1 Jan. 1840, and (after a visit to the Antarctic) from 17-25 Feb. 1840. Following this, D'Urville visited the Auckland Islands (11-20 March), Otago Bay (30 March-3 April), Akaroa (8-17 April) and the Bay of Islands in New Zealand, and then proceeded to France via Toud Island (now Warrior Islet) in Torres Strait. Most of the algae from this expedition were described by Montagne (1845), but several cases of mislabelling of specimens for localities occurred. These include *Chaetomorpha coliformis* (see p. 172) and several brown and red algae (see Womersley 1979, p. 501) which have been variously ascribed to the Auckland Islands, Akaroa or Toud Island, and which probably came from Tasmania. Labels (a small hand-written label for *C. coliformis*) were probably not attached until after sheets were dried, and in the above cases then associated with the wrong sheets.

The "United States Exploring Expedition" of 1838-1842, captained by C. Wilkes, visited Sydney and a few species were recorded from New South Wales by Bailey & Harvey (1874), but none from southern Australia.

Knowledge of Australian and New Zealand botany advanced markedly following the "Voyage of Discovery and Research in the Southern and Antarctic Regions, 1839-43", under Sir James Clark Ross, with J. D. Hooker as botanist. The expedition spent two lengthy periods in Hobart, from August to November 1840 and April to July 1841, as well as 3 weeks in Port Jackson (Sydney). Hooker made a comprehensive collection of marine algae, which were described by W. H. Harvey (1859b) in Hooker's "Flora Tasmaniae", as well as in Harvey's "Phycologia Australica". The marine algae of Tasmania were then the best known of all Australian algae.

A further expedition, the "Novara" of 1857-59, collected a few algae in Australia and they were described by Grunow (1870), but the period 1840-1850 saw developing interest in marine plants by Australian residents and initiated the second period of Australian phycology.

COLLECTIONS BY RESIDENT AUSTRALIAN NATURALISTS AND THEIR DESCRIPTION BY BRITISH AND EUROPEAN PHYCOLOGISTS (Latter half of the 19th Century)

The first collection of algae by a resident of Australia was that of Charles Fraser (Colonial Botanist in Sydney), from near the Swan River mouth in Western Australia; his collections were mentioned by Greville (1830), but mostly described by other authors. Also in Western Australia, Ludwig Preiss (see Ducker 1981a) collected from 1838 to 1842 between Fremantle and Cape Riche, resulting in the comprehensive accounts by Sonder (1845, 1846). Unfortunately, type localities for the Preiss material cannot be specified.

The arrival of Ferdinand Mueller (see Churchill, Muir & Sinkora 1978) in South Australia in 1847 marked an upsurge in botanical studies. During his four years residence in Adelaide he collected on nearby beaches, especially on Lefevre Peninsula. In 1852, Mueller moved to Melbourne and continued collecting algae though his main efforts were devoted to the land flora. Mueller's algal collections were described mainly by Sonder (1853, 1855, 1881) but many were also described by Kuetzing, J.G. Agardh, and others.

Several naturalists in Tasmania extended their land flora interests to the marine algae, and sent their collections to W.H. Harvey in Dublin. Notable among them were Ronald Gunn
(between 1832 and 1850), Charles Stuart, William Archer and John Fereday. George Clifton in Western Australia and David Curdie in South Australia provided Harvey with abundant material.

These numerous collections from Australia and Hooker's 1840 and 1841 collections from Tasmania showed Harvey that the Australian marine algae were especially rich in numbers, with many very distinctive taxa. Harvey's interest in the region, together with his poor health and desire for a warmer climate, resulted in his extensive visit to Australia in 1854-55. This marked a turning point in our knowledge of Australian marine algae, when for the first time a professional and expert phycologist saw the living algae and collected for himself. During Harvey's 18 months in Australia, he collected some 600 species and 20 000 specimens (Harvey 1858, "Advertisement"), which, allowing for travelling time, means that on many days he must have collected and prepared well over 100 specimens.

Harvey's specimens were sold or distributed as sets ("Algae Australicae Exsiccatae") and are available in many Herbaria, including MEL and NSW (also the Mitchell Library) in Australia. His types are considered to be those in TCD, but the sets contain many isotypes. A list of the species in the sets was printed by Harvey (1857). During his travels in Australia, Harvey used a "Travelling Set" of named specimens, each with a number (distinct from those in "Algae Australicae Exsiccatae"). These numbers were usually quoted in Harvey (1855c) where he described many new species from Western Australia and such specimens therefore must be regarded as the types. The "Travelling Set" is in TCD but unfortunately with many specimens removed—some of which are filed separately in the TCD Herbarium. However, in many cases Harvey kept duplicates of his travelling set numbers, and MEL contains many such duplicates, some of which are isotypes. They were probably the set presented to Mueller in Melbourne by Harvey in 1854 (see Mueller 1855, p. 6; Churchill, Muir & Sinkora 1978, p. 10).

Harvey arrived at King Georges Sound, Western Australia, on 7 January 1854 and left Sydney on 15 June 1855 after which he visited northern New Zealand for a month and then the Friendly Islands and Fiji before departing from Sydney in December 1855. On his Australian specimens, Harvey used a letter for locality following the number of the species, and some species came from different localities. The dates for the various localities (as extracted from Harvey 1855c and 1869) are as follows:

- A FREMANTLE, W. Aust., and vicinity, from 13 April to late July 1854, including ROTTNEST ISLAND, from 21 May to 2 July.
- B KING GEORGES SOUND, W. Aust. from 7 January (arrival) to 2 April 1854, during which March was spent at Cape Riche. Harvey revisited King Georges Sound in August.
- C CAPE RICHE, W. Aust., during March.

From late August, 1854 to 13 January 1855, and during most of April 1855, Harvey was based in Melbourne, making various field trips in Victoria.

- D PORT FAIRY, Victoria, from 1 to 15 October 1854.
- E PORT PHILLIP HEADS, Victoria, from 30 October for some days (?), and also from 30 November for a week.
- F PORT PHILLIP, Victoria | late August 1854 to 13 January 1855, and mid-
- G GEELONG, Victoria March to 1 May 1855, with visits elsewhere.
- H WESTERN PORT, Victoria, from 9 to 28 December, 1854.
- I/J GEORGE TOWN, Tasmania, from 13 January to 25 February, 1855, and briefly at Launceston in late March on the way back to Melbourne.
- K PORT ARTHUR, Tasmania (via Hobart), from 26 February to mid March, 1855, with a visit to Eaglehawk Neck.

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L	PORT	JACKSON.	N.S.W	from 1	to	16 May.	1855.
				******	•••		

Μ	NEWCASTLE, N.S.W.	from 17 May 1855 to mid-June 1855 (departed
Ν	KIAMA, N.S.W.	Sydney 15 June).

Harvey described a number of Australian algae in small papers in journals, followed in 1847 by his "Nereis Australis, or algae of the Southern Oceans" and by a more thorough account of his Western Australian algae in 1855c. Between 1858 and 1863, his five, beautifully illustrated (in colour) volumes of "Phycologia Australica" were published. Volume 5 included a synopsis of all known species. This is still a basic work for modern students of Australian algae since it illustrated some 300 species and demonstrated Harvey's excellent generic and specific concepts for that time. Unfortunately Harvey's health deteriorated and he died in 1866 at the early age of 55.

The middle and latter half of the nineteenth century saw the publication of several comprehensive algal floras of the world. In 1848 the Swedish phycologist, J.G. Agardh, commenced his "Species Genera et Ordines Algarum", which was to continue to 1901. J. Agardh described a large number of Australian species; a few were sent to him by Harvey, but most were received from Australian collectors (via Mueller) after Harvey's death, in particular from F. Mueller himself and J. Bracebridge Wilson in Victoria, and also from Jessie Hussey at Port Elliot in South Australia. J. Agardh's publications under the titles of "Till Algernes Systematik" (1872-1890) and "Analecta Algologica" (1892-1899) contain many descriptions of Australian species, and, of more importance, revisions of major groups. His studies were noteworthy for their morphological contributions, which helped to found the present day classification of marine algae. A particularly important monographic work was that on *Sargassum* (J.G. Agardh 1889).

In Germany, F.T. Kuetzing (see Ducker 1981b) published his "Species Algarum" in 1849 and later his massive series of 20 volumes of algal descriptions and illustrations, "Tabulae Phycologicae" (1851-71). Kuetzing described numerous Australian species, mostly from the herbarium of O.W. Sonder, the greater part of which is now in the National Herbarium, Melbourne.

Apart from the comprehensive accounts of Sonder, Harvey, J.G. Agardh and Kuetzing, and De Toni's "Sylloge Algarum" (1889-1924) which brought together the systematic knowledge of algae to that time, publications on Australian algae in the latter part of the nineteenth and early twentieth centuries consist of lists, sometimes involving new species. These were based on collections sent to various phycologists (e.g. Areschoug 1854; Gepp & Gepp 1906) and some made by expeditions visiting Australia. A number of generic revisions (e.g. Weber van Bosse 1898, on *Caulerpa*; Kjellmann 1900, on *Galaxaura*; Barton 1901, on *Halimeda*) also dealt with Australian species.

In South Australia, the most important accounts are those of Reinbold (1897, 1898), based on collections from Lacepede and Guichen Bays in the south-east of the State, and in 1899 from the south coast of Yorke Peninsula facing Investigator Strait. In Victoria, J. Bracebridge Wilson, who was Headmaster of Geelong Grammar School, dredged for algae near Port Phillip Heads and in Western Port for a number of years, gathering fine collections which were described by J.G. Agardh (see Wilson 1895 for his dredging stations). Wilson collected many new species and genera, quite a number of which are still rare. Duplicate collections are in the Melbourne National Herbarium and in the British Museum.

THE PRESENT CENTURY (from 1890) WITH STUDIES BY AUSTRALIAN PHYCOLOGISTS

While this section deals with the contributions made by Australian phycologists, significant monographs on many groups of algae, including Australian taxa, were published between 1920 and 1960 by European phycologists. Outstanding were those from Sweden by H. Kylin, with revisions of the Delesseriaceae (1924), Rhodymeniales (1931), Gigartinales (1932) and

Chordariales (1940), culminating in his 1956 monograph on the genera of Rhodophyta. Contributions were also made by De Toni & Forti (1923) and by Levring (1953).

(a) The first part of this period overlaps with the previous one in that J.B. Wilson gained considerable knowledge of the algae he collected and published a list of the algae of Port Phillip Heads in 1892. He was, however, clearly dependent very largely on J.G. Agardh's determinations. Tisdall (1898) apparently used Wilson's paper extensively in his list of Victorian algae, and Bastow (1898, 1899) presented illustrated keys to the brown and red algae, based on Sonder (1881).

The early 1900's saw a gap in phycological studies in Australia, until A.H.S. Lucas, a school teacher and naturalist, turned his attention to the algae. Lucas was the only Australian researcher on the algae for nearly 30 years. In 1909 and 1912 he published a list of the marine algae of Australia, extracted from De Toni's "Sylloge Algarum". Unfortunately his list gave no references and distributions were severely abbreviated, making it of very limited value. Lucas later published accounts of certain genera (*Caulerpa* of Victoria, 1931, *Nitophyllum*, 1926; *Spongoclonium*, 1927) as well as various notes and descriptions of new species. Lucas collected widely, often with his co-worker Mrs Florence Perrin from Launceston, and published in 1929 lists of Tasmanian and of South Australian algae. The algae of Lord Howe Island were described in 1935, and the first part of the "Seaweeds of South Australia" was published in 1936. This was the first descriptive account of any major group of Australian algae for over half a century, and was followed in 1947 by a second part on the red algae, completed by Mrs Perrin after Lucas's death. This contains little original work, being mainly a translation of the relevant descriptions from De Toni.

(b) Studies by University trained phycologists commenced in the mid 1930's by Valerie May in New South Wales, who published keys to the Chlorophyta (1938) and Phaeophyta (1939) of that State. These were followed in 1948 by a revision of the Australian species of *Gracilaria*. A key to the genera of red algae (May 1953) was followed by a supplement (May 1965a) and key to the species of red algae (May 1965b). Her papers on new geographical records and ecological studies have continued to the present day.

Studies by the present author on the marine algae of Kangaroo Island commenced in 1945, and the intertidal ecology of the very varied coastline of the island was surveyed (Womersley 1947). These studies spread to the rest of the South Australian coastline (Womersley & Edmonds 1958), but it was becoming apparent that ecological studies were limited by the lack of a sound taxonomic basis. Studies in Adelaide therefore turned more to the comparative morphology and taxonomy of our marine algae (the Phaeophyta and Rhodophyta in particular). The whole of southern Australia (including Tasmania) was recognised as a biogeographical region and most publications dealt with the species of genera or families within this region.

Following establishment of a comprehensive card index of all species recorded for this region, including synonyms, references and type data, studies by the author in British, European, and certain North American Herbaria in 1952 enabled the types of most southern Australian species to be checked against specimens from ADU, and notes incorporated into the card index. Following this, critical surveys were published on the Chlorophyta (Womersley 1956) and Phaeophyta (Womersley 1967), and our state of knowledge of Australian marine algae was also reviewed (Womersley 1959).

These studies began to attract graduate students from other countries as well as from Adelaide. Higher degree studies were carried out by Ann Shepley on the Sarcomenieae of the Rhodophyta, M. Nizamuddin on the Fucales, R.N. Baldock on the Griffithsieae, Elise Wollaston on the Ceramiaccae (*Antithamnion* etc.), A. Bailey on the Chordariaceae, Elizabeth Gordon on the Ceramiaccae (*Wrangelia* etc.), W.J. Woelkerling on the Acrochaetiaceae, M.J. Parsons on the Dasyaceae and Lophothalieae, Min Thein on the Gigartinales (Solieriaceae etc.), G.T. Kraft on the Gigartinales (Mvchodeaceae etc.) and S. Skinner on pulvinate Phaeophyta.

Within the Department of Botany of the University of Adelaide, the present author and his colleagues (Dr Elise Wollaston, Dr Elizabeth Gordon-Mills) have continued studies in comparative morphology and taxonomy. Since the late 1960's interest by SCUBA divers has developed strongly, resulting in studies of the subtidal ecology of several localities on the South Australian coast (e.g. Shepherd & Womersley 1971, 1981). SCUBA collections of algae, from known depths and sometimes from relatively deep water, have made significant contributions to taxonomic studies.

All three Universities in Melbourne have now developed phycological studies. At the University of Melbourne, Dr Sophie Ducker's publications include revisions of *Chlorodesmis* and *Metagoniolithon*, and studies on seagrass biology and on the history of phycology in Australia, and Dr G.T. Kraft continues with broad interests in the Rhodophyta of southern Australia, and the marine algae of Lord Howe Island, the southern Great Barrier Reef and the Coffs Harbour region of New South Wales. At Monash University, Dr Margaret Clayton is making significant advances in our knowledge of brown algae, particularly the Scytosiphonales and related groups, on the basis of culture studies; such studies are also being applied in the Ulvales. At La Trobe University, Dr W.J. Woelkerling is undertaking morphological and taxonomic studies of the crustose coralline algae, and of algae associated with mangrove communities.

Following the collections of Tasmanian algae by Lucas and Mrs Perrin, and the list of Lucas (1929a), only sporadic interest has been shown within Tasmania. E.R. Guiler (1952) published a further list of Tasmanian algae and studied the intertidal ecology of several coastal areas. A.B. Cribb (1954, 1956) contributed an ecological survey of Port Arthur and new records for the island. The algae of Tasmania are included within the region covered by the present Flora.

Phycological interests are also well developed at the University of Sydney with Dr A.W.D. Larkum (physiology and ecology), at the University of New South Wales with Dr R.J. King (ecology), and in Queensland with Dr A.B. Cribb (taxonomy and ecology) in the University of Queensland and Dr I. Price (tropical algae) at James Cook University in Townsville. In Western Australia, interest in the rich western algal flora has been followed at the University in Western Australia by Professor A. McComb (physiology) and Mr G. Smith (taxonomy) and is currently developing at Murdoch University.

The past 30 years have seen a great expansion of interest in southern Australian marine algae, especially in the Universities within this region. However, our current knowledge of the taxonomy of most groups is far from satisfactory and much remains to be accomplished. As our knowledge of the flora improves, so ecological and biogeographical studies will be better based.

4. THE ECOLOGY OF MARINE PLANTS ON SOUTHERN AUSTRALIAN COASTS

Taxonomic knowledge of plants is greatly assisted by a good understanding of their ecology; likewise, every ecologist should be able to identify accurately at least most of the organisms involved in a study and know their taxonomy well enough to be sure that the same name is always being applied to the same species and to only that species. This is not difficult for the larger, more conspicuous algae and seagrasses, but often great care is needed with smaller taxa where microscopic examination is usually essential for determination. A knowledge of habitats of marine plants, and the variation in form of plants in different habitats, is helpful for most taxonomic studies.

This Chapter gives a brief account of the intertidal and subtidal habitats and the associated flora on southern Australian coasts. While the emphasis here is on the plants, ecological studies should not ignore the animals since the occurrence and growth of plants is often influenced by associated animals. This is particularly true in the mid and upper eulittoral regions (see Table 1) where grazing animals are dependent on algae for food and also control or prevent the growth of algae. Grazers can also be important in some subtidal communities.

For a more detailed account and review of previous studies of the marine ecology and zonation of southern Australian coasts, Womersley (1981a) should be consulted. Many common animals of the subtidal and intertidal regions are described by Shepherd & Thomas (1982).

ECOLOGICAL FACTORS OF THE MARINE ENVIRONMENT

Any organism is subjected to the combined interaction of factors which form its total environment, and many algae (less so the seagrasses) can vary in size and form depending on their environment. An understanding of how the various aspects of the marine environment interact is, therefore, necessary for development of good taxonomic hypotheses at the species level.

Tides and Water Movement

Tides are the major factor in determining the position of algae in the intertidal region, though tidal effects are modified by various other factors such as wind, humidity, wave force, and biotic effects. The intertidal is in general a harsher environment than the shallow subtidal, and many algae which occur in both regions are more luxuriant in the subtidal. Others however (e.g. *Hormosira*) are essentially confined to the intertidal, as also are many blue-green algae.

For intertidal collecting, a knowledge of the local tidal fluctuations is essential. Tides on southern Australian coasts are mostly semi-diurnal with two high tides and two low tides per lunar cycle of 24 hours and 50 minutes. The successive highs and lows are of different magnitude and, because of the lunar cycle, successively later each day. The spring (maximum) tidal range is 1.0 to 1.4 metres along most of southern Australia, but is only about 0.4 metres near Perth (where there is usually only one tide per day and the water level is more dependent on winds and barometric pressure) and about 2.5 metres on Wilsons Promontory and the north coast of Tasmania. In the South Australian Gulfs, tidal range reaches 3 metres at Port Wakefield and 4 metres at Port Augusta, and when "dodge" tides occur during the neap (minimum range) periods there may be little tidal movement for 24 hours or so, or only one tide in this period.

Certain levels on shores have been referred to as "critical levels" and considered to represent significant changes in the length of emergence of organisms just above and below these levels. Changes in zones of organisms may be associated, at least in part, with such critical levels.

Water movement is often just as important as tidal fluctuations in determining the height of the zones and form of organisms in the intertidal, and it is also a very important factor in the subtidal. Southern Australian coasts have a wide range of variations in water movement, from almost completely sheltered bays and inlets such as American River inlet on Kangaroo Island, parts of Port Phillip and Westernport Bay in Victoria and similar bays on the Tasmanian coast, to surf beaten rocky coasts facing south or south west. Some of the latter coasts are extremely dangerous and it is not possible to collect in the lower intertidal or shallow subtidal except on rare occasions.

Rough-water (high wave energy) areas usually bear a distinctive flora of species adapted to such conditions as also do very calm water areas. Very few species occur in both calm water and surf conditions, and rough-water habitats usually are by far the richest in species. The effect of increasing surf action is to elevate and broaden intertidal zones (Fig. 9).

Water movement in the subtidal region decreases with depth, and within the photic zone it may be as important as light (essentially correlated with depth) in determining the occurrence of particular species.

In recording data on herbarium sheets, the locality will usually indicate the type of coast, but unless this is clear then a note on the degree of water movement is helpful. Similarly, the particular intertidal zone or depth should always be stated for *in situ* collections.

Physical factors: Substrate, Light and Temperature

Substrate. Rocky substrate forms the backbone of most coastline, and two main types occur in southern Australia. Many capes or promontories on rough-water coasts consist of Precambrian granites or gneisses, usually steeply sloping. Between such areas and often occurring over hundreds of kilometres of coast, horizontal calcareous rock platforms derived from consolidated sand dunes occur at about low tide level, backed by cliffs and with the seaward edge of the platform dropping vertically and often undercut. Such platforms, almost invariably on surf beaten coasts, are rich habitats for marine algae, especially in the dissected pool areas on their edges.

On more sheltered coasts, other types of rock occur with the sea floor often grading more gently into deeper water. At Flinders and on Phillip Island in Victoria, mid eulittoral basalt platforms are noteworthy.

Between the rocky areas, loose sandy (or occasionally pebbly) beaches occur, but mobile sandy beaches or subtidal sandy bottoms bear few algae other than microscopic forms.

Sandy mud tidal flats, often extending well into the sublittoral, occur in areas of slight water movement, within protected bays and inlets. Here the seagrasses in particular, and some algae which are adapted to attachment in such substrate (e.g. some species of *Caulerpa*) often colonise considerable areas, and in turn (especially the more robust seagrasses) provide a substrate for many other algae. Some epiphytic algae are confined to a single host, others can grow on many hosts.

Light is, of course, a vital factor for plant growth. The depth of the photic zone on southern Australian coasts is usually between 10 and 50 metres, but may be greater in clear, offshore waters, or less in some inshore waters.

Each algal species has its light preference, even within the one genus. In general, the Chlorophyta grow in shallow water, the Phaeophyta extend from low water level to some depth (to 10-50 m), and the Rhodophyta occur from shallow to deep water (where the bright red taxa are found). However, there are many exceptions to these generalisations, and some green algae (e.g. *Palmoclathrus, Ulvaria shepherdii* and *Caulerpa hedleyi*) are amongst our

deepest growing marine algae. Many algae which normally grow in fairly deep water may be found in shallow water in heavily shaded situations.

Temperature is fairly uniform subtidally over long distances of open coast, but varies considerably in the intertidal region with both sea and air temperatures being important.

In the intertidal region temperature and humidity are closely associated, and depend also on the sea and wind conditions on the coast. Southern Australian coasts in general have more severe conditions than many northern hemisphere temperate coasts where fog and cloud are more frequent, and this accounts for the general lack of algae in summer above the lower eulittoral zone. On sheltered coasts in particular (for example the upper sections of the Gulfs in South Australia), rocky intertidal areas have very few algae (and few animals) above low tide level, for the summer sun conditions with high temperatures and low humidity are too severe for any except the most hardy organisms. The prime reason for lack of animals in such areas may well be the lack of algal food.

Subtidally, water temperature is relatively uniform within the photic zone, but decreases with depth.

On rough-water coasts of southern Australia, surface water temperature monthly means range from about 14° C in winter to 19° C in summer (Fig. 7) along the western and central parts, and from about 10° C to 17° C on Tasmanian coasts. In sheltered bays or inlets, temperature ranges are much greater. Half way up Spencer Gulf the temperature range is about 12° C to 25° C, and at the head it is 13° C to 28° C.



Fig. 7. Surface water temperature means for summer; in °C (after Jeffrey 1981, Fig. 10.2).

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While sea temperatures are between 14°C and 19°C along most of southern Australia, they increase fairly rapidly passing up both the east (New South Wales) and west coasts of Australia.

Only recently has evidence been presented for onshore upwelling of deeper water, with consequent lower temperatures and higher nutrients, on temperate Australian coasts. Two small areas occur on the New South Wales coast, another in eastern Victoria (between Lakes Entrance and Gabo Island) and one (Fig. 8) on the south-east coasts of South Australia (Lewis 1981). The upwelling occurs largely during summer, and temperatures are several degrees (usually 3-5°C) lower than in adjacent coastal areas or ones further offshore.



Fig. 8. Surface water temperatures off the South Australian, Victorian and western coasts of Tasmania for January 1974, showing upwelling centred near Robe; in °C (after Rochford 1977, Fig. 6).

Temperature ranges in isolated shallow bays, or in rock pools, are considerably greater than in deep water. In winter, pools are affected by the lower air temperatures and in summer by the much higher air temperatures and insolation, often reaching over 30° C during the day. Organisms in these areas must be adapted to such temperature ranges, and among the green algae, species of *Enteromorpha* are common in rock pools.

Chemical factors: Salinity, Nutrients, Oxygen

While chemical factors may vary locally, they are probably of minor importance in causing variations in morphology of algae. However, some species are tolerant of salinity variations, others are not.

Salinity varies comparatively little on southern Australian coasts, due largely to the absence of significant river discharge over most of the coast. The average salinity is $35-36^{0}/_{00}$ on open coasts, increasing to $45^{0}/_{00}$ in summer at the head of Spencer Gulf. American River inlet (which is not a river) has normal to slightly higher salinity. Salinity on tidal flats or in rock pools can be reduced by heavy rain during low tide, and organisms in these habitats as well as the intertidal region must either be adapted to such changes or else able to recover after damage due to lower salinity.

Nutrients (such as phosphate and nitrate) are generally low on southern Australian coasts except where upwelling occurs or pollution from the land exists.

Oxygen levels on rough-water coasts are near to saturation, but vary greatly from day to night in calm shallow water over algal or seagrass beds.

Sea water is well buffered and the pH lies between 8.1 and 8.3.

Biotic factors: Competition, Grazing

Factors such as competition and grazing are important, especially in the intertidal region, in delimiting zones. In the subtidal, additional effects are the shading influence of larger algae in determining strata, and epiphytism of smaller algae on larger taxa.

The absence of many obvious algae above the lower eulittoral zone is due to the grazing activities of limpets and other molluscs, as well as to the less favourable environment compared with the lower zones. If grazers are eliminated, a fine algal turf usually develops in the mid eulittoral. On southern Australian coasts, grazing effects on algae in the sublittoral appear to be inconspicuous or minor.

In sublittoral regions dominated by larger brown algae, two or three strata of algae usually occur. This is due largely to the lower light intensity under the algal canopy, but water movement is also lessened by the canopy. In many areas, however, understorey plants are not prominent, because of the low light conditions and the damaging effects of the swaying fronds of certain of the dominants.

Many larger algae provide the substrate for smaller taxa, with diatoms (and bacteria) providing a microscopic surface layer in many cases. Epiphytes occur under all conditions of water movement, but are particularly frequent under rough-water conditions in the uppermost sublittoral; in most cases one epiphyte can occur on a variety of hosts, but in a few cases (for example *Notheia* on *Hormosira*) there is an obligate relationship.

ZONATION IN THE INTERTIDAL AND SUBTIDAL

When any alga is collected growing, the zone should be given on the herbarium sheet with notes as to depth (if subtidal), aspect (shaded etc.) and whether it is an understorey plant or not.

Zonation or horizontal banding of intertidal organisms is shown on all coasts, being best defined where tidal ranges are large and desiccation slight. With small tidal range and strong wave action, zonation is less clear-cut, and on irregular rocky substrate it is further obscured. Zonation is primarly due to the degree of desiccation and is related to the tidal fluctuations, but zones are elevated by strong and consistent wave action and under hot, dry intertidal conditions on sheltered coasts they may be depressed. Whatever their relation to the actual tide levels, the zones of organisms reflect the total effect of all the environmental factors acting at that point. In many cases, therefore, the zones are best based on the dominant organisms present, using them as "indicator organisms". The height in relation to mean sea level and the extent of the zones may, then, differ considerably on different coasts and even in closely adjacent areas.

Rock pools present specialised habitats, depending largely on their size and the height at which they occur. Their flora, at least in larger pools, is related to the sublittoral flora rather than the intertidal flora.

Subtidal zonation is less distinct than that intertidally, and there is usually more gradation between broad zones. This is due to the gradual decrease with depth of the two important environmental factors, light and water movement. Sharp changes can be seen, however, on the different faces of rocks, where shaded areas occur and water movement may differ considerably.

Within each zone, one or more communities of species can be recognised. A community is a distinctive assemblage of interacting organisms, usually with one or a few dominants which govern the appearance of the community and usually account for a high proportion of the biomass. Gradation occurs between many communities, especially subtidally, and distinct communities are usually associated with particular environmental regimes.

Zones of the intertidal region

The following zones (Fig. 9) are recognised on most coasts of the world and are best shown on rocky, evenly sloping areas.

Littoral fringe (supralittoral or supralittoral fringe).

This is the zone dominated by organisms of marine affinities, and which is wetted only by extreme high tides or by spray. Since the affinities of organisms of this zone are related to those lower in the intertidal, the zone is really a fringe of the eulittoral. The dominant organisms in this zone on rocky coasts are littorinid snails, often with dark patches of bluegreen algae at slightly higher levels and above them crustose grey, orange or yellow lichens. On sandy mud tidal flats, angiosperms are usually the dominants, with various species of mangroves (extending down to and mainly within the eulittoral) in the tropics, and samphires (Chenopodiaceae) on temperate Australian coasts.

Eulittoral zone

This comprises most of the intertidal zone and is subject to varying degrees of emergence. Above, there is only irregular wetting, and below the organisms are immersed except on rare occasions.

On temperate Australian coasts, and on many other coasts of the world, three zones of organisms occur within the eulittoral. These are conveniently designated the upper, mid, and lower eulittoral zones. On Australian shores, the upper zone is often dominated by small barnacles, the mid eulittoral by larger barnacles, limpets and blue-green algae, and the lower zone by an algal mat (*Gelidium* or coralline algae) or by *Hormosira*, with the large *Balanus* barnacle on coasts subject to strong surf.

A feature of most temperate Australian coasts is the lack of conspicuous algae above the lower eulittoral at least during summer, though thin crusts of brown or red algae (such as *Hildenbrandia*) may be prominent in the mid eulittoral, along with blue-green algae.

On sandy mud shores, mangroves often extend well into the intertidal region, and seagrasses become prominent in the lower eulittoral. Few macro-algae occur on the generally unsuitable muddy substrate, and where they do they are usually attached to firmer substrates (for example *Hormosira* on large mussels).



Fig. 9. The relation of intertidal zones to tidal level and degree of water movement. (E.H.W.S.-Extreme High Water Spring tides; E.L.W.S.-Extreme Low Water Spring tides.)

Zones of the sublittoral region

The sublittoral zone is normally immersed, and only at extreme low tide or momentarily during the suck-back of waves at low tide is the uppermost margin emergent. The organisms present are not tolerant of more than this very brief air exposure, and if extreme conditions (such as hot offshore winds coinciding with very low tides in summer) do occur, damage to the organisms is usually obvious.

On some rocky temperate Australian coasts, the laminarians *Ecklonia* and *Macrocystis* mark the upper limit of the sublittoral. In other areas, the sublittoral is often dominated by fucoid algae and these (for example *Cystophora, Sargassum, Phyllospora* and *Durvillaea*) are appropriate indicators of the boundary.

On most rocky coasts, the dominant larger brown algae descend for 10 to 15 metres, forming a relatively uniform upper sublittoral zone. On some rough-water coasts, however, the zone emergent during suck-back of waves at low tide may be characterised by dominants

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(e.g. *Cystophora intermedia*) which do not descend below this zone of 0.5 to 1 metres height. Such a zone is conveniently referred to as the *sublittoral fringe zone*.

On sandy mud tidal flats, the top of the sublittoral zone is usually well marked by the upper limit of the seagrasses *Posidonia* or *Heterozostera*, but a fringe zone is usually not evident.

Zones within the sublittoral can usually be distinguished on the basis of dominants, but such zones show considerable gradation. Upper, mid and lower sublittoral zones have been recognised by Shepherd & Womersley (1970) on South Australian coasts, and the depth of these zones is partly dependent on the degree of water movement.

DOMINANT ORGANISMS OF THE ZONES ON SOUTHERN AUSTRALIAN COASTS

Tables 1 and 2, and comments given here, offer a brief outline of the dominant organisms of the various intertidal zones on southern Australian coasts, and examples of zones in the subtidal. Intertidal zonation and many of the dominant organisms are illustrated in Plates 1-11. For a more detailed account, reference should be made to Womersley (1981a) and the ecological papers cited therein.

Rough-water coasts

Two main types of coastal topography occur on these coasts of high wave energy, viz. steeply sloping rock (Pl. 1) or boulders often of Precambrian age (granites or gneisses), and horizontal rock platforms at about low tide level (Pl. 1 fig. 1; Pl. 3 fig. 1).

Littoral Fringe

This is invariably a zone of littorinid snails, but coasts of ancient rock, smoothly sloping, often have extensive black patches (Pl. 1 fig. 1; Pl. 2 fig. 1) of the blue-green alga *Calothrix* fasciculata above the littorinids. In some localities, the blue-green *Entophysalis deusta* occurs instead, and the edges of such patches are often abrupt due to the grazing of the littorinids.

The lower part of the littoral fringe (and the upper culittoral) often have patches of the small, black, branched lichen *Lichina pygmaea* (Pl. 4 fig. 1), especially at the rear of calcareous platforms.

On Tasmanian coasts, orange and grey lichens are common above the littoral fringe zone, and on some rocks where birds roost in southern Tasmania and off the Victorian coasts, the green alga *Prasiola* (Pl. 12 fig. 2) occurs several metres above high tide level.

Eulittoral zone

The eulittoral zone is animal dominated in the upper two thirds, with the lower third or so covered by an algal mat or by *Hormosira*. In the mid eulittoral, blue-green algae do occur as scattered colonies, with occasional limited (often seasonal) occurrences of other algae.

Upper eulittoral zone (Pl. 1 fig. 2) is dominated by the small barnacles *Chthamalus* and *Chamaesipho* ("honeycomb" barnacle), with occasional patches of the lichen *Lichina*. In hot summer weather the *Littorina* in the littoral fringe often migrate downwards so that many occur in the upper eulittoral. The south-east coast of South Australia has very few small barnacles in the upper eulittoral; the reason for this is uncertain, but this coast is known to be an area of upwelling.

Mid eulittoral zone (Pl. 1 fig. 2) is a zone of larger barnacles where surf conditions are strongest, changing to a mollusc (mainly limpet) dominated zone under slightly less rough conditions. The surf barnacle (*Catophragmus polymerus*) (Pl. 2 fig. 2) occurs around most of temperate Australia.

Table 1. The intertidal zones and their dominants on Australian temperate rocky coasts subject to strong to moderate wave action. Names in brackets are either less conspicuous or seasonal taxa. Algal names are given in italics, animals in roman (after Womersley 1981a).

		Western Australia		South Australia		
		Granite, sloping	Rock platforms	Steeply sloping	Rock platforms	
	Littoral fringe	blue-green algae (Calothrix etc.) Littorina unifasciata	blue-green algae (Calothrix etc.) Littorina unifasciata	Calothrix or Entophysalis Littorina unifasciata	Littorina unifasciata Lichina [Verrucaria]	
E	Upper		Nodilittorina rugosa	[Chthamalus antennatus]	Chthamalus antennatus	
U		Notoacmea	Notoacmea	Chamaesipho columna	Chamaesipho columna	
I	Mid	onychitis	onychitis Siphonaria	Catophragmus polymerus [Splachnidium rugosum]	[Catophragmus polymerus] molluscs	
T T		blue-green algae (Rivularia)	kurracheensis (luzonica) Patelloida	blue-green algae	blue-green algae	
O R		Balanus nigrescens	alticostata	Galeolaria caespitosa	Galeolaria caespitosa	
A L	Lower	Clavarizona hirtosa Patellanax laticostata	algal mat (corallines etc.) Patellanax laticostata lithothamnia	Balanus nigrescens	algal mat	
		algal mat (Laurencia) coralline algae	Haliotis roci Balanus nigrescens Pterocladia capillacea	coralline mat	Hormosira banksii	
	Sub- littoral fringe	Cystophora spp. Acrocarpia	Caulocystis uvifera Sargassum spp.	Cystophora intermedia	Cystophora intermedia	
U S lit	lpper Sub- Itoral	robusta Platythalia angustifolia Ecklonia radiata	Ecklonia radiata Scytothalia dorycarpa	Cystophora spp. Ecklonia radiata	Cystophora spp. Sargassum spp. Ecklonia radiata	

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Table 1.—continued

Victoria	Tasmania			
	Rough-water (West and South)	More sheltered (North and East)		
Littorina unifasciata L. praetermissa	Littorina praetermissa	Littorina unifasciata		
Lichina [Verrucaria]				
Chthamalus antennatus	Lichina Chthamalus antennatus	Lichina Chthamalus antennatus		
Chamaesipho columna	Chamaesipho columna	Chamaesipho columna		
Catophragmus polymerus	Patelloida latistrigata	Patelloida latistrigata		
[Splachnidium rugosum] limpets Austromytilus rostratus	various limpets [Catophragmus polymerus]	various limpets blue-green algae		
blue-green algae [Porphyra columbina]	blue-green algae [Porphyra columbina] Scytothamnus	[Porphyra columbina] Scytothamnus		
Galeolaria caespitosa	Galeolaria caespitosa	rostratus Galeolaria caespitosa Patelloida alticostata		
	Ulva Balanus Lithophyllum	Ulva Balanus Lithophyllum		
Corainne mai Hormosira banksii	Patellanax peroni	Patellanax peroni		
[Pyura stolonifera] [Balanus nigrescens]	coralline mat Poneroplax costata Hormosira banksii Xiphophora gladiata	coralline mat Poneroplax costata Hormosira banksii [Xiphophora gladiata]		
Poneroplax spp. [Cystophora Durvillaea intermedia] potatorum	Durvillaea potatorum lithothamnia	Cystophora torulosa		
Phyllospora comosa		Cystophora spp. Phyllospora comosa Ecklonia		
Macrocystis angustifolia	Macrocystis pyrifera	radiata Macrocystis angustifolia		

A variety of molluscs, mainly limpets (e.g. the genera *Cellana* and *Patelloida*), are conspicuous in the mid eulittoral, and the white, calcareous tubes of the polychaete worm *Galeolaria caespitosa* form scattered to thick, often massive, patches in the lower part of the mid eulittoral. Mussels such as *Austromytilus rostratus* may also form extensive black patches (Pl. 2 fig. 2) in this zone.

The most conspicuous algae of the mid eulittoral are blue-green algae of the genera *Rivularia* (Pl. 4 fig. 2), *Isactis* and *Symploca*, occurring as scattered colonies amongst the limpets or barnacles. Crustose red algae such as *Hildenbrandia* and cruorioid taxa, as well as crustose brown algae, are also not uncommon in the mid eulittoral, but are often overlooked.

Several algae appear seasonally in winter in the mid eulittoral, including Ulva (Pl. 3 fig. 1), Enteromorpha (both of which can occur throughout the year), the brown Petalonia and the red Bangia. In South Australia, Splachnidium rugosum occurs in summer, as the macroscopic phase, as does Nemalion helminthoides. On cooler coasts of Victoria and Tasmania and spreading into New South Wales and South Australia, Porphyra columbina is prominent in winter in the mid eulittoral, and Scytosiphon lomentaria also appears at this level in conspicuous patches. Scytothamnus australis is often common on Tasmanian coasts on otherwise bare mid eulittoral rock.

Lower eulittoral zone is dominated by algae though under very strong wave action the large barnacle Balanus nigrescens (Pl. 9 fig. 2) is often conspicuous in and just above the algal mat.

Algae in this zone are usually coralline algae such as *Haliptilon roseum* (syn. Corallina cuvierii) and Jania micrarthrodia, with crustose corallines (e.g. Lithophyllum hyperellum Pl. 9 fig. 2) prominent in the upper part of this zone on Tasmanian coasts. Amongst them occur other small taxa such as *Gelidium pusillum*, Laurencia spp., Wrangelia plumosa, Dasya clavigera, Centroceras clavulatum, and several taxa of Chlorophyta such as species of Enteromorpha, Ulva, Cladophora (Pl. 9 fig. 3) and Chaetomorpha. This mat of fairly short algae retains water well when emergent.

On rock platforms, *Hormosira banksii* is usually dominant in the lower eulittoral, often forming an almost pure community (Pl. 3 fig. 2), with *Notheia anomala* as a common epiphyte. The southern Australian rock platforms bear a great variety of algae.

On Tasmanian coasts, with their slightly cooler conditions, larger algae such as *Xiphophora gladiata* (Pl. 10 fig. 2) and *Cystophora torulosa* are just emergent at low tide and probably do enter the lower eulittoral; they are essentially, however, upper sublittoral inhabitants.

While the algae are the conspicuous organisms of the lower eulittoral along southern Australia, chitons (such as *Poneroplax* spp.), some molluscs, and numerous crustaceans occur amongst them. On parts of eastern Tasmania (and New South Wales) however, the sessile, leathery ascidian *Pyura stolonifera* forms a dense and pure community in the lower part of the lower eulittoral.

Sublittoral zone

This region on temperate Australian coasts is dominated generally by the larger brown algae, and usually has a sharply defined upper boundary.

On rough-water coasts of south-east Australia, from Bermagui in New South Wales to Cape Jaffa in South Australia and on western, eastern and southern shores of Tasmania, the giant "bull kelp", *Durvillaea potatorum* (Pl. 10 figs. 1, 3) is dominant in the uppermost sublittoral and usually excludes most other large algae from under its fronds. In slightly calmer areas, the large fucoid *Phyllospora comosa* is often found. Its range coincides with that of *Durvillaea* in the west, but it extends considerably further north up the New South Wales coast than *Durvillaea*.

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PLATE 1 fig. 1. Coast at Point Sinclair, S. Aust., with granite cape in the background and calcareous rock platform in the foreground; a rough-water locality;

fig. 2. Zonation on the granite cape of Figure 1, showing the uppermost littoral fringe above the upper person (with black band of *Calothrix*), the upper eulittoral (small barnacles) between the two persons, the mid eulittoral below the lower person, and the dark brown algal mat of the lower eulittoral; the sublittoral fringe is covered by wave wash.



PLATE 2 fig. 1. Calothrix mat in the littoral fringe on the granite cape of Point Sinclair, S. Aust. The well defined but irregular lower edge is probably due to grazing by Littorina;

fig. 2. Mid eulittoral zone of surf barnacles (Catophragmus) and black mussels, at Point Sinclair, S. Aust;

fig. 3. Sublittoral fringe zone of Cystophora intermedia at Vivonne Bay, Kangaroo Island.

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PLATE 3 fig. 1. Rock platform at Elliston, S. Aust., at low tide; note pool microhabitats and green carpet of Ulva;

fig. 2. Rock platform at Pennington Bay, Kangaroo Island, showing *Hormosira banksii* in the lower eulittoral with fucoids (mainly species of *Cystophora*) just covered at low tide and calm water conditions.



PLATE 4 fig. 1. Lichina in the littoral fringe at Robe, S. Aust;

fig. 2. Rivularia firma in the mid eulittoral (with Hormosira) at D'Estrees Bay, Kangaroo Island;

fig. 3. Hormosira banksii (lower eulittoral, left) and Cystophora subfarcinata and Caulocystis uvifera (upper sublittoral, right).





PLATE 5 fig. 1. Coast inside Waterloo Bay, Elliston, S. Aust., subject to moderate wave action;

fig. 2. Outer platform at Aldinga, S. Aust., subject to slight to moderate wave action, showing the lower eulittoral mat of *Gelidium pusillum*.



PLATE 6 fig. 1. The mid eulittoral zone with limpets (Cellana) and lower eulittoral zone of Hormosira and Gelidium pusillum, at Elliston, S. Aust;

fig. 2. The upper sublittoral on Aldinga platform, S. Aust., with *Ecklonia radiata, Sargassum* and other fucoids.



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PLATE 7 fig. 1. Aerial view of the very calm tidal flats and lagoon at American River inlet, Kangaroo Island. (Photo. by M. McKelvey.)

fig. 2. The intertidal region in Pelican Lagoon, American River inlet. Samphires (Sarcocornia) are present in the upper eulittoral. (Photo. by M. McKelvey.)



PLATE 8 fig. 1. The lower eulittoral in American River inlet, Kangaroo I., S. Aust., with the calmwater form of *Hormosira banksii* and old, yellow mats of *Chaetomorpha billardierii*;

fig. 2. A bed of *Posidonia australis* at Aldinga, S. Aust., with the stiff leaves just projecting above the water level at low tide.



PLATE 9 fig. 1. The granite coast at Bicheno, Tasmania, showing *Durvillaea* in the upper sublittoral, and *Ulva* in the mid eulittoral with barnacles and mussels; taken during a very low tide and calm sea;

fig. 2. The large barnacle *Balanus nigrescens*, the hemispherical mounds of the coralline alga *Lithophyllum hyperellum* and tufts of *Ulva*, in the lower eulittoral at Bicheno, Tasmania;

fig. 3. Green tufts of Cladophora crinalis in the lower eulittoral at Bicheno, Tasmania.



PLATE 10 fig. 1. Durvillaea potatorum emergent during a very low tide at Bicheno, Tasmania, with Ulva in the lower eulittoral;

- fig. 2. Xiphophora gladiata as a dense belt just above the Durvillaea at Bicheno, Tasmania;
- fig. 3. Durvillaea potatorum at Bicheno, Tasmania.



PLATE 11 fig. 1. Palmoclathrus stipitatus. Mature plant with stipes and clathrate cups (ADU, A44197 collection);

fig. 2. Younger branches of *Palmoclathrus* with stipes bearing solid membranes before seasonal development of clathrate cups (ADU, A44197 collection). (Both photos by K.L. Branden.)



PLATE 12 fig. 1. Ulva australis in a mid eulittoral pool, Sorrento, Victoria (ADU, A51984 collection);

fig. 2. Prasiola crispa (and yellow lichen) on a rock 3-4 m above high tide level, Lady Bay, Southport, Tasmania (ADU, A53837 collection). (Photo by M.J. Parsons.)

fig. 3. Urospora penicilliformis on a lower eulittoral rock, Tesselated Pavement, Eaglehawk Neck, Tasmania (ADU, A54021 collection).



PLATE 13 fig. 1. Chaetomorpha coliformis. Robe, S. Aust., from the upper sublittoral, Sept. 1981;
fig. 2. Chaetomorpha linum. Port MacDonnell, S. Aust., drift (ADU, A53159 collection);
fig. 3. Dictyosphaeria sericea. Victor Harbor, S. Aust., 1 m deep (ADU, A53381 collection).
(Photo by A.C.U.E.)

fig. 4. Codium galeatum (lower), C. mamillosum (upper left) and C. capitulatum (upper right). Elliston, S. Aust.



PLATE 14 fig. 1. Caulerpa scalpelliformis. Elliston, S. Aust., in pools;

- fig. 2. Caulerpa longifolia. Sorrento, Vic., from rock pools on outer coast;
- fig. 3. Caulerpa cactoides. Sorrento, Vic., from rock pools on outer coast;
- fig. 4. Caulerpa simpliciuscula. Sorrento, Vic., from rock pools on outer coast.



PLATE 15 fig. 1. Polyphysa peniculus. Coobowie, S. Aust., upper sublittoral in lagoon, Feb. 1964; fig. 2. Avicennia marina. Northern Spencer Gulf, S. Aust., upper eulittoral;

fig. 3. Halophila australis. Off Seacliff, Adelaide, S. Aust., 7-8 m deep. (Photo by S.A. Shepherd.)

fig.4. Posidonia australis. Proper Bay, Port Lincoln, S. Aust., 4 m deep. (Photo by S.A. Shepherd.)



PLATE 16 fig. 1. Posidonia sp. (probably P. angustifolia) and Amphibolis antarctica. Off Seacliff, Adelaide, S. Aust., 5 m deep. (Photo by J.E. Johnson.)

fig. 2. Posidonia balls (close up). Middleton beach, near Port Elliot, S. Aust. (Photo by E.M. Wollaston.)

fig. 3. Posidonia balls. Middleton beach, near Port Elliot, S. Aust. (Photo by E.M. Wollaston.)

fig. 4. Heterozostera tasmanica and Halophila australis community. Carcase Rock, off Eyre Peninsula, S. Aust., 6 m deep; (34°44'S, 136°05'E.) (Photo by S.A. Shepherd.)

fig. 5. Zostera mucronata with Lepilaena marina and Ruppia tuberosa in foreground, and mangrove seedlings in the background. Mid eulittoral tidal flats, Port Clinton, S. Aust. (Photo by E.L. Robertson.)

West of Cape Jaffa, the upper boundary of the sublittoral is marked by other fucoid algae, especially several species of *Cystophora* and *Sargassum* and *Scytothalia dorycarpa*, which are frequently co-dominant with the true kelp *Ecklonia*. Where *Durvillaea* occurs east of Cape Jaffa, the above genera are usually well represented in deeper water.

The south-east Australian coasts (from Robe to Wilsons Promontory), including Tasmania, are characterised also by the giant kelp, *Macrocystis*. On the Victorian and northern Tasmanian coasts *M. angustifolia* occurs from low water level down, and *M. pyrifera* occurs on the southern and eastern coasts of Tasmania. On the south-west coast of Western Australia, *Cystophora* spp., *Acrocarpia robusta*, in some places *Platythalia angustifolia* and to a lesser degree *Sargassum* spp., dominate the upper sublittoral zone. From Point Peron north, however, this zone is dominated by species of *Sargassum*.

On most temperate Australian coasts the dominants descend from about mean low water to several metres deep. However, a striking sublittoral fringe zone is that of *Cystophora intermedia* on rough-water coasts of South Australia.

		Extreme to strong wave action		Moderate wave action	Slight wave action	
		Steeply sloping palaeozoic rock	Horizontal rock platforms	Sheltered coasts	Sandy or muddy flats	
	Littoral fringe	Calothrix fasciculata or Entophysalis deusta Littorina	Littorina unifasciata	Littorina unifasciata	Relatively bare when rocky	
		unifasciala	Lichina [Verrucaria]	Lichina	samphires	
		[Chthamalus antennatus]	Chthamalus	Chthamalus antennatus	samphires [Avicennia]	
E U	Upper	Chamaesipho columna	Chamaesipho columna	Chamaesipho columna	Bembicium melanostomum	
ι		Catophragmus polymerus	[Catophragmus polymerus]	molluscs	Bembicium melanostomum	
т т т	Mid	[Splachnidium rugosum] blue-green algae [molluscs]	molluses blue-green algae	blue-green algae	Avicennia. Enteromorpha spp.	
0		Galeolaria caespitosa	Galeolaria caespitosa	Galeolaria caespitosa	Modiolus inconstans	
R A		Balanus nigrescens	algal mat Hormosira	Haliptilon roseum Hormosira banksii	Hormosira banksii Austromytilus erosus	
L	Lower	coralline mat	banksii	Gelidium pusillum	Katelysia spp. Pinna bicolor	
	Sub- littoral fringe	Cystophora intermedia	Cystophora intermedia	Cystophora spp.	Hypnea spp. Spyridia filamentosa, and other algae	
Uppe	:ť <u> </u>	Cystophora spp.	Cystophora spp.	other algae	Heterozostera tasmanica	
sub- littori	al	Ecklonia radiata	Sargassum spp. Ecklonia radiata		Posidonia australis	

Table	2.	The intertidal zones and their dominants on South Australian coasts subject to
		strong, moderate and slight wave action. Names in brackets are either less conspicuous or seasonal taxa. Plant names are given in italics, animals in roman (after Womersley 1981a)

The seagrass Amphibolis may occur as small patches (1-3 m across) in quite rough-water areas, just below low tide level, but on calmer coasts it can form a belt at this level.

Chlorophyta are often prominent in the uppermost sublittoral zone, with some extending above low water level. Several species of *Caulerpa* and *Bryopsis, Codium fragile* in southeastern Australia, and species of *Ulva, Enteromorpha, Cladophora, Chaetomorpha* and others are common.

SCUBA investigations, down to the depth limit of most algae, have begun to give a glimpse of the deeper water algal ecology of our coasts (for references, see Womersley 1981a).

Three algae-dominated subtidal zones are distinguished on rocky coasts, and these are referred to as the upper, mid and lower sublittoral zones. A significant feature is the effect of water movement on the depth of both zones and their constituent species. In very strong surge, many algae occur deeper, but can grow in shallower water as water movement becomes less.

The following zones have been recognised.

Upper sublittoral zone. On rough-water coasts, this zone is characterised by a short, dense turf of coralline algae, often underlying larger algae. At West Island in South Australia the zone extends to 3 to 5 metres deep and has three subzones. The uppermost is the fringe zone with Cystophora intermedia and Balanus barnacles amongst articulate coralline algae, with lower zones (i) of turf-like Gelidium glandulaefolium and Curdiea gymnogongroides, and (ii) of Melanthalia spp., Sargassum spp. and Zonaria sinclairii. On less rough areas of West Island, the upper sublittoral is only about one metre broad; Cystophora intermedia disappears and is replaced by other species of Cystophora or other fucoid genera. With further lessening of surge, the zone is about half a metre broad, with dense Pterocladia capillacea in the lower part.

The coralline mat of the upper sublittoral extends (along with *Balanus*) above low tide level to form the distinctive lower eulittoral zone on rough-water coasts.

Mid sublittoral zone. Under strong surge, this zone (5-15 m deep) is dominated by Ecklonia radiata, with other large brown algae and also Melanthalia. As surge lessens, the zone is both narrower and at a higher level. On Pearson Island and St Francis Island, the mid sublittoral is from 5 to 8 metres to about 50 metres deep and is typically a zone of larger brown algae, dominated by Ecklonia radiata, Scytothalia dorycarpa, Acrocarpia paniculata, Cystophora spp. Myriodesma spp. and other taxa. These communities often show subzones; Pearson Island has three subzones, the upper dominated by Acrocarpia, the middle one by Ecklonia and the lower by Myriodesma quercifolium, Scytothalia, Cystophora platylobium and Sargassum bracteolosum.

On calmer coasts, this zone of brown algae comes to low tide level, and the upper sublittoral zone of a coralline algal mat is replaced (though it may occur in the lower eulittoral). The vertical position of this zone is clearly dependent more on water movement than on light, and some reports of the absence of *Ecklonia* on rough-water coasts are probably due to its restriction to the deeper sublittoral.

Lower sublittoral zone. This region lies below the zone of larger brown algae and consists of a dense cover of diverse red algae, including especially species of *Plocamium* and other small, delicate species, and encrusting coralline algae. At West Island it occurs from 17 to 29 metres deep, and at St Francis Island it is 47 to 57 metres deep. While red algae are prominent, the fauna becomes more conspicuous as the limits of the photic zone are approached.

Moderately sheltered to calm-water coasts

The intertidal zonation of coasts of moderate to slight wave action is well known for southern Australia. Such coasts include the north coast of Kangaroo Island (Pl. 7), the South Australian gulfs, and various bays. In Victoria, Port Phillip Bay and Westernport Bay provide calm-water areas, as do areas on the north coast of Tasmania and other inlets around the Tasmanian coast.

The situation in South Australia (Table 2) provides an example of the zonation and changes as wave action decreases, together with the change in topography from rocky coast to sandy mud tidal flats. The main differences from rough-water coasts are as follows.

Littoral fringe

Under moderate wave action and on rocky coast, *Littorina* is still the most conspicuous organism, with some *Lichina pygmaea*. However, under very calm conditions the rock is relatively bare and the more usual substrate is sandy mud, bearing samphires (*Sarcocornia* and *Arthrocnemum*).

Eulittoral zone

Upper eulittoral zone. On rocky coast with moderate wave action, the barnacles Chthamalus and Chamaesipho occur in the upper eulittoral, but they disappear on very sheltered coasts. The littoral fringe samphires often extend below high water level, and under their shade occur mats of the red algae Gelidium pusillum, Bostrychia simpliciuscula and occasionally the green alga Chaetomorpha capillaris. The common mollusc in the upper eulittoral is Bembicium, occurring on rock or the sandy mud substrate where there is probably a rich micro-flora of diatoms and other micro-algae. In the South Australian gulfs and in parts of Westernport and Port Phillip Bays, the mangrove Avicennia marina var. resinifera (Pl. 15 fig. 2) occurs in the upper and mid eulittoral. In Westernport Bay, the red algae Bostrychia and Caloglossa are common on the lower stems and pneumatophores of the mangrove. They are less frequent but occur in some gulf localities in South Australia. Rhizoclonium may also be present on the lower trunks and pneumatophores.

Mid eulittoral zone. On rocky coasts subject to some wave action this is essentially a mollusc, blue-green algae and Galeolaria zone, often rather sparse. On sheltered tidal flats there are few macro-algae except for Enteromorpha, and the mollusc Bemblicium is usually prominent, often with beds of mussels (Modiolus). In suitable areas, Avicennia extends into this zone.

Lower eulittoral zone. The characteristic mat of coralline algae or Gelidium pusillum, and species of Ulva, are usually common on rocky coasts. Gelidium pusillum (Pl. 5 fig. 2) may form a pure community over considerable areas (as on Aldinga platform in Gulf St Vincent). Hormosira banksii is also a feature of most eulittoral areas, usually as a short and often stunted form. On tidal flats, Hormosira is also the main alga, but here it occurs as the large spherical vesicle form attached to pebbles or the large mussel Austromytilus in the mud. Other common macro-algae are Enteromorpha, Ulva at lower levels and sometimes Chaetomorpha billardierii (Pl. 8 fig. 1), and beds of the seagrass Zostera (Pl. 16 fig. 5) may also occur.

Sublittoral zone

Upper sublittoral zone. On rocky coasts with some wave action, this zone extends down for several metres and is dominated by larger brown algae (Pl. 6 fig. 2), especially Ecklonia radiata, Cystophora subfarcinata, C. retorta, C. polycystidea, C. moniliformis, Caulocystis cephalornithos, Cystophyllum onustum and Sargassum spp. (such as S. decipiens, S. lacerifolium), with an understorey of coralline algae (e.g. Amphiroa anceps, Cheilosporum elegans), Cladostephus spongiosus and often species of Caulerpa. On a sandy bottom below rocky areas, the

seagrasses Amphibolis and Posidonia often cover very extensive areas as dense, usually pure, communities. Their distribution in Gulf St Vincent is indicated by Shepherd & Sprigg (1976).

The upper sublittoral on sandy mud tidal flats is characterised by the virtual absence of any larger brown algae and the presence of extensive beds of seagrasses. Only a few fucoid algae appear able to tolerate lack of water movement. The common algae at and just below low tide level are the red algae *Hypnea musciformis, Spyridia filamentosa* and *Centroceras clavulatum*, and the green algae *Ulva* spp., *Enteromorpha clathrata, Cladophora* spp., and often *Polyphysa peniculus* on old cockle shells.

In some areas, *Hypnea* and *Spyridia* may be limited to 20 to 40 centimetres below mean low tide level, and characterise a rather poorly defined sublittoral fringe zone.

Seagrass beds are well developed on sandy mud areas of tidal flats, extending to several metres depth. Zostera (Z. muelleri and Z. mucronata in southern Australia), usually occurs above low tide level (Pl. 16 fig. 5), but may extend below. The most important "eelgrass" of the sublittoral is *Heterozostera tasmanica* which forms dense and pure masses in thick, firm mud from low tide level down for 3 to 4 metres (Pl. 16 fig 4) with occasional plants as deep as 30 metres. The greatest areas of this sheltered environment are, however, covered by the "tape weed" Posidonia (several species) which is attached from about 0.5 metres below low tide to 20 metres or so deep. Posidonia australis is the most widespread species, and in many shallow areas the stiff leaves just project above low water level at low tide (Pl. 8 fig. 2). Other species tend to grow in deeper water. The Posidonia leaves often carry a wealth of epiphytes, but only a few macro-algae (for example Caulerpa cactoides, C. remotifolia) occur in or adjacent to the beds.

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5. MARINE BIOGEOGRAPHY OF SOUTHERN AUSTRALIAN COASTS

The rich and highly endemic Australian marine algal flora has long been of interest to phycologists, especially in the relationships within the Australasian region and to other areas of the world. The temperate coasts are most noteworthy, covering the whole of southern Australia, including Tasmania. The algae of tropical coasts of Australia are comparatively little known, but it is clear that there are considerably fewer taxa and a lesser degree of endemism.

Biogeography is dependent on good taxonomy and extensive well documented collections; without these, conclusions are dubious and often misleading. The extensive unpopulated coasts of Australia, both around northern Australia and in the Great Australian Bight, have resulted in very limited collections from these areas. Biogeography within such regions is more likely to be the biogeography of the collectors than of the algae. The distribution given for species in many monographic revisions reflects this, and often also the location of the author. Thus it is to be expected that many species ranges will be modified (usually extended) with future collections and further revisions.

It is important that biogeographic conclusions be based on as much information as possible. Many such studies have been based on the intertidal flora and fauna of "open" coasts (that is, excluding bays and inlets) and thus take account of a limited range of conspicuous organisms. Ideally, the whole flora and fauna (as far as it is reliably known) as well as the intertidal organisms should be assessed, and account taken also of near-shore plankton. Floras and faunas may differ markedly depending on topography of the coast and degree of water movement, and comparisons should take account of this. Broad biogeographical provinces are usually based on the flora and fauna of open coasts, but the total benthic flora can be validly used (see below), provided this applies to all comparisons. While most marine algae grow on any hard substrate under suitable water movement, a few may be restricted to particular rock types in certain areas. An example is the brown alga *Splachnidium*, which on South Australian coasts grows almost entirely on Precambrian rock, mainly granite, and not on other rock such as limestone or sandstone. On Victorian coasts, however, it does occur on limestone.

This analysis includes the main groups of benthic algae, the Chlorophyta, Phaeophyta and Rhodophyta. The Cyanophyta are not considered, since, although often common, the taxonomic confusion in this group and the widespread distribution of most taxa renders them of little value in biogeographical analyses. For a more detailed analysis, Womersley (1981b) should be consulted.

RELATIONSHIPS OF SOUTHERN AUSTRALIAN ALGAE WITH THOSE OF OTHER REGIONS OF THE WORLD

The southern Australian algal flora is essentially temperate in its affinities, with only a slight subantarctic element (e.g. *Prasiola crispa, Codium dimorphum*) in south-east Tasmania, and a subtropical element (e.g. *Acetabularia calyculus*) in some bays and gulfs in South Australia. The Tasmanian and Victorian coasts (extending into South Australia) are cold temperate, characterised by the giant brown algae *Macrocystis* and *Durvillaea*, while most of the South Australian and southern coast of Western Australia tends to be intermediate between cold and warm temperate.

The southern Australian algal flora is one of the richest of any part of the world, in spite of the restricted temperature range along the coast. The comparison in Womersley (1981b) credited southern Australia with 30 genera and 97 species of Chlorophyta, 86 genera and 203
species of Phaeophyta, and 284 genera and 800 species of Rhodophyta, giving a total of 400 genera and 1 100 species. The Chlorophyta, however, have now increased to 39 genera and 123 species in this Flora, and will increase further as little known groups are studied.

Other noteworthy regions of the world are the Japanese region with some 411 genera and 1 452 species (but with conditions ranging from subarctic to subtropical), Pacific North America with 366 genera and 1 254 species (arctic to tropical conditions) and the comparatively well known British flora with 261 genera and 604 species. South Africa also has a distinctive algal flora with 254 genera and 539 species.

BIOGEOGRAPHY OF THE AUSTRALIAN COASTS

The following marine biogeographical provinces (Fig. 1) have been recognised around Australia. They are based more on the intertidal and the just subtidal organisms than on assessment of whole floras and faunas, but the distribution of the algal floras appears to agree with most of these provinces.

A province is regarded as a coastal region characterised by a relatively distinct and homogeneous flora and fauna, with only a small percentage of species common to adjacent provinces, and usually differing in temperatures from adjacent provinces by more than 5° C.

Tropical and subtropical coasts

The marine algae of northern Australia are very little known, except for the eastern Queensland coast. Tropical and subtropical coasts are not rich in taxa and most areas of the north coast of Australia probably have only 200 or so species, while the Queensland coast has about 400 species. Three provinces have been recognised.

1. Dampierian Province, from the Abrolhos Islands (28°50'S) off Western Australia around northern Australia to Torres Strait.

2. Solanderian (or Banksian) Province, the mainland coast from Torres Strait south to about 25°S in southern Queensland.

3. Great Barrier Reef Province, comprising the Great Barrier Reef and associated islands.

It is doubtful if the widespread distribution of most Indo-Pacific algae would support recognition of these distinct provinces, and the whole of the tropical Australian coasts is probably best regarded as one province, with possibly sub-provincial regions if these can be justified by more comprehensive faunistic and floristic studies.

Warm temperate coasts

Peronian Province, from the southern coast of Queensland and along the New South Wales coast, changing to cool temperate near the Victorian border.

In Western Australia, a *West Australian Province* (from the Abrolhos Islands south, and extending just to the south coast) has been recognised, and it has been suggested that the distribution of ascidians justified recognition of a *Baudinian Province* from Fremantle to Albany. From an algal viewpoint there are inadequate data to support either of these provinces. The southern Australian algal flora and the subtropical flora of the western coast show a gradual transition, but there is a group of species (especially of the Fucales) apparently confined to the Baudinian region, and this coast merits detailed study.

Cold temperate coasts

Flindersian Province comprises the southern coast of Australia with the south-east coasts (Victoria and Tasmania) showing cold temperate affinities (sometimes referred to as the

Maugean Province or Subprovince). The relationships of this region are further discussed below, but southern Tasmania is distinctly cold temperate, grading to marginally cold temperate on the Victorian coast and to transitional warm temperate coasts further west.

DEGREE OF ENDEMISM OF THE SOUTHERN AUSTRALIAN MARINE ALGAE

The southern Australian algal flora is highly endemic, especially in the Phaeophyta and Rhodophyta, less so in the Chlorophyta. Previous analyses (Womersley 1981b) gave endemism levels of:

Chlorophyta-genera 11%, species 46%

Phaeophyta-genera 19%, species 70%

Rhodophyta-genera 30%, species 75%

In the present account of the Chlorophyta, the genus *Cladophora* is shown to have numerous cosmopolitan species on southern Australian coasts, and several genera are now credited with species on coasts of other countries. This results in the generic endemism dropping to about 5% (*Palmoclathrus* and *Callipsygma* only) and the species endemism to about 30%.

Noteworthy taxa

Within the Chlorophyta, the coenocytic groups are noteworthy as being of higher endemism as well as in some cases being particularly well represented. *Codium* with 16 species (11 endemic or largely so) and *Caulerpa* with 19 (15 endemic) are particularly well represented. *Caulerpa* is richest in species on the slightly cooler south-eastern coasts, and many species attain their largest size in this region. The Udoteaceae are quite well represented with 8 genera, but a total of only 9 species, and many of these are apparently of restricted distribution. Several other genera of Chlorophyta are also distinctive, e.g. *Palmoclathrus* and *Pedobesia*.

In the Phaeophyta, most orders are well represented in southern Australia (Womersley 1981b), especially the Ectocarpales, Sphacelariales, Dictyotales, Chordariales, Sporochnales and Fucales.

The highest degree of richness and endemism, for both genera and species, occurs in the Rhodophyta, especially in the large and most advanced order (Ceramiales) in which over 40% of the world's genera and nearly 20% of the species occur in southern Australia (Womersley 1981b).

In future Parts of this Marine Flora, clarification of the taxonomy of brown and red algae on southern Australian coasts should permit a better analysis of the biogeography of the taxa.

BIOGEOGRAPHY OF THE ALGAL FLORA WITHIN SOUTHERN AUSTRALIA

The southern Australian macro-algae can be grouped as follows:

- Cosmopolitan-widely distributed at least in the temperate oceans of the world,
- Southern Australian—found in suitable habitats from the south coast of Western Australia to Victoria and often also in Tasmania,
- Eastern element—on Victorian and Tasmanian coasts and usually extending into eastern South Australia and in some cases to Kangaroo Island and the west coast of Eyre Peninsula,
- Western element—on the south (and often south-west) coast of Western Australia and extending into South Australia, usually to the west coast of Eyre Peninsula or Kangaroo Island,
- Restricted—known only from isolated occurrences, with inadequate data for the above groupings.

	No. of species	Cosmo- politan	Southern Australian	Eastern Element	Western Element	Restricted
Chlorophyta Phaeophyta Rhodophyta	123 203 800	33% 13% 5%	30% 29% 34%	20% 46% 43%	10% 12% 18%	7%
Total	1 126	10%	32%	41%	17%	

These distributional groupings for the three phyla give the following results.

The much higher proportion of cosmopolitan species of Chlorophyta and lower proportions of both southern Australian, eastern, and also the western elements are evident in comparison to both the Phaeophyta and Rhodophyta.

The figures also emphasise the widespread distribution of a large proportion of the species along southern Australia, and the richness of the eastern region. In the Chlorophyta, 67% occur generally along the coast and 90% occur in the eastern region; some 75% occur in the western region. For the macro-algae as a whole, 40% are generally distributed and 82% in the eastern region.

These figures support the recognition of one province (the Flindersian) for southern Australia, and a subprovince only for the eastern region.

OTHER ELEMENTS IN THE SOUTHERN AUSTRALIAN ALGAL FLORA

The southern Australian algal flora includes a small number of typically tropical species. These are mostly confined to sheltered bays and inlets where summer temperatures are apparently high enough, for a sufficient period, for such species to survive. The Spencer Gulf region in South Australia is noteworthy in this respect, with Acetabularia calyculus, Hormophysa triquetra and Sargassum decurrens; other tropical species known from South Australia include Asparagopsis taxiformis, Liagora farinosa, Sarconema filiforme, Taenioma perpusillum, Laurencia brongniartii and L. paniculata. Such taxa may be relicts from earlier periods of warmer conditions along southern Australia. As well as the above species, two tropical genera represented by single and isolated species in southern Australia are Dasycladus (D. densus) and Avrainvillea (A. clavatiramea).

The closest relationships of the southern Australian algal flora are with New Zealand, and perhaps 20% of the species are in common. Womersley & Edmonds (1958) found that some 24% of the then known Kangaroo Island algae occur in New Zealand, but only 22% in New South Wales. Small groups of well known southern Australian species, usually between 20 and 35, have been reported from the subantarctic, South Africa, the Arabian Sea, Malaysia-Indonesia and Japan, though taxonomic doubts exist in some cases (Womersley 1959). There is also a small element of colder water (subantarctic) species present, especially in Tasmania, but often widespread in at least the Maugean subprovince.

In some cases it is likely that species have been spread by shipping, both from and to southern Australia. Asparagopsis armata, a common southern Australian species, was found near Naples in 1925 and has since spread to Britain (Dixon & Irvine 1977, p. 155), and several northern hemisphere species now found near Australian ports (for example Antithamnionella spirographidis, Polysiphonia brodiaei, P. pungens) may well have come on ships' hulls. Spread by ocean currents over long distances, especially through the temperature barrier of the tropics, seems to be of rare occurrence due to the short life of algal spores and drifting fragments. Spread by migratory sea birds may be effective in rare cases.

Some authors regard continental drift as a possible explanation for the distribution of some marine algae, but this is likely to apply at a generic level rather than at a species level, and appears to be a possibility for only very few algal genera.

6. SEAGRASSES

by Enid L. Robertson[†]

Seagrasses are flowering plants adapted to living completely submerged in the marine environment. In his comprehensive monograph "Seagrasses of the World", den Hartog (1970) described 12 genera and 49 species. Eight of these genera are represented in southern Australia, and two additional genera, *Ruppia* and *Lepilaena* are also discussed here. These latter two genera, which frequently grow in close association, are generally not recognised as seagrasses. They are unique in tolerating and growing successfully in a wide range of salinities from fresh water through to hypersaline inland waters. In southern Australia both genera have species occurring in marine habitats and hence are included here with the purely marine genera.

South-western Western Australia is particularly rich in seagrass species and since 1970 two new species of *Posidonia* have been described from this region (Cambridge & Kuo 1979). It is anticipated that a forthcoming paper by the same authors will increase the number still further.

Traditionally the characters used in classifying flowering plants are the floral and fruiting parts (e.g. petals, sepals, stamens, fruits and seeds) and these are used here in the various synoptic keys. However, flowers and fruits of most seagrasses are not often collected and when found they are mostly small and inconspicuous.

Alternative vegetative characters with which to identify the seagrasses have been examined. Seagrass leaf apices are very useful diagnostically. Considerable variation in leaf apex shape can be found within a species or even on one plant, but none-the-less if used in conjunction with other features this character is valuable taxonomically. Longitudinal air lacunae or air canals are present in the leaves of all seagrasses and their size and arrangement may be characteristic for a particular species. Separating the air canals are blocks of cells or diaphragms, some running longitudinally and others transversely. Vascular tissue may pass through these, e.g. the transverse veins in Zosteraceae. Minute scale-like structures, the squamules (squamulae intravaginales), are found in the axils of foliage and scale leaves of all seagrasses (and most other non-marine aquatics as well). Their exact function is not known but it is probable that they are primarily secretory (see Tomlinson 1982, p. 46). The number, shape and arrangement of squamules is constant for any one genus and may vary between species. Other useful vegetative characters include leaf venation, blade L/B* ratio, the nature of the sheath and the number and arrangement of roots.

The key on p. 58, based entirely on vegetative characters, enables sterile material to be identified to genus. Later taxonomic keys are based on both vegetative and floral characters, and these in conjunction with the illustrations enable specific determinations to be made. The illustrations have been drawn either from fresh specimens or liquid preserved material. Many of the species have been maintained in culture for considerable periods of time at the University of Adelaide.

Seagrasses are all monocotyledons. Traditionally flowering plants as a whole have been known as Angiospermae but following the more modern classification they are here referred to the Division Magnoliophyta (Cronquist, Takhtajan & Zimmermann, 1966) which is divided into two natural Classes, the Liliopsida (= Monocotyledonae), and the Magnoliopsida (= Dicotyledonae). Within the Liliopsida there are five major groups or subclasses and the seagrasses belong within the subclass Alismatidae Takhtajan (= Helobiae).

^{*} L/B i.e. length/breadth ratio.

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KEY FOR STERILE MATERIAL OF SOUTHERN AUSTRALIAN SEAGRASSES

1.	Leaf with a distinct broad blade and narrow petiole, without a definite sheathing base, auricles absent
1.	Leaf more or less the same breadth throughout its length, not petiolate, with a well- developed sheathing base, auricles present, one either side of the sheath
	2. Ligule absent
	2. Ligule present at junction of blade and sheath
3.	Leaf blade more or less terete, or strongly convex on one or both faces
3.	Leaf blade flat, or somewhat concavo-convex, with upper and lower faces parallel5
	4. Leaf blade soft and succulent, in cross section showing a central vascular bundle surrounded by a ring of 5-7 air canals and an outer ring of 7-10 peripheral vascular bundles
	4. Leaf blade tough and fibrous; in cross section showing a row of 3-9 longitudinal vascular bundles
5.	Leaf blade less than 1 mm broad with a single median vein LEPILAENA
5.	Leaf blade 1-15 mm broad, in cross section showing a row of 3 or more longitudinal veins
	6. Leaf blade and sheath falling together, leaving a clean scar on the stem7
	6. Leaf blade falling first, sheath remaining persistent on the stem for some time and always with some hairy fibres remaining, never leaving a clean scar (except in <i>Halodule uninervis</i>)
7.	Leaf margin entire, apex bi-dentate or concave; roots usually at every node, branched and often somewhat coiled
7.	Leaf margin with numerous truncated denticulations, apex rounded; roots at every fourth internode, unbranched, not coiled
	8. Leaf apex tri-dentate
	8. Leaf apex rounded or truncate, with or without a notch, not dentate10
9.	Base of leaf sheath finally falling and leaving a clean scar; leaf blade with 3 longitudinal veins, the 2 lateral ones marginal and each ending in a lateral tooth, not uniting with the midvein, transverse veins absent, tannin cells numerous and appearing as dark spots scattered on the blade
9.	Base of leaf sheath remaining as persistent hairy fibres on the stem; leaf blade with 3 longitudinal veins, the 2 lateral ones submarginal and uniting with the midvein near the apex, transverse veins connecting the lateral veins to the midvein at more or less regular intervals, tannin cells absent
	10. Leaf blade with 3 longitudinal veins, the 2 lateral ones submarginal (so that the blade appears single-veined to the naked eye), or the lateral veins, if not submarginal, at least much closer to the margin than to the midvein
	10. Leaf blade with 5 or more longitudinal veins
11.	Rhizome in cross section showing 2 lateral vascular bundles, one either side of the central vascular bundle ZOSTERA
11.	Rhizome in cross section showing 6-12 cortical vascular bundles and a central vascular bundle
	12. Leaf blade with 7-20 longitudinal veins, uniting near the apex, tannin cells numerous, appearing as dark linear spots either side of each transverse vein POSIDONIA
	12. Leaf blade with 5 longitudinal veins, the veins either side of the midvein united to it near the leaf apex, the marginal veins joining the inner laterals some distance from the apex, tannin cells absent

SEAGRASSES

The system of classification adopted for the seagrasses in this Flora follows Cronquist (1981), in conformity with the treatment used in "Flora of Australia" (see Kanis 1981, p. 82), except that within the subclass Alismatidae the circumscription of orders and families follows Tomlinson (1982, p. 10). Accordingly *Ruppia* is included in Potamogetonaceae, and not in the segregate family Ruppiaceae, and the order Potamogetonales is used to embrace all the seagrass families except Hydrocharitaceae. This latter highly specialized and distinctive family is placed in the separate order Hydrocharitales. In both Cronquist and Tomlinson the subclass Alismatidae is essentially that of Takhtajan (1966) but Cronquist defines 4 orders and Tomlinson 5, within the subclass. The families to which the seagrasses belong are fairly clearly circumscribed but as Tomlinson observes "the task of assembling a totally acceptable arrangement of them into higher categories... seems impossible".

DIVISION MAGNOLIOPHYTA Cronquist, Takhtajan & Zimmermann 'Angiosperms'

Vascular plants, usually with roots, stems and leaves. Vascular tissue consisting of xylem (usually at least in part containing vessels), and phloem. Sexual reproductive structures characteristically aggregated to form flowers which are associated with specialised leaves; usually with a perianth forming the outer parts of the flower; male structures producing pollen and female structures producing ovules; fertilised ovules forming seeds which are enclosed in a fruit.

CLASS LILIOPSIDA Cronquist, Takhtajan & Zimmermann 'Monocotyledons'

Plants mostly herbaceous, without normal secondary growth; vascular bundles of the stem without cambium, scattered or in 2 or more rings. Roots all adventitious. Leaves usually with parallel venation. Floral parts usually in sets of 3; perianth frequently of 2 whorls of 3 parts each (but in some orders much modified); embryo with one cotyledon.

SUBCLASS ALISMATIDAE Takhtajan 'Helobiae' or 'Fluviales'

Plants herbaceous, more or less aquatic. Vascular system generally not strongly lignified, often much reduced; vessels confined to the roots or wanting. Leaves simple. Perianth frequently much reduced or absent; gynoecium mostly apocarpous, sometimes monocarpous (except in Hydrocharitales where carpels are weakly united to form a compound ovary); endosperm absent in most taxa; pollen trinucleate.

Two of the five orders are represented by seagrasses in southern Australia.

KEY TO ORDERS OF SEAGRASSES

- 1. Leaves linear to terete with a sheathing base, not differentiated into a petiole and a blade. Flowers usually ebracteate (bracts if present small and inconspicuous). Perianth when present generally much modified, never with distinct sepals and petals. Carpels 1-several, free, ovary superior **POTAMOGETONALES**

HYDROCHARITACEAE

ORDER HYDROCHARITALES Lindley 1833

The order consists of a single family, the Hydrocharitaceae.

FAMILY HYDROCHARITACEAE Jussieu, nom. cons.

Monoecious or dioecious; annual or perennial aquatic herbs. *Leaves* basal or arising along the stem, eligulate. *Squamules* present in each leaf axil. *Tannin* cells present or absent. *Flowers* actinomorphic, unisexual, trimerous, sessile or pedicellate, enclosed in a spathe of 2 bracts, free or fused together. Perianth in one or two whorls of 3 free segments. *Male flower* with anthers sessile or with slender filaments, bi- or quadrilocular, longitudinally dehiscent. Pollen grains globose to ellipsoid, frequently united by mucilage into moniliform chains; pollination hydrophilous. *Female flower* frequently with the perianth borne on a slender hypanthium; ovary inferior, compound (by loose union of the carpels), unilocular, placentation parietal. *Fruit* usually indehiscent.

A diverse family of cosmopolitan distribution with about 15 genera, both freshwater and marine, with one marine genus in southern Australia.

Genus HALOPHILA Thouars 1806: 2. "Paddleweed".

Monoecious or dioecious; annual or perennial, stoloniferous, marine herbs. Stolons bearing 2 scales with a lateral shoot and 1- few roots at each node. Roots unbranched with abundant root hairs. Scales usually hyaline, sub-opposite, one associated with the root(s) and clasping the stolon, the other embracing a lateral shoot (frequently very reduced) which bears the leaves. Leaves in pairs (in southern Australian species), sessile or more frequently petiolate, usually with a distinct blade, linear to ovate, with a midvein and an intramarginal vein connected by more or less parallel crossveins. Squamules (1-) 2-3, linear to lanceolate, attenuate at the base, about 1 mm long (in southern Australian species). Tannin cells absent. Inflorescence usually of a solitary unisexual flower, spathe of 2 sessile imbricate keeled bracts. Male flower subsessile at first, pedicel elongating considerably at time of anthesis; tepals 3; stamens 3, anthers sessile, the whole male flower caducous after dehiscence of the anthers. Pollen grains ellipsoid, united in moniliform chains when released but readily breaking up in contact with water; pollination hydrophilous. Female flower usually sessile; hypanthium bearing 3 minute tepals at its summit; ovary inferior, ovoid to ellipsoid, unilocular, placentation parietal, ovules numerous; styles 3 or 6, linear. Fruit thin walled, ellipsoid to ovoid or globose, rostrate due to the persistent hypanthium.

Type species: H. madagascariensis Steudel [= H. ovalis (R. Br.) J.D. Hooker] (see Doty & Stone 1967).

A genus of about 10 species, widely distributed in tropical and warm temperate waters. Some species are well defined and restricted in distribution but H. ovalis sensu lato* is widespread in the Indo-West Pacific and has great ecological tolerance. Den Hartog (1970, p. 250) referred to H. ovalis as a "collective species" in which a number of closely allied taxa are united. He recognized the populations growing in extra-tropical Australia as being relatively distinctive and having all parts generally larger, but still considered them as a subspecies, H. ovalis subsp. australis (Doty & Stone) den Hartog, within his broad concept of H. ovalis.

As usual with seagrasses, most herbarium collections are of sterile material as fertile material is frequently difficult to obtain. However, for the common southern Australian species of *Halophila*, good collections of fertile material are now available. The distinguishing features include a constant difference in style number and position of the female flower. The consistent characters of 6 styles and the green, foliose nature of the scales on the erect flowering branch (an extended lateral shoot), together with the generally more robust nature

^{*}i.e. in a wide or broad sense.

of the plant and the narrower leaves [L/B 3-4 (-6)] appear sufficient to warrant species status. The name H. australis is recognized for this taxon and applied here to most of the material from southern Australia.

However, specimens from the Perth region in Western Australia fall within H. ovalis, having female flowers with 3 styles, borne on the horizontal stolons. Although no material with six styles has been found from the west coast of Western Australia, the vegetative characters of some collections suggest that H. australis probably extends at least as far north as Dongara on the Western Australian coast and that there is a region of overlap of H. ovalis and H. australis from approximately Cowaramup Bay in the south to Dongara in the north. On the eastern coast of Australia overlap probably occurs in the Sydney region in New South Wales, and good fertile collections would clarify the limits of the two species.

KEY TO SPECIES OF HALOPHILA

- 1. Plants monoecious; leaf margins always finely serrulate; glabrous or hairy to a variable
- - 2. Female flowers borne on the prostrate horizontal stolons, styles 3; scales all hyaline, sessile; leaf blade oblong to obovate, mostly rounded at the base, L/B mostly 2. Female flowers borne on erect lateral branches, styles 6; scales at the first node of the fertile female branch usually green and foliose, subsessile or shortly

petiolate; leaf blade more or less elliptic, narrowed towards the base, L/B mostly

1. Halophila decipiens Ostenfeld 1902: 260, with fig. Aston 1973: 221. Beadle, Evans & Carolin 1972: 520. Green 1981: 6. den Hartog 1970: 254. Jacobs & Pickard 1981: 20. Sainty & Jacobs 1981: 236. H. baillonii sensu Holm 1885: 4, pls 1-3

FIGS 10A, 11A-C

Monoecious; stoloniferous perennial herb (Figs 10A, 11A,B), glabrous or with some unicellular hairs. Stolon about 1 mm in diameter. Roots 1 per node. Scales 3-5 mm long, obovate, keeled, glabrous or with scattered hairs on the outside particularly on the keel. Leaves (Fig. 11A,B) in pairs, delicate, bright green, glabrous or with scattered unicellular hairs on one or both faces, blade oblong-elliptical, rounded at the apex, 1-1.5(-2.5) cm long, 2.5-4 (-6) mm broad, L/B usually 3-4; margin finely serrulate, crossveins 5-7(-9) pairs. Petiole triquetrous, usually considerably shorter than the leaf blade. Squamules 1-2, linear, in the axil of the petiole. Spathes (Fig. 11A,C) enclosing one male and one female flower, borne on erect lateral shoots (3-)5-7(-10) mm long; spathal bracts 3-7 mm long, ovate, acuminate, glabrous or with scattered hairs on the oustide, keel usually finely serrulate. Male flower subsessile at first, with ovate tepals 1-1.5 mm long, pedicel 4-8 mm long at anthesis. Female flower solitary, sessile, hypanthium 1-2 mm long, tepals minute, styles 3. Fruit (Fig. 11A) ellipsoid, 3-5 mm long, at maturity splitting the spathe. Seeds about 30.

Flowering and fruiting: October to December.

Type from the Gulf of Thailand, off Koh Kahdat, on coral sand, 10 m deep (Schmidt 540, Feb. 1900); in C, L.

Distribution: A widespread pantropical species usually occurring only north of the Tropic of Capricorn. On the Western Australian coast it occurs south to Cockburn Sound and on the south-eastern Australian coast it occurs south to Mallacoota Inlet, Victoria.



Fig. 10. A. Halophila decipiens (MEL, 584594). Habit, showing female flower with 3 stigmas. B,C. Halophila ovalis. B. Habit, female plant showing flower with 3 stigmas (ADU, A53177 from Western Australia). C. Habit, small leaved plant (ADU, A52972 from Queensland).

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Fig. 11. A-C. Halophila decipiens. A. Habit of fertile plant with hairy leaves from Northern Territory. B. Portion of fertile plant with glabrous leaves from Mallacoota Inlet, Victoria. C. Portion of branch, with leaves removed, showing young male and female flowers. (A from ADU, A41255. B,C from MEL, 584594.) D-G. Halophila ovalis. D. Habit of female plant. E. Portion of stolon showing male flower on elongated pedicel. F. Variation in leaf shape on a plant from Queensland. G. Variation in leaf shape on a plant from ADU, A52975. F from ADU, A52972.)

Selected specimens: Gipsy Point, Mallacoota Inlet, East Gippsland, Vic., 1.5-4 m deep (*McConchie & Macauley*, 10.xi.1980; MEL, 584594). Lee Point, Darwin, N.T., 0.5 m deep (*Must* 805, 6.x.1971; ADU, A41255). Punta Arenas, Mayaguez, Puerto Rico, dredged 15-20 m deep (*Diaz-Piferrer*, 31.viii.1963; ADU, A29123).

The population at Mallacoota Inlet has glabrous leaves (Fig. 11B,C). However, hairiness is a variable character in this species, and can vary considerably within a population and even on the same plant. The leaf margins are consistently serrulate.

 Halophila ovalis (R. Brown) J.D. Hooker 1858: 45. Beadle, Evans & Carolin 1972: 519. Blackall & Grieve 1954: 10. Green 1981: 6. den Hartog 1970: 240, fig. 62. Jacobs & Pickard 1981: 20. Ostenfeld 1916: 38. Sainty & Jacobs 1981: 236, with fig. Willis 1970: 77 (in part). Caulinia ovalis R. Brown 1810: 339.

FIGS 10B,C, 11D-G

Dioecious; annual or perennial glabrous herbs (Figs 10B,C, 11D,E); with much-branched stolons forming extensive beds. Stolons 1-2 mm in diameter. Roots usually 1 at each node. Scales hyaline, (2-)3-5 mm long, suborbicular to obovate, notched at the summit. Leaves in pairs, glabrous, usually oblong to obovate with a rounded apex and base, 1-3(-4) cm long, 0.5-2 cm wide, L/B 2-3 [but considerable variation can occur even in one population (Fig. 11F,G)]; margin entire; crossveins (7-)10-12(-19) pairs, arising at angles of 45-60°, some crossveins forked. Petiole terete. Squamules 2, lanceolate in axil of petiole. Spathes enclosing either a male or a female flower, sessile on the prostrate stolon; spathal bracts 5-8(-10) mm long, lanceolate, keeled. Male flower (Fig. 11E) at first subsessile, pedicel up to 2.5 cm long at anthesis; tepals 3-4(-6) mm long, membranous with a prominent central vein, hooded, imbricate; pollen grains ellipsoid. Female flower (Figs 10B, 11D) solitary, sessile on a horizontal stolon with hyaline scales at each node. Ovary ovoid, 1.5-2 mm long, hypanthium 3-5(-8) mm long; tepals up to 1 mm long; styles 3, 10-25(-40) mm long. Fruit ovoid to globose, 3-5 mm long, with a persistent hypanthium. Seeds 20-30, subglobose.

Flowering and fruiting: August to April.

Type from Queensland, Australia (exact locality unknown) (R. Brown 5816); in BM.

Distribution: Widely distributed in tropical and warm temperate waters of the Indo-Pacific region and extending down the Western Australian coast as far as Cowaramup Bay and down the eastern Australian coast to about the Victorian border (Jacobs & Pickard 1981, p. 20).

Selected specimens: Whitfords Beach, Perth, W. Aust., 5 m deep on sand (Lipkin, 2.ii.1982; ADU, A52975). Freshwater Bay, Swan River estuary, W. Aust., 1.5 m deep (Hillman, 21.iv.1982; UWA, 3163 and ADU, A53177). Point Walter, Swan River estuary, W. Aust. (Allender, 28.i.1969; UWA, A1208 and A1209). Cowaramup Bay, W. Aust., 2-3 m deep (Clarke & Engler, 1.ix.1979; ADU, A50666). Shelley Beach, Pallarenda, Queensland (Birch, 22.viii.1978; ADU, A52972). Tetel I., Florida Is, Solomon Is, in pools on reef (Bailey 91, 9.vii.1965; ADU, A53388).

In the absence of fertile material, H. ovalis may usually be distinguished by the leaves which are generally more ovate-oblong with a rounded apex and frequently more rounded at the base than H. australis. However, as discussed earlier, the species exhibits great morphological variation in leaf size, leaf shape, L/B ratio and also the ratio of leaf blade to petiole length. A determination cannot be made with a single leaf but needs to take into account the whole population.

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Fig. 12. A-C. Halophila australis. A. Holotype specimen. The erect stem (arrowed) bears a mature fruit and a horizontal branch (stolon) with roots at the nodes. B. Habit (ADU, A52605), female plant showing flower with 6 stigmas. C. Habit (ADU, A51935).

3. Halophila australis Doty & Stone 1966: 306, fig. 2.

H. ovalis sensu Aston 1973: 221, fig. 87. Jessop 1978: 86, fig. 53.

H. ovalis (R. Brown) J. D. Hooker, subsp. australis (Doty & Stone) den Hartog 1970: 251. Jacobs & Pickard 1981: 20.

PLATES 15 fig. 3, 16 fig. 4; FIGS 12, 13

Dioecious; perennial glabrous herb (Pls 15 fig. 3, 16 fig. 4; Figs 12, 13A,B) forming extensive beds. Stolons much-branched, 1-2 mm in diameter, internodes (1-) 2-6 (-8) cm long. Roots one at each node. Scales (3-) 4-5 (-8) mm long, suborbicular, notched at apex but with the central vein extending into a short mucro, distinctly keeled. Leaves in pairs, glabrous, linear-lanceolate to narrow elliptical, (2.5-) 5-6 (-7) cm long, narrowed towards the base, 6-15 mm wide, L/B 3-4 (-6); margin entire; crossveins (10-) 14-16 (-20) pairs arising at angles of 45-60°, some crossveins forked near the base. Petiole terete, up to 10 cm long, usually distinctly longer than the blade. Squamules (Fig. 13C) 2-3, linear to lanceolate, about 1 mm long, in the axil of the petiole. Spathes enclosing either a male or a female flower; spathal bracts (4-) 5-7 (-10) mm long, lanceolate, strongly keeled. Male flower (Fig. 13B, D-F) subsessile within the spathe, borne on a prostrate stolon and frequently at first embedded in sediment, pedicel elongating to about 2 cm carrying the anthers above the sediment at anthesis; tepals 0.5-0.7 mm long, membranous, imbricate, hooded; pollen grains (Fig. 13E) ellipsoid, adhering in short moniliform chains. Female flower (Fig. 13A) solitary, sessile in the spathe, borne on an erect extended lateral shoot 5-15 cm long, which may produce one or more successive, erect, flowering shoots. Scales at first node of the flowering shoot sometimes scarious but more usually green and foliose, subsessile (occasionally shortly petiolate) with the blade (3-) 4-5 cm long. Ovary ovoid, 1-2 mm long, hypanthium 2-5 mm long (sometimes elongating in the fruit), tepals (0.3-) 0.5-1 mm long, styles (Figs 12B, 13A) 6, 6-15 (-20) mm long. Fruit (Figs 12A, 13G-I) ovoid, (7-) 9-11 (-13) mm long, rostrate due to the persistent hypanthium 5-7 mm long. Seeds (Fig. 13J, K) 50-60, subglobose with a reticulate surface, immersed in a gelatinous mucilage. In the mature fruit the seeds are clearly visible through the thin wall.

Flowering and fruiting: October to January.

Type from Queenscliff, Vic. (Lucas, Jan. 1922); holotype in NSW, 3214, and isotypes.

Distribution: Widespread around southern Australia, including Tasmania, extending at least as far north as Dongara, W. Aust. and probably into the central coast of N.S.W.; in both sand and mud from low tide level to 23 m deep, usually in calm water situations.

Selected specimens: Point Valliant, Two People Bay, W. Aust., in sheltered pool (Womersley, 30.vii.1979; ADU, A50946). Waterloo Bay, S. Aust., 150 m off end of jetty, 9 m deep (Shepherd, 8.xi.1980; ADU, A51901). East Cove, Pearson I., S. Aust. 20-23 m deep (Shepherd & Turner, 29.iii.1982; ADU, A53022). Farm Beach, Coffin Bay, S. Aust., 5 m deep (Shepherd, 3.xi.1981; ADU, A52605). Quarry Point Reef, Wallaroo, S. Aust., 1-2 m deep (Gill, 21.xii.1980; ADU, A52045). Tiparra reef, Spencer Gulf, S. Aust., 5 m deep (Shepherd, 30.x.1980; ADU, A51825). Brighton, Adelaide, S. Aust. (H.H.D.G. [Griffith], 2.ii.1917; AD, 97507186). Wright I., Encounter Bay, S. Aust., 8-10 m deep (Clarke, 23.xii.1981; ADU, A52823). Encounter Bay, S. Aust., 7 m deep (Clarke, 7.xii.1980; ADU, A51935). Somers, Mornington Pen., Vic., drift (Wetherill, Feb. 1969; MEL, 589102).

Fig. 13. Halophila australis. A. Habit of female plant. B. Portion of plant, showing young male flower within a spathe. C. Squamules. D. Young male flower removed from spathe. E. Male flower at anthesis, releasing pollen grains in moniliform chains. F. Withered male flower after anthesis with anther remnants. G. Spathe enclosing young fruit, with hypanthium projecting. H. Cross section of young fruit showing arrangement of the seeds. I. Mature fruit, with seeds visible through the thin wall. J. Seeds enclosed in testa. K. Seeds with testa removed. L. Variation in leaf shape on one plant. (A from ADU, A52605. B,D-F from ADU, A51901. C from ADU, A52823. G,H from ADU, A51825. I-K from ADU, A52045. L from ADU, A53022.)



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POTAMOGETONACEAE

This description is based on the form most commonly occurring in southern Australia. Some specimens [e.g. from Partney I., Sir Joseph Banks Group, S. Aust., 10-12 m deep (*Baldock*, 13.xii.1977; ADU, A48932)] have leaves L/B about 2, more or less ovate, and appear closer to *H. ovalis*, and others [e.g. from Tapley Shoal, Gulf St Vincent, S. Aust., 15 m deep (*Shepherd*, 2.ii.1969; ADU, A33485)], with linear-lanceolate leaves 1-2 cm long, represent a small-leaved form of the species. Considerable variation of leaf size and shape can also occur on one plant as is shown in the specimen from Pearson I. (Fig. 13L).

Doty & Stone's type description of H. australis refers only to vegetative characters although the holotype bears a mature fruit which is mentioned in their caption of the accompanying photograph. It is apparent on examining the holotype (Fig. 12A) that this specimen is part of an erect extended lateral branch, similar to that shown in Fig. 12C, but which has become detached from the prostrate stolon. After flowering, the branch has continued growth, as is typical for this species, producing a horizontal branch with roots at the nodes. The collection of isotype specimens, also in NSW, contains a number of similar erect shoots, each with a mature fruit. In some fruits, seeds are obvious through the thin wall.

ORDER POTAMOGETONALES sensu Tomlinson 1982

Perennial (or rarely annual) herbs, aquatic or semi-aquatic, rooted to the substrate. *Leaves* basal or cauline, commonly sheathing at the base, mostly ligulate (ligule absent in Potamogetonaceae); venation parallel, sheathing base generally subtending squamules at the node. *Flowers* unisexual or bisexual, mostly small and inconspicuous, usually ebracteate (or bract small and inconspicuous). Perianth absent or when present generally much modified. Pollination anemophilous or hydrophilous. Carpels 1-several, free, uni-ovulate; ovary superior. *Fruit* usually achenous.

Six families widely distributed around the world; 5 of these contain marine species in southern Australia.

KEY TO FAMILIES OF POTAMOGETONALES

1.	Pollen grains globose to spherical, or reniform, not filiform, although sometimes adhering
	in chains
1.	Pollen grains filiform
	2. Flowers bisexual POTAMOGETONACEAE
	2. Flowers unisexual. Plants monoecious or dioecious ZANNICHELLIACEAE
3.	Flowers bisexual. Stamens 3 POSIDONIACEAE
3.	Flowers unisexual. Plants monoecious or dioecious. Stamens 1, or 2 and connate4
	4. Flowers solitary or in a loose compound inflorescence CYMODOCEACEAE
	4. Male and female flowers arranged alternately on a spadix enclosed in a
	spathe

FAMILY POTAMOGETONACEAE Dumortier, nom. cons.

Submerged or floating, annual or perennial, aquatic herbs, with monopodial or sympodial rhizomes rooting at the nodes. *Roots* unbranched. *Leaves* with sheathing base, eligulate. *Squamules* 2-many at each node, enclosed within the leaf sheath. *Tannin* cells present. *Inflorescence* a simple terminal spike. *Flowers* usually bisexual. Perianth present or absent. Stamens 2 or 4, anthers sessile each with 2 bilocular pollen sacs, longitudinally dehiscent; pollen grains globose to spherical or reniform. Carpels usually 3 or 4 (in some species considerably more), free; ovules solitary, pendulous, orthotropous or campylotropous. *Fruit* an achene, exocarp membranous or spongy, endocarp usually bony. Vegetative perennating organs sometimes present.

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A family of three genera which are widely distributed in temperate and subtropical regions, mostly in freshwater and sometimes in brackish or saline water. One genus, *Ruppia*, has marine representatives in southern Australia.

Ruppia has been placed in the monogeneric family Ruppiaceae (Hutchinson 1959, p. 558). However, more recent authors including Gamerro (1968), Thorne (1976) and Dahlgren (1980) have questioned the distinctions separating the Ruppiaceae from the Potamogetonaceae. In a revision of Ruppia in Australia, Jacobs & Brock (1982) consider Ruppia should be retained in the Potamogetonaceae and their treatment has been followed here.

Genus RUPPIA Linnaeus 1753: 127. "Sea tassel".

Annual or perennial, submerged rhizomatous herbs. Rhizomes monopodial. Roots 1-2 per node, unbranched; root-hairs abundant. Stems very short or absent, or up to 2.5 m long and flexuous with branches in one plane. Leaves alternate (except the 2 immediately below the inflorescence which are sub-opposite); sheath open, edges overlapping, eligulate, auriculate; blade narrow-linear to filiform, more or less concavo-convex in cross section with a large air canal either side of an inconspicuous median vein. Prophylls commencing each branch, always inserted between the branch and the main axis. Squamules paired, laterally opposed in each leaf axil. Tannin cells present in most tissues, particularly conspicuous in the epidermis as dark-brown elongate cells. Inflorescence a spike of (1-)2 flowers on opposite faces of the axis, enclosed at first in the inflated sheathing leaf bases; peduncle short, stout, erect, or elongating greatly before anthesis to a fine thread raising the flowers to the water surface, and becoming tightly spirally coiled retracting the developing fruits after pollination. Flowers bisexual; perianth absent; stamens 2; anthers each with 2 bilocular pollen sacs, longitudinally dehiscent; pollen grains elongate-reniform with a reticulate exine; pollination hydrophilous (either below or on the water surface). Carpels (2-)4-12(-26), free, sessile or subsessile at first, often becoming stalked in the fruit; ovary ovoid, 1-celled; stigma sessile, thick, peltate. Fruit an achene, not floating, sessile or with a distinct stalk (podogyne) which remains attached to the fruit and falls with it. Exocarp spongy, disintegrating; endocarp bony, beaked, persistent, with a triangular depression either side of the base of the beak. Turions (starch-filled perennating organs) produced terminally on the rhizomes, or at the junction of the leaf sheath and rhizome, are present in 2 species.

Type species: Ruppia maritima Linnaeus.

Two to ten species in temperate and subtropical regions throughout the world, in both ephemeral and permanent water bodies. Two species occur in marine habitats in southern Australia. In some localities *Ruppia* spp. are known as "Widgeon grass".

Ruppia is tolerant of a wide range of salinity, occurring in fresh, brackish, marine and sometimes in hypersaline situations to ten times the salinity of seawater (Brock 1982a). Some morphological variations appear to be associated with fluctuations in the environment (Brock 1981, 1982a, 1982b).

In Ruppia, pollination may occur either below, or on, the water surface. After detailed studies Setchell (1946) concluded that the genus (as known then) contained two species distinguished on the inflorescence position at pollination, and the associated peduncle length, viz. R. maritima Linnaeus with a short peduncle, permanently submerged inflorescence and pollination below water, and R. spiralis Linnaeus ex Dumortier [= R. cirrohosa (Petagna) Grande] with an elongate flexuous peduncle, elevating the inflorescence on to the water surface for pollination. Verhoeven (1979, p. 253) demonstrated that the submerged pollination in R. maritima takes place at the air-water interface of a gaseous bubble liberated from the air canals of the plant itself. The cosmopolitan R. maritima, although not common in Australia, has been recognized by Jacobs & Brock (1982) from all mainland States in permanent inland waters (i.e. salt lakes, mound springs and artesian bores) and also from estuaries in subtropical

and tropical regions of Australia. There are no marine collections of this species from southern Australia but it has been found in Sydney Harbour, e.g. Parramatta, N.S.W. (Betche, Nov. 1881; NSW, 2437).

KEY TO SPECIES OF RUPPIA

- - 2. Mature fruiting carpel sessile or subsessile; podogyne absent or, if present, always much shorter than the carpel; carpels (6-)8-12(-26) 2. R. tuberosa
 - 2. Mature fruiting carpel with a well-developed podogyne; podogyne straight, slender, mostly 1-2 cm long, always much longer than the carpel; carpels (4-)6-8(-16).

* *R. polycarpa* (Fig. 15A-C), first described from New Zealand (Mason 1967), is common in southern Australia in fresh to brackish water and also in salinities up to 66^{9}_{00} (see Brock 1982a, p. 221), occurring in coastal lakes, lagoons and estuaries. *R. polycarpa* has filiform leaves less than 0.5 mm broad with obtuse or acute apices, flowers with (4-)6-8(-16) carpels, and fruits 2-3 mm long on slender straight podogynes mostly 1-2 cm long. Turions are frequently produced.

Selected Specimen: Peel Inlet, W. Aust., in freshwater 30 m from sea (Carstairs, 12.ix.1982; ADU, A53396).

R. polycarpa may be difficult to distinguish from R. tuberosa unless fruits are present. It has not been found in normal marine situations.

1. Ruppia megacarpa Mason 1967: 525, fig. 3. Green 1981: 5. Sainty & Jacobs 1981: 394 (figs), 395.

Ruppia maritima sensu Aston (in part) 1973: 290, fig. 116 a,b,d-f.

FIGS 14A, 15D-M

Rhizomatous robust perennial herb (Figs 14A, 15D); rhizomes 1-1.5(-2.5) mm in diameter. Stems 0.5-1(-2) mm in diameter, 20-30 cm (and up to 2.5 m) long, branched, flexuous. Turions absent. Leaves filiform; sheath 1-3(-5) cm long with 2 short rounded auricles (Fig. 15F); blade 5-10(-25) cm long, 0.4-0.5(-1) mm broad; apex (Fig. 15E) mostly bidentate, sometimes truncate, finely serrulate. Prophylls (Fig. 15F, G) (4-)6-10 mm long, lanceolate, often conspicuous. Squamules (Fig. 15H) 0.2-0.5 mm long, ovate. Inflorescence (Fig. 15D) 2-flowered, at first enclosed in the enlarged sheaths of two sub-opposite leaves; peduncle at first rigid, erect, becoming lax and flexuose, elongating rapidly to reach the water surface where fertilisation occurs (peduncle length very variable depending on water depth and often to 1 m long). After anthesis the peduncle (Figs 14A, 15D) becomes tightly spirally coiled withdrawing the inflorescence below the surface. Pollen grains (Fig. 15I, J) elongate-reniform, adhering in chains. Carpels (2-)4(-6) at first sessile, after fertilisation the base elongating into a podogyne (Fig. 15K, L) 2-4(-5) cm long, about 0.3 mm in diameter, attached to the fruit by a broad base about 0.8 mm across. Fruit (Fig. 15M) asymmetric, usually 3-4 mm long with a distinct stylar beak up to 0.5 mm long; podogyne persistent in the mature fruit after the exocarp has decayed; endocarp dark-brown, rough, with a deltate perforation on each side.

Flowering: October to March.

Type from Taumutu, Lake Ellesmere, New Zealand (J. Clarke, 9.ii.1966); in CHR, 150818A.

Distribution: W. Aust., S. Aust., Victoria and New South Wales in permanent water bodies such as estuaries, coastal salt-lakes and inland lakes, brackish to hypersaline with salinities up to $46^{\circ}/_{00}$. New Zealand.

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Fig. 14. A. Ruppia megacarpa (ADU, A46713). Habit, plant with mature fruits. B-D. Ruppia tuberosa. B. Habit, plant with mature fruits on short stiff peduncles (ADU, A52729). C. Habit, plant with young inflorescence on short peduncle (arrowed) and older inflorescences with young fruits on elongate flexuose peduncles (ADU, A51909). D. Vegetative plants showing turions (ADU, A53621).

The marine material of R. megacarpa is from depths up to 2 m in sheltered areas influenced by the tides but not continuously in contact with the open sea.

Selected specimens: Coodanup, Peel Inlet, W. Aust., 0.5 m deep (Carstairs, 12.ix.1982; ADU, A53397). West Lakes, Adelaide, S. Aust., 1.5-2 m deep (Thomas & P. Womersley, 22.xii.1975; ADU, A46713). Coorong, S. Aust., (Womersley, 17.ii.1974; ADU, A50543). Pelican Point, St Georges Basin, near Jervis Bay, N.S.W., 0.5 m deep (Roberts, 8.x.1979; ADU, A53232).

R. megacarpa and R. tuberosa grow sympatrically in some localities but are reproductively isolated as flowering times do not overlap (Brock 1982a).

2. Ruppia tuberosa Davis & Tomlinson 1974: 60, figs 1-10. Green 1981: 5. Ruppia maritima sensu Aston (in part) 1973: 290.

PLATE 16 fig. 5; FIGS 14B-D, 16, 17

Annual or delicate short-lived perennial (Figs 14B-D, 16A, B) with slender rhizomes 0.5-1.5 mm in diameter. Stems very short, not conspicuous. Turions (Figs 14D, 16C, D) falcate, asymmetric, 2-6 mm long, 0.5-1 mm broad. Leaves (Fig. 16E-G) filiform; sheath 1-2 cm long, auricles rounded, 0.5-1.5 mm long, often unequal in length; blade (6-)8-10 cm long, (0.1-)0.2-0.3(-0.5) mm broad; apex (Fig. 16H) rounded to acute, frequently finely serrulate. Prophylls (Fig. 16I, J) lanceolate, 5-6 mm long. Squamules (Fig. 16K, L) ovate, 0.2-0.3 mm long. Inflorescence (Figs 14C, 16A, B, 17A, B) with 1-2 flowers, enclosed in the inflated leaf sheaths at first, peduncle 3-30 cm or more in length (dependent on water depth), becoming tightly spirally coiled (Fig. 16B) and retracting the fruits after fertilisation. Carpels (Fig. 17B, C) (6-) 8-12(-26), sessile or subsessile. Fruits (Figs 14B, 17C, D) pyriform, usually symmetric, (1.2-) 1.8-2.0(-2.5) mm long; exocarp fleshy, decaying early; endocarp (Fig. 17E) dark-brown or black, smooth, (1.0)1.4-1.7(-2.0) mm long, with a short thin beak about 0.1 mm long, a longitudinal ridge and an ovate perforation on each side; podogyne absent (or rarely about 1.5 mm, but never as long as the fruit, and not persistent after the exocarp decays).

Flowering: September to November.

Type from Shark Bay, W. Aust. (J. S. Davis, 5.ix.1970), apparently lost; neotype in FLAS, 137470 (see Jacobs & Brock 1982, p. 331).

Distribution: W. Aust., S. Aust. and Victoria. In ephemeral, or at the margins of permanent, saline water bodies such as lakes, inlets, estuaries and tidal lagoons in water from 10 cm to 1 m deep, and also in the mid to lower eulittoral on tidal flats in sheltered bays (Pl. 16 fig. 5) where it grows in association with Lepilaena marina and Zostera mucronata. This latter intertidal form of R. tuberosa (Fig. 14B) has rigid, short (3-10 cm) peduncles, inflorescences frequently 1-flowered, and numerous (up to 26) carpels per flower; it does not appear to produce turions.

Selected specimens: Goldsmith Beach (near Edithburgh), Yorke Peninsula, S. Aust., mid eulittoral (*Robertson*, 14.xi.1981; ADU, A52729). Coobowie Inlet, S. Aust., connected with sea

Fig. 15. A-C. Ruppia polycarpa (ADU, A53396). A. Leaf apices. B. Inflorescence of two flowers soon after fertilisation. Note short podogynes (po.). C. Mature fruits with elongated podogynes (po.). D-M. Ruppia megacarpa. D. Portion of plant showing one young inflorescence with short peduncle and one inflorescence after anthesis with spirally coiled peduncle. Note pollen sacs (p.s.) and carpels (ca.). E. Leaf apices. F. Prophyll (p.) in leaf axil embracing young branch (b.). (Leaf sheath with auricles (a.) pulled to one side). G. Prophyll removed from leaf axil. H. Squamules. I. Pollen grains adhering in a chain. J. Pollen grain. K. Young fruits showing podogynes (po.). M. Endocarp of ripe fruit, after decay of exocarp. (D-J from ADU, A50543. K-M from ADU, A46713.)



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Ruppia

POTAMOGETONACEAE

at high tide only, 0.5 m deep (van der Ster & Snoejs, 25.xi.1980; ADU, A51909 and Robertson, 2.x.1982; ADU, A53652). Port Clinton, S. Australia, mid eulittoral (Robertson, 2.x.1982; ADU, A53655). Camp Noonameena, North Lagoon, Coorong, S. Aust., lower eulittoral (Robertson, 18.ix.1982; ADU, A53621).

In R. tuberosa pollination always takes place at the air-water interface on the surface of the water. Plants which remain submerged (Fig. 16B), growing in enclosed water bodies, present the inflorescence on the water surface by elongation of the peduncle. Plants with short peduncles growing on intertidal flats (Fig. 16A) become emergent with the falling tide and remain exposed during low tide. In both cases the inflorescence floats on the water surface with the stigmas exposed to the large quantities of pollen liberated during anthesis. The reniform pollen grains are united in short chains which drift onto the peltate stigmas effecting pollination.



Fig. 17. Ruppia tuberosa (ADU, A53655). **A.** Portion of plant showing young inflorescence seen through swollen leaf sheath. Note emerging root (*rt.*). **B.** Inflorescence of 2 flowers just before anthesis. Note carpels (*ca.*) with peltate stigmas (*st.*) and bilocular pollen sacs (*p.s.*) with lines of dehiscence (*de.*). **C.** Developing fruits. Note some unfertilised carpels (*ca.*) remaining in the flower and tannin cells (*t.c.*). **D.** Fruits covered by spongy exocarp. **E.** Endocarp of fruit exposed after exocarp decay.

⁻Fig. 16. Ruppia tuberosa. **A.** Portion of plant with short peduncle, from intertidal region. **B.** Portion of plant with elongated peduncle, from sub-tidal area. **C.** Turion inside swollen leaf sheath. Note tannin cells (*t.c.*) appearing as dark streaks. **D.** Turion removed from sheath. **E.** Portion of leaf (adaxial face). Junction of blade and sheath showing auricles (*a.*) and T.S. of blade. Note auricles, vascular bundle (*v.b.*) and large air canals (*a.c.*) **F.** Portion of leaf, abaxial face. Junction of blade and sheath showing auricles (*a.*). and T.S. of blade. Note auricles, vascular bundle (*v.b.*) and large air canals (*a.c.*) **F.** Portion of leaf, abaxial face. Junction of blade and sheath showing auricles (*a.*). **G**₁, **G**₂. Portion of leaf. Two side views of blade-sheath junction with auricles (*a.*). **H.** Leaf apices. **I.** Prophyll (*p.*) shown in position in leaf axil. **K.** Squamules in position at node (subtending leaf removed). **L.** Squamules. (**A, E-G, I-L** from ADU, A53655. **B, H** from ADU, A53652. **C, D** from ADU, A53621.)

Turions in *Ruppia* spp. act as perennating organs allowing the plant to withstand desiccation. They appear to be initiated as salinity increases but may sometimes be formed at salinities less than that of seawater (Brock 1982b). The term "turion" was first applied to these starch-filled storage organs in *R. tuberosa* by Davis & Tomlinson (1974). However, their presence, under the name of "tubers" has been known for many years. In the Coorong, South Australia, they form an important food item of duck and other waterfowl which congregate in the late spring and summer, and systematically graze on *Ruppia* spp., eating both seeds and turions (Delroy, Macrow & Sorrell 1965, Delroy 1974).

FAMILY ZANNICHELLIACEAE Dumortier, nom. cons.

Monoecious or dioecious; annual or frequently ephemeral, rarely perennial, slender, submerged, rhizomatous, aquatic herbs. *Rhizomes* creeping, usually sympodially branched, rooting at the nodes and giving rise to erect, much-branched, leafy and flower-bearing shoots. *Roots* unbranched, 1-several per node. *Leaves* alternate, more or less distichous, sheathing at the base; sheath open, margins overlapping, ligulate, auriculate; blade linear. *Squamules* usually a pair at each node. *Tannin* cells rare or absent. *Flowers* usually terminal. *Male flower* perianth present or absent; one stamen with 1-6 pollen sacs (each containing a pair of microsporangia); pollen grains globose. *Female flower* perianth of 3 free tepals or a membranous cupule; carpels 1-8, free, short-stalked; ovule 1, anatropous and pendulous. *Fruit* an achene.

A family of four genera mostly in fresh or brackish water, widely distributed in temperate and tropical regions. One genus, *Lepilaena*, has marine representatives in southern Australia.

Zannichelliaceae is a distinct family with no close relatives and no obvious ancestors (Tomlinson 1982, p. 34). Generic limits within the family, and some aspects of morphological development are discussed by Tomlinson & Posluszny (1976) and Posluszny & Tomlinson (1977).

Genus LEPILAENA Drummond ex Harvey 1855d: 57. "Water-mats".

Monoecious or dioecious; annual or perennial rhizomatous herbs. *Rhizomes* much-branched bearing at the nodes roots, scale leaves and erect leafy shoots. *Leaves* alternate, with the floral leaves often apparently sub-opposite and frequently crowded towards the apex of the stem. Sheath with ligule well developed, frequently bifid; blade linear, a single median vein and a fibrous strand on either margin. *Prophylls* enclosing younger organs at first, sometimes prominent. *Squamules* filiform, a pair at each node. *Flowers* inconspicuous, solitary, each flower at first enclosed in a leaf sheath. *Male flower* pedicellate, consisting of a single stamen with a minute cup-like perianth or 3 minute tepals; anther sessile, with 6 (2 only in *L. bilocularis*) pairs of microsporangia united longitudinally and dorsally, appearing at dehiscence as one six-loculed anther; pedicel at first very short, elongating considerably at anthesis to extend above the foliage. Pollen grains globose. *Female flower* with 3 tepals, membranous, persistent; carpels 3, free; each carpel with 1 ovule, style slender, stigma expanded, obliquely peltate or funnel-shaped. *Fruit* an achene.

Type species: L. australis Drummond ex Harvey.

A genus of four or more species confined to Australasia, mainly in fresh or brackish water. Two species are marine in southern Australia.

Species of *Lepilaena* tolerate a wide range of salinity from fresh water through brackish water to salinities exceeding those of seawater. They occur in both temporary and permanent inland waters, in salt lakes and estuaries and also sometimes in truly marine habitats subject to tidal influences. The marine species commonly found around the southern Australian coast is a previously undescribed species (*L. marina*, see below).

Tomlinson (1982, p. 339) discusses the stamen of *Lepilaena*, which has been variously interpreted by different workers. He describes it as having 6 units (2 only in *L. bilocularis)*, with each unit or pollen sac consisting of a pair of microsporangia, i.e. a total of 12 microsporangia. These are clearly seen in the cross section of the young stamen (Fig. 20K). The wall separating the 2 microsporangia within the pollen sac breaks down at maturity leaving a single locule in each pollen sac, i.e. a total of 6 locules from which the pollen grains are released.

KEY TO SPECIES OF *LEPILAENA*

- 1. Mature fruit L/B usually 3-4(-6), fruit longer than the tepals and projecting beyond them; pedicel elongating after fertilisation, fruits extending well beyond the leaf sheath.
- 1. L. cylindrocarpa 1. Mature fruit L/B usually 1.5-2.5(-3), fruit shorter than the tepals and remaining enclosed within them; pedicel remaining short, fruits usually not extending beyond the leaf sheath _____2
- Lepilaena cylindrocarpa (Koernicke in Walpers) Bentham 1878: 180. Aston 1973: 316, Fig. 129. Green 1981: 5. Jessop 1978: 76. Willis 1970: 70. Zannichellia cylindrocarpa Koernicke in Walpers 1861: 3. Althenia cylindrocarpa (Koernicke in Walpers) Ascherson 1889: 213.

FIGS 18A, 19A-I

Dioecious in marine specimens examined (Fig. 18A); herb, probably annual. Rhizomes 0.3-0.5 mm in diameter with an amplexical scale 1-5 mm long at each node, and usually at every alternate node 1-4 roots and an erect shoot 5-15(-25) cm tall. Leaf sheath (Fig. 19A,B) inflated, membranous, 4-6 mm long, ligule 1-2 mm long mostly deeply cleft; blade linear, 2-8 cm long, 0.1-0.2(-0.3) mm broad; apex (Fig. 19C), acute to acuminate or tapering to a very short mucro. Squamules (Fig. 19A,B), filiform, mostly about 2 mm long, sometimes projecting from the sheath (Fig. 19D,E). Male flowers (Figs 18A, 19D,E) on slender flexuous, branched shoots 15-35 cm tall, borne singly on very short pedicels, at first enclosed within the inflated leaf sheath; tepals minute, united into a cup; stamen with 6 pollen sacs, 1.2-1.6 mm long; at anthesis the pedicel elongates to about 1 cm long and carries the flower well beyond the leaf sheath. Female flowers (Figs 18A, 19F,G) on slender flexuous branched shoots 15-25 cm tall, on pedicels 5-10 mm long frequently elongating in the fruit to about 2 cm, to project the mature achenes well beyond the leaf sheath; tepals 2.5-4 mm long, membranous, ovate-lanceolate, apex serrate; carpophore 0.5-1 mm long, sometimes elongating in the fruit to 3-4 mm long, style 2-3 mm long, stigma narrow, obliquely funnel-shaped with an irregularly serrate margin, ovary at first enclosed within the tepals but after fertilisation enlarging considerably to project well beyond them (Fig. 19H). Fruit (Fig. 19H,I) an achene, darkbrown, cylindrical, 2.0-3.0 mm long, usually L/B 3-4(-6).

Flowering and fruiting: August to November.

^{*} L. preissii is included here for comparative purposes although no truly marine specimens have been seen.

Type from "Australia felix"*F. Mueller n. 52 (Herb. Berlin-presumed destroyed).

Distribution: In marine estuaries around southern Australia from the Inman R. estuary, Encounter Bay, S. Aust. to Yarra R. estuary, Vic., and in the North Lagoon, Coorong, S. Aust. which is influenced by tides but not exposed to open seas. Also in fresh to brackish to saline inland waters, in swamps and lakes.

Selected specimens: Inman River mouth, Encounter Bay, S. Aust., in brackish water billabong (Skinner, 2.x.1978; ADU, A49572). Camp Noonameena, North Lagoon, Coorong, S. Aust., 0.5 m deep, in mud (Robertson, 18.ix.1982; ADU, A53620). Coorong, S. Aust. salinity 50-58%/00 (Snoejs & van der Ster, 29.xii.1980; ADU, A53214). Yarra River delta, Victoria (Clifford, 1.ix.1948; MEL, 578049).

2. Lepilaena preissii (Lehmann) F. Mueller 1874: 217. Aston 1973: 318, fig. 128 (i-p).

Bentham 1878: 180. Green 1981: 5. Jessop 1978: 76. Willis 1970: 70.

Zannichellia preissii Lehmann 1846: 3.

Althenia preissii (Lehmann) Ascherson & Graebner 1907; 160. Blackall & Grieve 1954; 8.

FIGS 18B, 19J-R

Monoecious; slender rhizomatous herb (Figs 18B, 19J), probably annual. Rhizomes very fine, 0.3-0.5 mm in diameter, with an amplexicaul scale at each node, and usually at each alternate node 1-4 roots and an erect shoot 5-20(-50) cm tall. Leaf sheath (Fig. 19J,N) membranous, somewhat inflated, 3-10 mm long, ligule deeply bifid; blade narrow-linear, 1-8 cm long, mostly 0.1-0.2 mm broad; apex (Fig. 19K,O) usually tapering to an acute or acuminate tip. Squamules (Fig. 19J) filiform, 1.0-2.0 mm long. Fertile shoots (Fig. 19J) flexuous, muchbranched, 20-50 cm tall, most branches bearing 1 or 2 female and 1 or 2 male flowers clustered together within the subtending leaf sheaths, some clusters with all female flowers particularly in the upper branches of the inflorescence. Male flower (Fig. 19L) with pedicel 3-5 mm long at anthesis; tepals 3, united in lower part, 0.2-0.4 mm long; stamen with pollen sacs about 1 mm long. Female flowers (Fig. 19L,P) on pedicels 0.5-1 mm long, not (except for the styles and stigmas) projecting beyond the leaf sheaths; tepals 1-2.5 mm long, elliptic, apex deeply bifid and irregularly dentate; carpophore 0.2-0.5 mm long; style slender, stigma narrow, obliquely funnel-shaped with a serrate margin. Fruit (Fig. 19M,Q,R) asymmetric oblong, about 2 mm long, L/B 1.5-2.5(-3), shorter than (or equal to) the tepals and remaining enclosed within them. Tepals frequently whitish and conspicuous around the dark-brown to black fruits.

Flowering and fruiting: September to November.

Type from the Canning River estuary, Perth, W. Aust., in salt water. (*Preiss* No. 1879, Nov. 1841); in LD.

Distribution: No marine specimens have been seen. The type locality in the Canning River estuary has been greatly modified in the past few decades and no *Lepilaena* has been found in that locality recently.

L. preissii occurs in fresh to brackish to saline water of seasonal or intermittent coastal and inland waters in W. Aust. (in the Perth to Esperance area), S. Aust. (south east), Vic. (western shores of Port Phillip Bay), Flinders I. (Bass Strait) and Tas.. Brock & Lane (1983) record L. preissii in salinities up to $150^{9}/_{60}$.

Selected specimens: The type and Peel Inlet, W. Aust., 1 m deep, temporary freshwater pool (*Carstairs*, 12.ix.1982; ADU, A53395).

Aston (1973, p. 318) records monoecious and dioecious plants in Victoria. The type (Figs 18B, 19N-R) is monoecious and all Western Australian specimens examined are also monoecious. L. cylindrocarpa and L. preissii have frequently been confused and further work on the genus is essential.

^{* &}quot;Australia felix" was used broadly to denote the area of grasslands and coastline of southern Victoria from Melbourne westwards to Portland.



Fig. 18. A. Lepilaena cylindrocarpa (ADU, A53620). Habit of male (lower left) and female plants. B. Lepilaena preissii. Part of the type sheet. C. Lepilaena marina. The type sheet.

3. Lepilaena marina E.L. Robertson sp. nov.

PLATE 16 fig. 5; FIGS 18C, 20

Dioecious; rhizomatous marine herb (Fig. 18C), probably annual. Rhizomes about 1 mm in diameter, much-branched, bearing at each node a membranous amplexicaul scale 3-5 mm long, and at usually every alternate node 1-4 (-5) unbranched roots and an erect leafy shoot (2-) 3-5 (-10) cm tall. Leaf sheath (Fig. 20A-C) membranous, 4-5 (-10) mm long, ligule about 2 mm long, usually deeply cleft so as to appear bi-auriculate; blade (Fig. 20D) linear, (1-) 2-3 (-5) cm long, (0.2-) 0.3-0.4 (-0.5) mm broad, entire, in cross section showing a median vascular bundle and marginal fibre strands; apex (Fig. 20E, F) usually truncate with a central mucro (but considerable variation in apex shape can occur on the one plant -Fig. 20F). Squamules (Fig. 20G) filiform, about 1 mm long. Male flowers (Fig. 20H-K) in densely leafy shoots 3-5 (-10) cm tall; axillary, subtending leaves scarcely if at all modified; arising singly in a series of successive leaf axils with only 1 (rarely 2) mature at a time; shortly pedicellate at first, pedicel elongating and becoming filiform and 1-1.5 cm long at anthesis; tepals 3, minute; stamen with 6 pollen sacs, 1.0-2.5 mm long, connective not extended. Female flowers (Fig. 20L-N) borne on slender erect leafy shoots 5-10 (-25) cm tall, frequently projecting above the vegetative shoots; each flower axillary, borne on a short pedicel 1-2 (-5) mm long, usually closely adpressed to the axis with the flower extending well beyond the leaf sheath, subtending leaves reduced and sub-opposite; tepals (1.5-) 2.5-3 (-3.5) mm long, membranous, elliptic, apex mostly deeply bifid and somewhat dentate; carpophore up to 1 mm long; styles projecting the stigmas well beyond the tepals; stigmas obliquely funnel-shaped with an irregularly dentate margin, Fruit (Fig. 20 O,P) an achene, dark-brown, asymmetric oblong, (1.1-) 1.3-1.7 (-2.0) mm long, L/B 1.5-2 (-2.5), shorter than or equal to the tepals, smooth with a slight dorsal ridge, carpophore not elongated, fruits enclosed within the tepals with only stylar remains projecting. Tepals frequently becoming scarious and whitish and very conspicuous around the dark-brown fruits.

Flowering and fruiting: September to December.

Diagnosis: Herba annua dioecia marina repens, 5-10 (-25) cm alta. Rhizomata ramosissima, ad nodum quemque squamam membranaceum amplexicaulem et ad nodos alternos radices 1-4 simplices surculumque ramumve foliosum erectum ferentia. Folia vagina membranacea, ligula bifidissima, lamina lineari, 0.2-0.5 mm lata, integra, plerumque truncata, mucronata. Flores masculini in surculis dense foliosis portati, axillares, pedicello usque ad 1-1.5 cm longo sub anthesi elongato; tepala 3 minuta; stamen 1 sessile, anthera 6 paria microsporangiorum longitudinaliter connata continenti. Flores feminei in surculis gracilibus portati, axillares pedicellati, e vaginis excedentes, erecti; tepala 3 elliptica bifida, carpella 3 libera, carpophoro ca. 1 mm longo, in fructu non elongato, stylis tepalis longioribus, stigmatatibus oblique infundibularibus. Fructus achenium brunneum, oblique oblongum, 1-2 mm longum, 1.5-2.5 plo longior quam latior, quam tepala cingentia brevior aequilongumve, laevis, costa dorsali exigua.

Fig. 19. A-I. Lepilaena cylindrocarpa (ADU, A53620). A. Portion of leaf (adaxial view) showing blade (bl.) and sheath (sh.) junction. Note ligule (l.) deeply cleft into 2 auricles (a.) and a pair of squamules (sq.) adhering to the sheath base. **B.** Junction of leaf blade and sheath (side view) showing ligule (l.), auricles (a.) and squamules (sq.). **C.** Leaf apices. **D.** Portion of male inflorescence. **E.** Portion of male inflorescence showing 3 male flowers, lowest (oldest) with dehisced pollen sacs, mature flower with ripe pollen sacs and immature flower enclosed in sheath. Note pedicel (pe.), pollen sacs, tepals (t.) and squamules (sq.). **F.** Portion of female inflorescence. **G.** Young female flowers showing 3 achenes projecting beyond tepals. **I.** Mature achene. Note carpophore (c.p.) and stylar beak (be.).

J-M. Lepilaena preissii (ADU, A53395). J. Portion of monoecious plant with inflorescence. K. Leaf apices. L. A mature male and an immature female flower in position, subtending leaves removed. Note squamules (sq.), tepals (t.) and pedicels (pe.). M. Mature fruit showing 3 achenes enclosed within the tepals. N-R. Lepilaena preissii (Type specimen). N. Junction of leaf blade (bl.) and sheath (sh.) showing ligule (l.) and auricles (a.). O. Leaf apices. P. Female flower (two stigmas damaged, one missing), with pedicel (pe.) and tepals (t.). Q. Mature fruit showing achenes enclosed within tepals (t.). R. Single achene showing stylar beak (be.) and carpophore (c.p.).





Type locality: Port Clinton, Yorke Peninsula, S. Aust., mid eulittoral. (*Robertson*, 18.xi.1981). Growing with *Zostera mucronata* and *Ruppia tuberosa*.

Holotype: ADU, A52656. Isotypes in AD, MEL, PERTH.

Distribution: From Sceale Bay, Eyre Peninsula, S. Aust. eastwards to Port Phillip Bay, Victoria, on Bass Strait Islands and Boomer, Blackmans Bay, Tas. L. marina forms extensive low turfs in mid and lower eulittoral zones on sandy mud tidal flats, growing in association with Ruppia tuberosa and Zostera mucronata in S. Aust. (Pl. 16, fig. 5) or with Zostera muelleri in Vic. and Tas. It also occurs just subtidally in some localities.

Selected specimens: The type and Tulka, Proper Bay, Port Lincoln, S. Aust., low eulittoral (*Womersley*, 21.viii.1967; ADU, A46522). Eastern flats, American River inlet, Kangaroo I., S. Aust., mid eulittoral (*Womersley*, 26.viii.1948; ADU, A46521). Barker Rocks, Yorke Peninsula, S. Aust., sandy platform on mid eulittoral flats (*Robertson*, 15.xi.1981; ADU, A52723). Coobowie Bay, Yorke Peninsula, S. Aust., mid eulittoral (*Robertson*, 18.ix.1981; ADU, A52652). Coobowie inlet, S. Aust., uppermost sublittoral, 0.5 m deep (*Robertson*, 2.x.1982; ADU, A53653). Port Gawler, S. Aust., mid eulittoral (*Robertson*, 16.xii.1981; ADU, A52793). Swan Bay, Queenscliff, Vic. (*King*, 17.ix.1969; MELU, 4682 and MEL, 103509). Boomer, Blackmans Bay, Tas., in tidal water (*Curtis*, 1.xi.1947; HO, 58750).

The fruit of *L. marina* is very similar in shape and proportions to *L. preissii*. However, *L. marina* is clearly distinguished from *L. preissii* by its consistently dioecious character, the densely leafy branches bearing the male flowers, and its broader leaf blade with a more truncate apex.

FAMILY POSIDONIACEAE Lotsy, nom. cons.

Robust perennial marine herbs with stout rhizomes. *Rhizomes* irregularly monopodially branched, rooting at the nodes. *Roots* simple or branched. *Leaves* alternate with distinct blade and sheathing base. *Tannin* cells numerous. *Inflorescence* racemose, of several spike-like units. *Flowers* actinomorphic, bisexual, or sometimes male only; perianth absent; stamens 3 (rarely 4), sessile; pollen filiform; pollination hydrophilous; carpel one, 1-ovuled with a sessile ornate stigma. *Fruit* a drupe.

Only one genus, Posidonia.

Fig. 20 Lepilaena marina. A. Portion of leaf (adaxial view). Junction of blade (bl.) and sheath (sh.) opened out showing ligule (l.) deeply bifid into 2 auricles (a.). B. Junction of blade and sheath opened out (abaxial view). C₁, C₂ Junction of leaf blade (bl.) and sheath (sh.) (side view). D. T.S. leaf blade showing median vascular bundle (v.b.) and marginal fibre strands (f). E. Leaf apices (juvenile). F. Leaf apex variation (mature leaves). G. Squamules in position at node (subtending leaves removed). H. Male inflorescence showing mature male flower on elongated pedicel releasing pollen, and young male flower enclosed in sheath. I. Two male flowers before anthesis, one enclosed in sheath. Note tepals (t.), pedicel (pe.) and squamules (sq.). J. Male flower from above showing connective (c.), 12 microsporangia (m.s.) and line of dehiscence (de.). K. T.S. through a young male flower showing connective (c.) and wall (m.w.) between a pair of microsporangia (m.s.) Note line of dehiscence (de.) and which breaks down at maturity to leave a 6-loculed structure. L. Female inflorescence. M. Female flower on pedicel (pe.) showing tepals (t.) enclosing 3 carpels with styles projecting. N. Single carpel removed from tepals. Note carpophore (c.p.). O. Mature fruit showing achenes enclosed within tepals. P₁-P₃. Achenes showing carpophore (c.p.). and stylar beak (bc.). (A-G, I-K, M-P from the type. H, L from ADU, A52793.)

POSIDONIACEAE

Genus POSIDONIA Konig 1805: 95, nom. cons. "Tapeweed".

Perennials, forming extensive marine meadows. Rhizomes herbaceous at first, usually becoming lignified, frequently compressed laterally, bearing a scale at each node, with age becoming covered with senescent scales and leaf sheaths. Roots 1 or 2 at each node, arising in 2 alternate series, simple or branched, root hairs infrequent. Prophylls undifferentiated, conspicuous in some species. Leaves alternate; sheath open, more or less amplexicaul, ligulate, auriculate, persistent after the fall of the blade, the line of abscission frequently conspicuous; blade linear and flat, or biconvex to terete, longitudinal parallel veins 5-21, united near the apex, connected by numerous transverse veins (which are frequently conspicuous due to the accumulation of tannin on either side); apex rounded to truncate, or spathulate. Tannin cells present in all parts but especially in the epidermis, appearing as dark dots or stripes, increasing with senescence of the plant. Squamules numerous, palisade-like. Inflorescence borne on a flattened, leafless peduncle, subtended by 2 unequal bracts; each spike-like unit of 2-6 sessile flowers terminating in an acuminate spur. Flowers bisexual (or male only); perianth absent; stamens usually 3 (or 4), sessile, 2 bilocular anthers longitudinally dehiscent, caducous, separated by a broad, apically elongate connective which persists at the base of the fruit; carpel one, 1-ovuled, stigma lobes 1-3, fleshy, vertucose, sometimes with spur-like processes, persistent on the developing fruit. Fruit a drupe with a spongy pericarp, free floating for a time, eventually dehiscent. Seed with a ventral wing, remaining attached to the young plant for 1-2 years after germination.

Type species: P. oceanica (Linnaeus) Delile.

At least 5 species in temperate waters, all endemic to Australia except *P. oceanica*, which is restricted to the Mediterranean region.

Encrusting coralline algae frequently cover the older leaves of *Posidonia* spp.. Many other algae are epiphytic either on the encrusting corallines or directly on the *Posidonia* leaves.

"Posidonia balls" or "marine balls", 7-10 cm in diameter, composed principally of drift material of *P. oceanica*, have been recorded from Mediterranean beaches since ancient times. Similar balls (Pl. 16 figs 2,3), common on southern Australian shores near *Posidonia* marine meadows, are produced from detrital remains, particularly fibres, of *P. australis*. The combs of the grappling apparatus of *Amphibolis* spp., as well as fragments of other seagrasses, algae and shells, are often firmly enmeshed in the balls. Cannon (1979) ingeniously demonstrated the formation of "Posidonia balls" using the oscillating action of a domestic washing machine to simulate the action of waves and water eddies.

KEY TO SPECIES OF *POSIDONIA*

- 1. Leaf blade thick and tough, biconvex to round in cross section . 2. (P. ostenfeldii group)
- - Leaf blade biconvex (in cross section) throughout its length, not terete in any part, (1.5-)2-5(-7) mm broad when fresh; leaf blade with 5-9(-11) longitudinal vascular bundles.
 P. aff. *ostenfeldii

*aff. = affinis i.e. a species having an affinity with, or close to another species.

5. P. angustifolia

1. **Posidonia ostenfeldii** den Hartog 1970: 139, fig. 42. Aston 1973: 270 (in part). Green 1981: 5. Jessop 1978: 77 (in part).

FIGS 21A, 22A-G

Robust rhizomatous perennial herb (Fig. 21A). *Rhizomes* 1–3 mm thick, oval in cross section, with long internodes 2–3 cm long separated by a series of several short internodes 0.5–3 mm long. *Roots* arising irregularly, 1–2 per node, pale-brown in colour, coarse, 1–2.5 mm in diameter, becoming wrinkled and hollow with age. *Leaves* (1-) 2 (-3) per shoot; sheath (Fig. 22A) 12–18 cm long, margins overlapping for their entire length; ligule about 1 mm long; auricles (Fig. 22B, C) 2–2.5 mm long, 2–3 mm wide, dark-brown; after fall of the blade the sheath gradually disintegrates into numerous pale hair-like fibres; blade (Fig. 22D) (40-) 60–135 cm long, terete and 1–1.5 mm in diameter near the base, becoming somewhat flattened (biconvex in cross section) and gradually tapering higher up (when dry, biconvex in cross section throughout except near the base which remains terete), longitudinal vascular bundles 5; apex (Fig. 22E, F) flattened, spathulate. *Squamules* (Fig. 22G) linear-lanceolate, 0.5–1.4 mm long. *Inflorescence* borne on a flattened peduncle 30–35 cm long, considerably shorter than the leaf-canopy; subtending bracts 2, unequal, the longer bract about 20 cm in length greatly exceeding the spikes; spikes 3–7, each terminating in a spur about 4 mm long. *Flowers* bisexual, 3–4 per spike. *Fruit* 2–4 cm long, ovate with a recurved tip.

Flowering and fruiting: November to December.

Type from Esperance Bay, W. Aust. (J. Firman, Dec. 1951); in AD, 96404336.

Distribution: From Cape Leeuwin to Israelite Bay, W. Aust. P. ostenfeldii grows in areas of strong wave action usually below 10 m deep.

Selected specimens: The type and Bremer Bay, W. Aust., 10 m deep (Cambridge, 28.xi.1979; ADU, A50854).

P. ostenfeldii is known mostly from sterile drift material; floral parts when present are frequently damaged.

2. Posidonia aff. ostenfeldii

FIGS 21B,C, 22H-Z, 23

Robust rhizomatous perennial herbs (Figs 21B,C, 23A). *Rhizomes* (Fig. 22H) somewhat compressed, more or less oval in cross section, 2-4 (-5) mm thick, internodes variable in length, frequently an elongate internode 1.5-6 cm long alternating with a series of 2-4 short internodes 0.5-2.5 mm long. *Roots* arising irregularly, 1-2 per node, frequently pale-brown to reddish-brown in colour, 1-4 mm in diameter, with a few fine laterals, becoming hollow with age. *Leaves* 1-3 per shoot; sheath (Fig. 22I) 5-20 cm long, with margins overlapping for about 3/4 to the entire length; ligule 1-1.5 mm long; auricles 2-2.5 mm long, 2-3 mm wide, mostly dark-brown; the abscission line between the blade and the sheath usually conspicuous; after

fall of the blade the sheath disintegrates to a greater or less extent into numerous pale hairlike fibres; blade (Fig. 22J-O) 40–125 cm long, 1.5–8 mm broad, biconvex in cross section (not round in any part); longitudinal vascular bundles 5–11 (clearly seen in cross section of the blade, but inconspicuous in surface view, except near the apex); apex (Fig. 22P) somewhat flattened, usually spathulate with slightly recurved margins, occasionally rounded. *Squamules* (Fig. 22Q) lanceolate about 1 mm long. *Inflorescence* (Figs 21B,C, 23B,C) on a flattened peduncle 30–40 cm long, usually shorter than the foliage leaves, subtending bracts 2, unequal; spikes (Fig. 22R,S) 6–10 (-14), each terminating in a spur 0.5–1.5 cm long. *Flowers* 3–4 (-6) per spike; stamens 3, connective (Fig. 22T,U) 5–8 mm long, linear-lanceolate, with a shallow keel; ovary about 5 mm long, oblong-ellipsoid; stigma (Fig. 22V,W) lobes 3, irregularly verrucose. *Fruit* (Figs 21B, 22X-Z, 23B) 3–4 cm long, more or less ellipsoid, somewhat falcate.

Flowering and fruiting: September to January.

Distribution: From Carnarvon, W. Aust., southwards and eastwards to Backstairs Passage, S. Aust. Drift material has been collected eastwards to South End, Rivoli Bay, S. Aust. P. aff. *ostenfeldii* grows from the upper sublittoral to a depth of about 27 m, mostly in areas of strong wave action.

Selected specimens: Collie Head, Garden I., Cockburn Sound, W. Aust., 6 m deep (Humphries, 20.i.1971; ADU, A50861). Middleton Beach, Albany, W. Aust., upper sublittoral (Womersley, 29.viii.1979; ADU, A51381). Fowler Bay, near Point Fowler, S. Aust., 9 m deep (Shepherd, 28.iii.1980; ADU, A51942). Wittlebee Point, S. Aust., drift (Skinner, 29.xi.1977; ADU, A48914). Hotspot, 10 km NW Flinders I., S. Aust., 27 m deep (Gray, 1.iv.1982; ADU, A53017). Waterloo Bay, S. Aust., 6 m deep (Shepherd, 2.iii.1980; ADU, A51949). Off Marino, Gulf St Vincent, S. Aust., 2-3 m deep (Owen, 30.xi.1969; ADU, A35726). Aldinga, S. Aust., drift (Womersley, 31.xii.1967; ADU, A46461). Pennington Bay, Kangaroo I., S. Aust., drift (Womersley, 21.xi.1968; ADU, A46464). Cooalinga, near Cape Jervis, S. Aust., 7 m deep (Shepherd, 13.xi.1981; ADU, A52748). Off Blowhole Creek, 10 km SE of Cape Jervis, S. Aust., 5-7 m deep (Shepherd, 19.i.1982; ADU, A52883) and 12-15 m deep (Shepherd, 15.ix1981; ADU, A52563). South End, Rivoli Bay, S. Aust., drift (H. Robertson, 14.ix.1982; ADU, A53639).

P. aff. ostenfeldii comprises a range of material of probably at least two species. Ostenfeld (1916) referred to and illustrated "aberrant" leaves of *Posidonia* from Carnarvon, W. Aust., which had distinctive apices and were stronger and thicker than *P. australis*. These undoubtedly belong to *P.* aff. ostenfeldii. Since den Hartog (1970) described *P. ostenfeldii* this name has been applied to all thick, tough *Posidonia* material having a narrow leaf blade, biconvex in cross section. Cambridge (1975, p. 155) referred to broad and narrow leaved morphs, within the species *P. ostenfeldii*, and suggested more than one species could be involved around the south-west corner of Western Australia. Kuo (pers. comm.) was the first to realise that den Hartog's type specimen of *P. ostenfeldii* (AD, 96404336) has terete leaves (not readily discernible in dried herbarium material), and that its leaf blades are at the extreme narrow end of the spectrum within the range of material generally lumped under that name. Since that time, Cambridge & Kuo have studied all available herbarium material and also collected fresh material extensively around southern Western Australia as far east as Eyre (32°15'S, 126°18'E) in the Great Australian Bight. The results of their anatomical, morphological and ecological investigations will help to elucidate the *P. ostenfeldii* complex.

Dry herbarium material of broader leaved specimens of *P.* aff. ostenfeldii, e.g. ADU, A51949 from Waterloo Bay, S. Aust., looks very similar to *P. angustifolia* but can readily be distinguished by cutting a transverse section of the blade. After soaking in water for a few minutes the section resumes the biconvex shape characteristic of the fresh leaf.



Fig. 21. A. Posidonia ostenfeldii (ADU, A50854). Habit. B. Posidonia aff. ostenfeldii (ADU, A52883). Habit, with mature fruits. C. Posidonia aff. ostenfeldii (ADU, A52563). Habit, with very young inflorescence.

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Fig. 22. A-G. Posidonia ostenfeldii (ADU, A50854). A. Portion of leaf (adaxial view). Junction of blade and sheath showing overlapping margins, auricles (a.) with accumulation of tannin cells (t.c.), and position of transverse veins marked by lines of tannin cells. B. Portion of leaf (abaxial view). Junction of blade and sheath showing the abscission line (ab.) and auricles (a.). C. Portion of leaf (side view). Junction of blade and sheath showing abscission line (ab.) and auricles (a.). D₁-D₇ T.S. leaf blade at 7 levels showing row of longitudinal vascular bundles (v.b.). D₁ 5 mm above ligule. D₂, 15 cm above ligule. D₃ 30 cm above ligule. D₄ 60 cm above ligule. D₅ 110 cm above ligule. D₆ 120 cm above ligule. D₇ 130 cm above ligule or 5 mm from apex. E. Apex of juvenile leaf (adaxial view). F. Apex of mature leaf (adaxial view). G. Squamules adhering to base of leaf sheath.

H-Z. Posidonia aff. ostenfeldii H. Portion of rhizome showing long internodes alternating with a series of short internodes, and the fibrous remains of sheaths at each node. I. Portion of leaf (adaxial view). Junction of blade and sheath showing overlapping margins, ligule (l), auricles (a) (with accumulation of tannin cells) and position of transverse vein marked by lines of tannin cells (*t.c.*) J-O. T.S. mid portion of leaf blade showing row of longitudinal vascular bundles (v.b.) (from 6 separate collections). **P.** Leaf apex (abaxial view) showing recurved margins, longitudinal veins (l.v.), transverse veins (t.v.)and tannin cells (t.c.). Q. Squamules adhering to base of leaf sheath. R. Portion of inflorescence showing spike of 2 flowers with dehisced anthers (an.). S. Portion of inflorescence showing spike of 3 flowers after anthers have fallen. Note scars (sc.) on persistent connective (c.), and terminal spur (sp.). T. Connective (abaxial view) with keel (k.) after anthers have fallen. Note scars (sc.). U. Stamen (adaxial view) showing connective and anthers. V. Ovary and lobed stigma. W. Ovary (after fertilisation) and persistent lobed stigma. X. Spike of 2 young fruits showing persistent connectives (c.) and stigma remnant (st.r.) Y. Mature fruit. Z. T.S. fruit showing pericarp (p.c.) and seed (se.) (H, I, L from ADU, A52563. J from ADU, A51381. K from ADU, A46461. M from ADU, A53639. N from ADU, A52883. O-Q from ADU, A51942. R, T-V from ADU, A46464. S, W from ADU, A52748. X-Z from ADU, A48914.)




Fig. 23. A. Posidonia aff. ostenfeldii (ADU, A51942). Habit. B. Posidonia aff. ostenfeldii (ADU, A48914). Inflorescence with mature fruits. C. Posidonia aff. ostenfeldii (ADU, A46464). Inflorescence.



Fig. 24. A. Posidonia sinuosa (ADU, A53018). Habit B. Posidonia australis (ADU, A46919). Habit. C. Posidonia angustifolia (ADU, A53021). Habit.

3. Posidonia sinuosa Cambridge & Kuo 1979: 309. Green 1981: 5.

FIGS 24A, 25, 26A,B

Rhizomes 3-8 mm thick, internodes 1-5 cm long, bearing short erect stems with very short internodes, crowded branches and numerous congested 1-2 leaved shoots, usually giving the appearance of discrete, tufted plants (Figs 24A, 26A). Leaves 1-2 per shoot; sheaths (Fig. 25A-D) 3-6 (-12) cm long, margins overlapping for about half their length, brown to dark reddish-brown in colour, remaining entire, not disintegrating into hair-like fibres, straw-like in texture when dry; ligule about 1 mm long; auricles 1-2 mm long, dark-brown; blade (Fig. 25C-F) linear, flat or somewhat concave-convex, lax, (20-) 25-50 (-120) cm long, 4-8 (-11) mm broad, longitudinal veins 8-11 (-13) uniting near the apex; epidermal cells (Fig. 25G) in surface view oblong, L/B 4-10, with sinuous margins; apices (Fig. 25H) rounded or truncate, frequently asymmetric. Squamules (Fig. 25I,J) lanceolate, 0.2-0.8 mm long. Inflorescence (Figs 25K, 26A,B) hidden beneath the canopy of leaves on a flat peduncle about 10 cm long, 2-4 mm broad; spikes 2-4 subtended by 2 bracts of unequal length, the longer one 6-25 cm long and exceeding the inflorescence; spike terminating in a short spur. Flowers (Fig. 25K) 3-6 per spike. Anthers deep red before dehiscence, connective (Fig. 25L,M) 4-6 mm tall, oblonglanceolate, with a shallow keel, apex tridentate. Ovary (Fig. 25N) 4-5 mm tall; stigma irregularly dentate with 3-5 spurs. Fruit (Figs 25O,P, 26B) ellipsoidal-terete, 2-3 cm long; seed (Fig. 25Q) ellipsoid, 1.5-2 cm long, ventral wing 2-3 mm wide, seed (Fig. 25R), remaining attached to the young plant for 1-2 years after germination.

Flowering and fruiting: August to January.

Type from Point Atwick, Garden I., W. Aust., 3 m deep (Cambridge, 20.xi.1971); in PERTH.

Distribution: From Shark Bay, W. Aust. around western and southern Australia to Kingston, S. Aust. *P. sinuosa* is widely distributed to a depth of 15 m in bays and other sheltered areas either in pure stands or growing sympatrically with *P. australis* or *P. angustifolia*. In more exposed areas it may form meadows with *Amphibolis* spp. The rhizome of *P. sinuosa* is firmly rooted in the substrate and usually only removed with great difficulty.

Selected specimens: Safety Bay, (near Penguin I. spit), W. Aust., 1.5 m deep (Cambridge, 23.ix.1976; UWA, 2840 and ADU, A51181). Warnbro Sound, W. Aust., 2 m deep (Cambridge, 26.x.1978; ADU, A50860). Main Bay, Pearson I., S. Aust., 7-10 m deep (Shepherd & Turner, 28.iii.1982; ADU, A53018). Tiparra reef, Spencer Gulf, S. Aust., 8 m deep (Shepherd, 12.i.1978; ADU, A49410). West I., Encounter Bay, S. Aust., 5 m deep (Shepherd, 28.xii.1973; ADU, A45288). Kingston, S. Aust., 6 m deep (Shepherd, 21.iii.1974; ADU, A46462).

Fig. 25. A-R. *Posidonia sinuosa.* A, B. Leaf sheath (sh.) (adaxial view) with auricles (a.) and ligule (l.) showing variation in amount of margin overlap. C. Portion of leaf (adaxial view). Junction of blade and sheath (sh.) showing auricles (a.), ligule (l.), longitudinal veins and transverse veins. D. Portion of leaf (abaxial view). Junction of blade and sheath showing auricles (a.), longitudinal veins and transverse veins. D. Portion of leaf (abaxial view). Junction of blade and sheath showing auricles (a.), longitudinal (l.v.) and transverse (t.v.) veins, tannin cells (t.c.) and abscission line (ab.). E. T.S. mid portion of leaf blade showing vascular bundles (v.b.). F. Portion of leaf blade showing tannin cells (t.c.) accumulated either side of transverse veins (t.v.) G. Epidermis of leaf blade (surface view) showing sinuose margins of epidermal cells. H₁-H₃. Leaf apices showing venation. I. Squamules in position adhering to base of sheath. J. Squamules showing variation in size. K. Inflorescence of 2 spikes showing terminal spur (sp.). L. Stamen (abaxial view) showing 2 bilocular anthers (an.) (dehisced), line of dehiscence (de.) and elongated connective with keel (k.). M. Connective (abaxial view) after anther connectives (c.). and stigma remnant (st.r.). P. T.S. fruit showing pericarp (p.c.) and seed (se.). Q. Seed showing ventral wing (w.), emerging root (rt.) and plumule (pl.). R. Young plant remaining attached to seed. (A-J from ADU, A49410. K-N from ADU, A45288. R from ADU, A46462.)



 Posidonia australis J. D. Hooker 1858: 43. Aston 1973: 270. Beadle, Evans & Carolin 1972: 522. Blackall & Grieve 1954: 9. Cambridge & Kuo 1979: 317. Green 1981: 5. den Hartog 1970: 132 (in part). Jessop 1978: 77. Ostenfeld 1916: 31. Sainty & Jacobs 1981: 366. Willis 1970: 67.

Caulinia oceanica sensu R. Brown (non DC.) 1810: 339.

PLATES 8 fig. 2, 15 fig. 4, 16 figs 2, 3; FIGS 24B, 26C, D, 27A-M

Rhizomes 5-15 mm thick, laterally compressed, internodes usually 1-4 cm long. Stems (Pl. 15 fig. 4) erect, short, sparingly branched; older stems and rhizomes both covered with senescent fibrous remains of leaf sheaths (Figs 24B, 26C). Leaves 2-3 (-4) per shoot; sheaths (Fig. 27A) 6-10 cm long, margins overlapping for about 1/3 of their length, persistent, finally disintegrating into a mass of shaggy pale-yellow to grey, hair-like fibres; ligule 1-1.5 mm long, auricles 3-4 mm long, usually dark-brown; blade (Figs 27B-D) linear, flat, frequently stiffly curved, (15-) 20-45 cm long, (6-) 10-15 (-20) mm broad, with 14-20 longitudinal veins uniting near the apex, epidermal cells (Fig. 27C) in surface view more or less isodiametric, L/B 0.5-1, with smooth margins; apices (Fig. 27D) rounded to truncate. Squamules (Fig. 27E) linear to lanceolate, 0.5-1 mm long. Inflorescence (Figs 26C,D, 27F) about the same height as, or extended above, the canopy of leaves, on a flattened peduncle 15-45 (-60) cm tall and 3-5 mm broad; 2-5 spikes subtended by 2 unequal bracts, the longer one up to 40 cm long; each spike terminating in an acuminate spur up to 1.5 cm long. Flowers (2-) 4 (-6) per spike; anthers (Fig. 27G,H) dark-brown before dehiscence, connective (Fig. 27I,J) 5-7.5 mm tall, lanceolate, usually strongly keeled, keel entire, serrate or with a coarse hook, sometimes winged, apex acute; stigma lobes (Fig. 27K) 3, irregularly papillose, frequently spurred; ovary about 2 mm long. Fruit (Fig. 27L,M) 2-3 cm long, oblong-ellipsoid, asymmetric, somewhat laterally compressed.

Flowering and fruiting: October to December.

Lectotype from Georgetown, Tas. (Gunn 1347); in K (see Cambridge & Kuo 1979, p. 317).

Distribution: Widespread from Shark Bay, W. Aust., southwards and eastwards around southern Australia, and north and east Tas., to Lake Macquarie, N.S.W., with some reports from localities further north on both the west and east coasts of Australia. It occurs from just below low water mark, where the tops of the leaves are emergent at low tide (Pl. 8 fig. 2) to about 15 m deep and grows sympatrically with both *P. angustifolia* and *P. sinuosa* in the shallower part of their range. The rhizomes of *P. australis* are usually not deeply buried but creep more or less horizontally just below the surface of the substrate at a depth of about 5–15 cm with the roots frequently penetrating to about 50 cm deep.

Selected specimens: Strickland Bay, Rottnest I., W. Aust., 0-1.5 m deep (Engler & Clarke, 5.ix.1979; ADU, A51108). Spalding Cove, Port Lincoln, S. Aust., 0.5 m deep (Womersley, 10.i.1976; ADU, A46919). Proper Bay, Port Lincoln, S. Aust., 3 m deep (Shepherd, 26.viii.1975; ADU, A46587). Red Cliff Point, Spencer Gulf, S. Aust., 0.4 m deep (Johnson, 18.ix.1974; ADU, A45924). Mangrove Creek, Spencer Gulf, S. Aust., 1 m deep (Shepherd, 12.ix.1973; ADU, A45287). Goose I., Spencer Gulf, S. Aust., 0.5 m deep (Shepherd, 20.xii.1971; ADU, A41271). Barker Rocks, Yorke Peninsula, S. Aust., 1.5-3 m deep (Lipkin, 20.ix.1981; ADU, A52645). Aldinga, S. Aust., S end of reef, 0-1 m deep (Womersley, 19.v.1977; ADU, A48004). Eastern Cove, Deal I., Bass Strait, Tas., 15 m deep (Shepherd, 23.iii.1981; ADU, A52049). Towra Point, Botany Bay, N.S.W., 1.5 m deep (Steffenson, 23.viii.1981; ADU, A52353).

P. australis is the commonest and most widespread species of *Posidonia*. Prior to the work of Cambridge & Kuo (1979) all flat-leaved material of *Posidonia* in Australian waters was referred to *P. australis*, although the existence of variants was recognised. Detailed ecological, morphological and anatomical studies led to the recognition of 3 species within the *P. australis* group, two narrow-leaved species (*P. sinuosa* and *P. angustifolia*) and the broader-leaved *P. australis*.

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Fig. 26. A, B. Posidonia sinuosa (ADU, A50860). A. Plant showing inflorescence shorter than foliage leaves. B. Inflorescence with fruits. C, D. Posidonia australis. C. Plant showing inflorescence taller than foliage leaves (ADU, A45924). D. Inflorescence (ADU, A52645).

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The cellulose-rich fibres of the persistent leaf sheaths of P. australis are very resistant to decay. As the plants die, sediment is trapped amongst the foliage and accumulates with the fibrous remains, gradually raising the level of the sea floor. Huge deposits, several metres thick, of fibre and sediment have built up in the shallow coastal waters of the South Australian gulfs. These deposits near Port Broughton were mined for several years from 1908-1914 and the fibre extracted. It had a number of industrial uses principally in the textile trade and as an insulation material. The venture proved uneconomic and was abandoned following the collapse of the European market in 1914 (Winterbottom 1917).

5. Posidonia angustifolia Cambridge & Kuo 1979: 312. Green 1981: 5.

PLATE 16 fig. 1; FIGS 24C, 27N-Y

Rhizomes (Fig. 24C) 4–10 mm thick, laterally compressed, internodes mostly 1–6 cm long. *Stems* short, erect, sparingly branched, both stems and rhizomes retaining the fibrous remnants of the leaf sheaths. *Leaves* 2–3 per shoot; sheaths (Fig. 27N) 5–14 cm long, with margins overlapping for about 2/3 the length of the sheath; ligule about 1 mm long; auricles 1–2(-5) mm long; persistent fine hair-like fibres remaining after senescence of the rest of the sheath, fibres pale-yellow to grey, hair-like in texture, less dense than in *P. australis;* blade (Fig. 27O) flat, linear, (10-)20–75(-120) cm long, mostly 4–6 mm broad with 7–11 longitudinal veins uniting near the apex, epidermal cells (Fig. 27P) in surface view elongate, L/B 3–6, cell margins smooth; apex (Fig. 27Q,R) truncate to slightly notched, mostly oblique. *Squamules* (Fig. 27S) linear-lanceolate, 1–2 mm long. *Inflorescence* (Fig. 27T) usually hidden beneath the canopy of foliage leaves, peduncle 10–20 cm high, flattened and about 2 mm broad, spikes mostly 2–4, each terminating in a short spur. *Flowers* (Fig. 27U) 2–5 per spike; anther connective (Fig. 27V) about 5 mm long, lanceolate, margins usually entire, keel shallow; stigma (Fig. 27W) with 2 or 3 spurs, somewhat papillose. *Fruit* (Fig. 27X,Y) asymmetrically pyriform, about 2.5 cm long, somewhat compressed laterally.

Flowering and fruiting: November to February.

Type from 4 km NE of Cape Naturaliste, W. Aust., 30 m deep (Cambridge, 22.xi.1976); UWA, 2856, in PERTH, isotypes in ADU, K.

Fig. 27 A-M Posidonia australis. A. Portion of leaf (adaxial view) showing sheath (sh.) margin overlap, ligule (l) and auricles (a.). B. T.S. mid portion of leaf blade showing vascular bundles (v.b.). C. Epidermis of leaf blade (surface view) showing isobilateral cells. D. Leaf apex showing longitudinal veins (l.v.), transverse veins (t.v.) and tannin cells (t.c.). E. Squamules showing shape and size variation. F. Inflorescence of 2 spikes showing terminal spur (sp.). G. Stamen showing 2 young anthers (an.), line of dehiscence (de.) and elongate connective with keel (k.). H. Stamen showing 2 dehisced anthers and connective with hooked keel. I₁,I₂. Connectives (abaxial view) showing scar (sc.) after anther fall. J₁,J₂. Connectives (side view) showing well-developed keel. K₁-K₄. Ovaries and stigmas showing variation in lobing. L. Fruit showing persistent anther connectives (c.) and stigma remnant (st.r). M. T.S. fruit showing pericarp (p.c.) and seed (se.). (A-G, J₁,J₂, K₂-K₄ from ADU, A45924. H, I₁, I₂, K₁ from ADU, A48004. L, M from ADU, A41271.)

N-Y Posidonia angustifolia. **N.** Portion of leaf (adaxial view) showing sheath (sh.) margin overlap, ligule (l.) and auricles (a.) **O.** T.S. mid portion of leaf blade showing vascular bundles (v.b.), **P.** Epidermis of leaf blade (surface view) showing elongate cells. **Q.** Leaf apex showing longitudinal veins (l.v.), transverse veins (t.v.) and tannin cells (t.c.) **R.** Leaf apices, variation in shape. **S.** Squamules showing dehiseed anthers (an.), elongate connectives (c.), ovary and lobed stigma (st.). V₁-V₅. Connectives after fall of anthers showing scars (sc.) and shallow keel (k.). W₁-W₃. Ovaries and stigmas, showing variation in stigma lobing. **X.** Fruit showing terminal spur (sp.), persistent connective (c.) and stigma remnant (st.r.). **Y.** T.S. Fruit showing pericarp (p.c.) and seed (sc.). (N-Q, S, U from ADU, A48844. **R** from ADU, A50924. **T.** V₁-V₅, W₁-W₃ from ADU, A46474. **X.** Y from ADU, A46466.)



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Distribution: From Houtmans Abrolhos, W. Aust., southwards and eastwards to Port MacDonnell, S. Aust. *P. angustifolia* grows subtidally from 2-35 m deep. It frequently grows in deeper water than *P. australis* but it can grow sympatrically with either *P. australis* or *P. sinuosa*. In its deeper range it is often found in association with *Heterozostera tasmanica* or *Halophila australis* and in sheltered positions in its shallower range in association with *Amphibolis antarctica* (Pl. 16 fig. 1). The rhizomes of *P. angustifolia* usually extend more or less horizontally within the substrate at a depth of about 10-20 cm with the roots penetrating to a depth of about 30-60 cm.

Some specimens from the eastern limit of its range, e.g. ADU, A48848 from Port MacDonnell, S. Aust., represent a very broad leaved form and may be intergrades between *P. angustifolia* and *P. australis*.

Selected specimens: The isotype and Ward I., W of Flinders I., S. Aust., 18-22 m deep (Shepherd, 3.iii.1980; ADU, A50924). East Cove, Pearson I., S. Aust., 20-23 m deep (Shepherd & Turner, 29.iii.1982; ADU, A53021). North Bay, Pearson I., S. Aust., 14 m deep (Shepherd, 12.i.1969; ADU, A46466). Investigator Strait, S. Aust., 32 m deep (Watson, 23.i.1971; ADU, A40993). Off Broadway, Glenelg, S. Aust., 8 m deep (Shepherd, 3.xi.1968; ADU, A46474). Off Semaphore, near Adelaide, S. Aust., 15 m deep (Shepherd, 8.xi.1977; ADU, A48844). Off Blowhole Creek, 10 km SE of Cape Jervis, S. Aust., 12-15 m deep (Shepherd, 15.ix.1981; ADU, A52562). Abalone Cove, West I., S. Aust., 5 m deep (Shepherd, 22.ix.1977; ADU, A48848).

FAMILY CYMODOCEACEAE N. Taylor, nom. cons.

Dioecious; marine perennial herbs with creeping, monopodially or sympodially branched rhizomes. *Leaves* distichous, with distinct blade and sheathing base; leaf sheath ligulate, auriculate; leaf blade flat and linear or terete and subulate. *Squamules* present in each leaf axil. *Tannin* cells numerous. *Flowers* solitary or in cymose inflorescences. Perianth absent or rarely of 1-few hyaline bracts. *Male flowers* subsessile or pedicellate, 2 anthers, longitudinally dehiscent. Pollen grains filiform and tightly coiled within the anther; pollination hydrophilous. *Female flowers* (1-) 2 carpels, free, sessile or stipitate; style 1; stigmas 2-3, filiform. *Fruit* a 1-seeded nut, viviparous in *Amphibolis* and *Thalassodendron*.

The five genera, with mainly tropical distribution, are all found on the Australian coast, with two genera occurring in southern Australia.

KEY TO GENERA OF CYMODOCEACEAE

- 1. Leaf blades terete, subulate; flowers in conspicuous cymose inflorescences
- Leaf blade shed before the persistent sheath; blade narrow (usually less than 3 mm broad); blade veins 3, longitudinal, a midrib and 2 submarginal veins . *HALODULE
- 2. Leaf blade and sheath shed together leaving conspicuous annular scars on the stems; blade usually more than 5 mm broad; blade veins 8-21, more or less parallel3
- 3. Leaf blades entire; apex bidentate. Stems much-branched, arising at irregular intervals of (1-)4-8 nodes. Roots branched, arising at each node. Flowers in axils of unmodified vegetative leaves. AMPHIBOLIS

^{*}For footnote see page 99 opposite.

CYMODOCEACEAE

Genus THALASSODENDRON den Hartog 1970: 186

Dioecious; perennials with robust, sympodially branched rhizomes bearing 1 or 2 erect unbranched (or little branched) stems at every fourth internode (Tomlinson 1974, p. 119). *Stems* with a tuft of leaves at the summit and scars of fallen leaves below. *Roots* 1–5 arising together, only at the internode preceding the stem-bearing internode. *Leaf* sheath compressed, ligulate, auriculate, amplexicaul; blade flat, linear with denticulate margins, primary veins numerous, parallel, connected by oblique crossveins; apex coarsely denticulate; blade and sheath shed together leaving an annular scar. *Squamules* present in each leaf axil. *Tannin* cells numerous. *Flowers* solitary and terminal on short lateral shoots, each flower enclosed by 4 leafy bracts. *Male flower* with 2 anthers, each with a terminal appendage. *Female flower* consisting of 2 free carpels each with a short style and 2 stigmas. *Fruit* a 1-seeded nut; seed viviparous, remaining attached to the parent plant after germination. *Seedling* free-floating for a time.

Type species: Thalassodendron ciliatum (Forskal) den Hartog.

Two species, one endemic to south Western Australia.

Thalassodendron pachyrhizum den Hartog 1970: 194. Green 1981: 5.

FIGS 28A, 29F-J.

Dioecious; rhizomatous perennial (Fig. 29F). *Rhizomes* robust, (3-)4-6 mm in diameter, becoming lignified with age. *Roots* arising in pairs, 3-5 mm thick, usually unbranched, becoming lignified, black when dry. *Leaf* sheath (Fig. 29G) compressed, (2-)3-4(-5) cm long, cuneate at the base, margins not overlapping; ligule obtuse, about 1 mm high; auricles obtuse; blade linear, falcate, 7-15(-20) cm long, (6-)8-10(-12) mm broad, midrib prominent, 7-9 inconspicuous, parallel veins on either side of the midrib, connected by oblique crossveins; ligule obtuse, 1 mm high; auricles obtuse; apex (Fig. 29H) rounded, bearing numerous square or trapezoid sclerenchymatous denticulations 0.1-0.2 mm long which continue at less frequent intervals down the margin. *Squamules* (Fig. 29I, J) linear, 1-4 mm long in 2 groups of 8-10 on either side of the node. *Male flower* not seen. *Female flower* enclosed by 4 leafy bracts; ovary ellipsoid, 2 mm long, style up to 1 mm long, 2 stigmas about 20 mm long. *Fruit* a one-seeded nut with a hard pericarp and surrounded by the fleshy innermost of the 4 floral bracts.

Flowering and fruiting: August to October.

Type from Leighton, W. Aust., drift (Baird, 30.vii.1941); in UWA.

Selected specimens: Whitfords Beach, W. Aust., 5 m deep (Lipkin, 2.ii.1982; ADU, A52953). Mangles Bay, Point Peron, W. Aust., drift (Royce 3051, 28.v.1949; PERTH s.n.).

Halodule uninervis (Fig. 29D) is a pioneer species and a rapid colonizer and may sometimes establish itself in temporarily denuded areas around Port Denison, prior to the establishment of other seagrass species (Kirkman, pers. comm.). It may be distinguished by its linear, three-veined leaves, with the submarginal veins ending in teeth (Fig. 29E).

Selected specimen: Seven Mile Beach, Dongara, W. Aust., low eulittoral to upper sublittoral (Womersley, 17.ix.1979; ADU, A51311).

^{*} The two widespread tropical species Syringodium isoetifolium (Ascherson) Dandy (1939, p. 116) and Halodule uninervis (Forskal) Ascherson (1882, p. 24) also occur in restricted areas on the temperate Western Australian coast.

Syringodium isoetifolium occurs to a depth of 5 m in mixed seagrass beds as far south as Rottnest I. and suburban Perth beaches. It may be distinguished by its cymose inflorescence (Fig. 29A) and its subulate-terete leaf blades (Fig. 29B, C), which in transverse section show a central vascular strand surrounded by 6-8 air canals and 7-10(-15) pericentral vascular bundles.

Distribution: Restricted to the temperate coast of W. Aust. from Geraldton southward to Cape Leeuwin and eastward to Bremer Bay. *T. pachyrhizum* commonly grows on rocks at the edge of limestone and granite reefs at depths up to 6 m. It has been found in regions of extreme turbulence at greater depths, to 40 m. It is a poor competitor and is not normally found growing in association with other seagrasses.

Selected specimens: Port Denison, W. Aust., drift (Gordon 8.xi.1968; ADU, A51965). Whitfords Beach, W. Aust., 4-5 m deep (Lipkin, 2.ii.1982; ADU, A52947). Sorrento Beach, Perth, W. Aust. (Royce 3063, 7.viii.1949; PERTH, s.n.). Cottesloe, W. Aust. (Glauert, Nov. 1922; PERTH, s.n.). Cowaramup Bay, W. Aust., 2-3 m deep (Clarke & Engler, 1.ix.1979; ADU, A50665). South coast, E. of Augusta, W. Aust. (Royce 3233, 26.vi.1950; PERTH, s.n.).

Kirkman (pers. comm.) has monitored a stand of *T. pachyrhizum* for a twelve month period and has recently made numerous collections of both male and female flowering material. His findings will help to enlarge our knowledge of this species.

Genus AMPHIBOLIS C. Agardh 1823: 474. "Wire-weed", "Sea-nymph".

Dioecious; perennials, rhizomatous, forming extensive meadows. Rhizomes much-branched, sympodial, lignified, with 1-2 roots at each node, producing numerous erect stems. Roots branched, lignified, wiry, often somewhat coiled. Stems lignified, wiry, marked by the annular scars of fallen leaves. Leaves alternate, distichous, borne in tufts at the ends of branches; sheath compressed, ligulate and auriculate, amplexicaul, leaving an annular scar on the stem when shed; blade flat linear, entire, shed with its sheath; veins inconspicuous, longitudinal veins 8-21, more or less parallel, joined irregularly by numerous oblique crossveins. Squamules present in the axil of each leaf. Tannin cells numerous. Flowers solitary and terminal on short lateral shoots, enclosed by normal (unmodified) vegetative leaves. Male flower subtended by a bract, subsessile at first, becoming pedicellate; 2 anthers, connate in their lower part, each with 2 pairs of microsporangia, dehiscing longitudinally, crowned by 2-3 appendages, anthers caducous at or immediately prior to dehiscence; pedicel elongating just prior to anthesis. Pollen grains filiform, individual grains up to 5 mm long, coiled into tight pollen masses. Pollination hydrophilous. Female flower consisting of 2 free carpels (usually one aborts) subtended by a circular bract which is initiated as a ring meristem but later becomes frayed (McConchie, Ducker & Knox 1982, p. 254) and may be very reduced in A. griffithii. Each carpel has a short style, and 3 (rarely more) stigmatic branches, and 4 (sometimes more) pericarpic lobes at the base of the ovary. The pericarpic lobes are fleshy at first, but a hard bony skeleton of more or less parallel bristles united at the base is revealed as the fleshy tissue disintegrates. These bristles form the 4-lobed "comb" which acts as a "grappling apparatus" (see Tepper 1882, p. 4) to anchor the young seedling to the substrate. Seedlings viviparous; almost immediately after fertilisation the seed germinates on the parent plant and develops into a leafy shoot which remains attached for about 7-12 months. The abscission laver forms immediately below the comb prior to the release of the seedling. The seedling is free floating until the grappling apparatus becomes caught in, and attached to, a substrate such as sand, an algal turf, a coralline alga or the fibrous leaf base of a Posidonia plant.

Type species: Amphibolis zosteraefolia C. Agardh = A. antarctica (Labillardiere) Sonder & Ascherson ex Ascherson (Ducker, Foord & Knox 1977, p. 68).

Two species, both endemic to southern Australia.

Black (1913, p. 3) was the first to accurately describe and illustrate the unique mode of reproduction and dispersal of *Amphibolis*. Recent studies by Ducker, Foord & Knox (1977), Ducker, Pettit & Knox (1978) and McConchie, Ducker & Knox (1982) have considerably enlarged our knowledge of the biology of the genus.

Huge mounds of drift often occur on beaches near *Amphibolis* meadows. These result both from branches torn off by storms and also from the vast quantities of lower leaves shed each winter. Sometimes marine balls are formed by wave action rolling fragments of *Amphibolis*



Fig. 28 A. Thalassodendron pachyrhizum (ADU, A52947). Habit. B. Amphibolis antarctica (ADU, A52563). Habit. C. Amphibolis griffithii (ADU, A35725). Habit.

stems into more or less spherical balls mostly up to about 7 cm in diameter. *Amphibolis* balls incorporate algal epiphytes, hydroids and other drift but are mostly composed of short lengths of *Amphibolis* stems (c.f. *Posidonia* balls (Pl. 16 figs 2,3) composed mainly of *Posidonia* fibres).

KEY TO SPECIES OF AMPHIBOLIS

- Amphibolis antarctica (Labillardiere) Sonder & Ascherson ex Ascherson 1867b: 164. Aston 1973: 302, fig. 120. Green 1981: 5. den Hartog 1970: 199, figs 54-56. Jessop 1978: 74, fig. 39.

Ruppia antarctica Labillardiere 1807: 116, pl. 264.

Caulinia antarctica (Labillardiere) R. Brown 1810: 339. Harvey 1855c: 427.

Cymodocea antarctica (Labillardiere) Endlicher 1837: 230. Blackall & Grieve 1954: 8. Ostenfeld 1916: 19. Willis 1970: 68.

Pectinella antarctica (Labillardiere) J. Black 1913: 1.

PLATE 16 fig. 1; FIGS 28B, 30, 31

Dioecious; perennial (Pl. 16 fig. 1, Fig. 28B) with creeping, lignified rhizomes (Fig. 30A) 2-3(-4) mm thick. Stems erect, much-branched, 1-1.5 mm in diameter, (0.2-)0.5-1.0(-1.5) m tall. Roots (Fig. 30A) 1 (rarely 2) at each node, branched, wiry. Leaves (Fig. 30B) in groups of (6-)8-10, loosely arranged at the ends of branches; sheath (Fig. 30C,D) 6-10 mm long, frequently slightly wider than the blade, margins overlapping at the base only, ligule about I mm long, auricles exceeding the ligule, usually about 2 mm long; blade (Fig. 30C,D) 18-30(-50) mm long, (2-)3.5-6(-10) mm broad, L/B 2.5-6(-10), flat, frequently twisted about 180° in the upper half; apex lunate to truncate, with 2 acute, marginal teeth (absent in juvenile leaves of the seedling). Squamules (Fig. 30E,F) usually 1-3 either side of the stem in the leaf axil, ovate to ovate-lanceolate, about 1 mm long. Male flower (Fig. 30G-J) with a subtending scarious bract; anthers 7-8(-10) mm long, with 2 or 3 branched appendages each (1-)2-3 mm long; pedicel (Fig. 30K) elongating to 5-6 mm prior to dehiscence of the anthers. Female flower (Fig. 31A-D) surrounded by a continuous, scarious bract up to 8 mm long, splitting into 2-several laciniate parts; style 4-6 mm long, stigmatic branches 3, about 3 mm long (one or more stigmatic branches may each divide again to form 2 or more secondary branches); pericarpic lobes (Fig. 31C-G) developing in 2 whorls, the outer whorl of 4 unequal lobes (a broad pair and a narrow pair), and the inner whorl of 4 (or more) shorter and narrower lobes, one pair of which is frequently bifid and the other pair trifid. Seedlings (Fig. 31E-J) viviparous, development continuing as described for the genus. Seedlings about 6-10 cm long when released, the leaves at first (Fig. 31H) linear, entire, the apex without the 2 acute marginal teeth characteristic of the adult leaf. The comb (Fig. 31H-K), which remains after the disintegration of the fleshy tissue of the pericarp lobes, is 8-10 mm long, with 13-18 bristles in each broad lobe and 7-11 bristles in each narrow lobe.

Fig. 29 A-C. Syringodium isoetifolium (ADU, A52953). A. Portion of male inflorescence. B. T.S. Leaf blade showing air canals (a.c.) and vascular bundles (v.b.). C. Habit. D, E. Halodule uninervis (ADU, A51311). D. Habit. E. Leaf apex. F-J. Thalassodendron pachyrhizum. F. Habit. Note leaf scars (l.sc.). G. Blade-sheath junction showing venation, ligule (l.) and auricles (a.). H. Leaf apex. I. Squamules (sq.) in position at node. J. A group of squamules from one side of node. (F, G, I, J from ADU, A52947. H from ADU, A51965.)



Flowering and fruiting: September to February. Seedlings released: July to December.

Type from "Ad terrae Van-Leuwin littora" (Esperance Bay, W. Aust.); holotype in FI, isotype in P. Labillardiere (1807) described and illustrated Ruppia antarctica (= Amphibolis antarctica) from material collected from New Holland, but some doubt exists whether he collected the specimen himself in 1791 or whether it was part of the collections of the Baudin expedition (see Baudin 1974, and Ducker, Foord & Knox 1977, p. 70).



Fig. 30. Amphibolis antarctica. A. Rhizome with branched roots. Note leaf scars (*l.sc.*). B. Portion of erect stem with lateral branch terminating in a tuft of leaves. Note leaf scars (*l.sc.*). C. Leaf (adaxial face) showing blade (*bl.*), ligule (*l.*), auricles (*a.*) and sheath (*sh.*). D. Leaf (abaxial face) showing venation and auricles (*a.*). E. Squamules (*sq.*) in 2 groups at a node (subtending leaf removed). F. Squamules showing variation in shape. G. Young male flower at apex of lateral branch with vegetative leaves pulled apart. Note squamules (*sq.*). H. Young male flower removed from branch showing subtending bract (*br.*). I. Mature male flower showing filiform pollen grains dehiscing from junction of two loculi. Note line of dehiscence (*de.*). and bract (*br.*) J. T.S. male flower showing 2 anthers each with 2 pairs of microsporangia (*m.s.*). Note vascular bundles (*v.b.*) and microsporangial wall (*m.w.*) K. Apex of lateral branch of male plant after anthesis, showing elongated pedicel (*pe.*) of fallen male flower in leaf axil. (A-D from ADU, A52219. E, F from ADU, A51989. G, H from ADU, A52622. I-K from ADU, A51990.)



Fig. 31. Amphibolis antarctica. A. Apex of lateral branch of female plant with stigmatic branch (s.b.) projecting from between terminal vegetative leaves. B. Vegetative leaves removed (from A) to expose young female flower of two carpels and surrounding bract (br.). Note squamules (sq.) and leaf scars (l.sc). C. Female flower with bract removed (from B) to show pericarpic lobes (pc.l.) at base of carpels. D. Female flower (from C) enlarged to show two whorls of pericarpic lobes (pc.l.). E. Apex of lateral branch of female plant (with vegetative leaves removed) to expose early viviparous development of seedling. Note enlarged pericarpic lobes (pc.l.) in 2 whorls (inner whorl stippled) with a plumule (pl.) in the centre. An aborted ovary remains enveloped in the bract on the right hand side. Note stigma remnants (st.r.). F. Apex of lateral branch of female plant (from E.-with one outer pericarpic lobe cut away) showing inner whorl of pericarpic lobes (pc.l.) and developing plumule (pl.). G. Developing seedling with stalk and several leaves remaining attached to parent plant H. Seedling released from parent plant; fleshy tissue remaining on inner whorl of pericarpic lobes (pc.l.) (stippled); fleshy tissue distintegrated from outer whorl of pericarpic lobes (all except one on right hand side) exposing the bony bristles of the combs (co.) of the grappling apparatus. I. Lower part of a free-floating seedling showing leaf scars (l.sc.) and the two whorls of combs (co.) of the grappling apparatus. One lobe (lo.) of the outer whorl cut away to show the inner whorl. J. Lower part of older seedling (already attached to substrate). Note roots (rt.) developing. K. Grappling apparatus after seedling has become detached, showing outer whorl of 4 irregular lobes and remnants of inner whorl. (A-F from ADU, A51989. G, I, K from ADU, A52620. H from ADU, A52219. J from ADU, A52726.)

Distribution: From Carnarvon, W. Aust. around the southern Australian coast to Wilsons Promontory in Victoria, Bass Strait islands and the northern coast of Tasmania. It grows in sandy mud bottoms, or as patches on flat rock under conditions of moderate to fairly strong water movement, from the uppermost sublittoral zone to 23 m deep. *Amphibolis antarctica* is frequently an early coloniser in denuded areas in *Posidonia australis* meadows (Cambridge 1975, p. 157).

Selected specimens: Whitfords Beach, W. Aust., 5 m deep (Lipkin, 2.ii.1982; ADU, A52978). Pondalowie Bay, S. Aust., drift (Robertson, 19.ix.1981; ADU, A52563 and A52620). Pondalowie Bay, S. Aust., 0.5-1 m deep (Johansen, 19.ix.1981; ADU, A52622). Pondalowie Bay, S. Aust., uppermost sublittoral (Robertson, 14.xi.1981; ADU, A52726). Groper Bay, near Pondalowie Bay, S. Aust., uppermost sublittoral (Robertson, 14.xi.1981; ADU, A52726). Groper Bay, near Pondalowie Bay, S. Aust., uppermost sublittoral (Robertson, 14.xi.1981; ADU, A52726). Aldinga Beach, S. Aust., drift (Gordon-Mills, 5.vii.1981; ADU, A52219). Victor Harbor, S. Aust., 0-3 m deep (Clarke & Engler, 7.xi.1981; ADU, A51989 & and A51990 &). Kelso, Tamar Estuary, Tas., drift (H. Robertson, 5.xii.1982; ADU, A53902).

Intergrades between *A. antarctica* and *A. griffithii* are rare but some deep water (20 and 23 m) specimens from Investigator Strait, S. Aust. (*Watson*, 7.i.1971; ADU, A38428 and 9.i.1971; ADU, A38434) exhibit some characters intermediate between these two species.

When A. antarctica male flowers are shed, the shoreline adjacent to a large Amphibolis meadow may be strewn with many thousands of yellow-green empty anthers.

2. Amphibolis griffithii (J. Black) den Hartog 1970: 208, fig. 58-59. Aston 1973: 305. Green 1981: 5. Jessop 1978: 75.

Pectinella griffithii J. Black 1915: 94.

Cymodocea griffithii (J. Black) J. Black 1929: 664.

FIGS 28C, 32

Dioecious; perennial (Fig. 28C) with creeping, lignified rhizomes (1-)1.5-2 mm thick; erect stems 1-1.5 mm in diameter, branched, 0.5-1 m tall. *Roots* (1-)2 at each node, branched. *Leaves* (Fig. 32A-D) in tufts of (3-)4-5 tightly grouped together at the ends of branches; sheath (Fig. 32A,B,D) clasping, 1.5-2 cm long with the margins overlapping for most of their length; ligule and auricles vestigial; blade (Fig. 32D) (3-)5-10 cm long, 3-7 mm broad, L/B 10-15, flat, not twisted or by $45-90^{\circ}$ in the upper part; apex (Fig. 32C) deeply notched with 2 obtuse marginal teeth (marginal teeth absent in juvenile leaves of the seedling). *Squamules* (Fig. 32E,F) 1-1.5 mm long, lanceolate, in 2 groups of 2-3. *Male flower* (Fig. 32G,H) anthers 8-10(-12) mm long, with 2-3 simple or laciniate appendages (2-)3-5 mm long with or without a small laciniate bract at the base, pedicel (Fig. 32I) elongating to 5-10 mm at the time of anthesis. *Female flower* (Fig. 32J) with (0-)1-several small, filiform bracts, 1-2 mm long, at the base of the carpels, each carpel with a style 3-5 mm long and 3 stigmatic branches 10-12(-14) mm long (rarely branching), pericarpic lobes (Fig. 32J,K) 4 (2 broad and 2 narrow) in one whorl. The development of the flower and of the viviparous seedling is similar to that

Fig. 32. Amphibolis griffithii. A. Leaf (adaxial face) showing blade (bl.), sheath (sh.), auricles (a.) and ligule (l.). B. Leaf (abaxial face). C. Variation in leaf apices. D. Leaf showing venation of blade. E. Squamules (sq.) in position at node (subtending leaf removed). F. Squamules. G. Male flower at the apex of a lateral shoot (leaves pulled apart to expose anthers). H. Male flower removed from surrounding leaves showing anthers and bract (br.). I. Apex of lateral shoot on male plant after anthesis, showing elongated pedicel partly removed from sheath. J. Female flower removed from parent plant, showing pericarpic lobes (pc.l.), 2 carpels (each with 3 stigmatic branches (s.b.) and a bract (br.). K. Developing seedling viviparous on female plant, surrounded by enlarged pericarpic lobes. Note leaf scars (l.sc.) on parent plant. L. Seedling after release from parent plant. Note bony comb-like lobes (co.) of grappling apparatus. (A,B,D-F, J from ADU, A51988. C from ADU, A49414. G-I from ADU, A51986. K from ADU, A35980. L from ADU, A52621.)



of *A. antarctica.* The pericarpic lobes lose their fleshy covering, exposing the bony comb (about 5-7 mm long) of the grappling apparatus, the 2 narrow lobes with 11-15 teeth, the 2 broad lobes each with 18-26 teeth. *Seedling* (Fig. 32K,L) leaves linear, entire, at first without the notched apex of the adult leaf.

Flowering and fruiting: February to March. Seedlings released: September to February.

Lectotype from Henley Beach, S. Aust. (Griffith, 1.xi.1913); in AD, 9642217.

Distribution: From Champion Bay, W. Aust. south and eastwards to Victor Harbor, S. Aust. *A griffithii* occurs in pure stands or in mixed communities with *A. antarctica* from low tide to a depth of 5 m. Below 5 m, *A. griffithii* extends into rougher localities and tolerates lower light intensities than *A. antarctica*. Cambridge (1975) records *A. griffithii* from 40 m deep in clear oceanic water.

Selected specimens: Cliff Head, W. Aust., 1-1.5 m deep (Kirkman & Joll, 18.ix.1979; ADU, A51170). W of Tiparra reef, Spencer Gulf, S. Aust., 12 m deep (Shepherd, 27.vii.1970; ADU, A35980). Tiparra reef, Spencer Gulf, S. Aust., 15 m deep (Shepherd, 11.i.1978; ADU, A49414). Pondalowie Bay, S. Aust., drift (Robertson, 19.ix.1981; ADU, A52621). Marino, S. Aust., 2-3 m deep (Owen, Jan. 1970; ADU, A35725). Victor Harbor, S. Aust., 0-3 m deep in a sheltered cove near the Bluff (Clarke & Engler, 7.ii.1981; ADU, A51986 & and A51988 9).

FAMILY ZOSTERACEAE Dumortier, nom. cons.

Monoecious or dioecious; marine herbs with creeping perennial rhizomes, rooting at the nodes, forming extensive beds. Roots unbranched. Erect shoots annual (or sometimes possibly perennial) and producing inflorescences. Leaves with a distinct blade and sheathing base; sheath ligulate, auriculate; blade linear, flat with 3-7(-11) parallel longitudinal veins. Between the veins longitudinal striations, clearly visible in fresh or liquid preserved material, indicate diaphragms separating longitudinal air canals. Transverse vascular strands occupy some of the transverse diaphragms and these are also frequently prominent. Tannin cells absent from the leaves, but present in some other parts of the plant. Sauamules present within each leaf sheath. Prophylls present at the base of each shoot. Flowers without a perianth, arranged on one side of a flattened spike (spadix) enveloped within a modified leaf sheath (spathe), the margin of the spadix incurved and usually bearing several intramarginal lobes (retinacules); in monoecious species male and female flowers arranged alternately in 2 longitudinal rows. Male flower of one stamen consisting of 2 free, bilocular, longitudinally dehiscent anthers with a ridge-like connective; pollen filiform; pollination hydrophilous. Female flower of a unilocular ovary with one ovule, a single short style and 2 long stigmatic branches. Fruit an achene.

A family of three genera, known commonly as "eelgrasses", distributed in temperate seas of both hemispheres; two of these genera occur in southern Australia where they are known locally as "garweed".

The Zosteraceae are a clearly circumscribed group. Its members are much reduced anatomically. Lignin is virtually absent (Tomlinson, 1982, p. 423). The highly specialised arrangement of the reproductive organs is quite distinct from that of any other family.

Many instances have been noted of adventitious shoots with horizontal rhizomes arising from mature erect fertile shoots. These adventitious shoots may develop roots, become detached and act as propagules.

ZOSTERACEAE

KEY TO GENERA OF ZOSTERACEAE

- 1. Internode in transverse section showing only 2 vascular bundles in the cortex, erect shoots always developing inflorescences; retinacules triangular to suborbicular.

Genus HETEROZOSTERA (Setchell) den Hartog 1970: 114. "Garweed", "Eelgrass".

Monoecious; perennials with extensively branched rhizomes. Vegetative shoots erect, unbranched; internodes of both rhizomes and erect stems in transverse section showing 4-12 vascular bundles in the outer cortex in addition to the central vascular bundle. Leaves alternate, distichous; sheath open, ligulate, auriculate; blade linear, deciduous, leaving a senescent sheath at the node. Squamules in pairs. Fertile shoots sympodially branched, forming cymose inflorescences; spathe stalked, inflated, enclosing the stalked spadix. Male and female flowers arranged alternately in 2 longitudinal rows on the spadix; retinacules present.

Type and only species: H. tasmanica (Martens ex Ascherson) den Hartog.

Heterozostera tasmanica (Martens ex Ascherson) den Hartog 1970: 116, figs 36-38. Aston 1973: 325, figs 134-136a,b. Green 1981: 5. Jacobs & Williams 1980: 454. Jessop 1978: 73. Sainty & Jacobs 1981: 429.

Zostera tasmanica Martens ex Ascherson 1867a: 15. Setchell 1933: 816. Willis 1970: 68.

PLATE 16 fig. 4; FIGS 33, 34

Monoecious; perennial (Fig. 33A-D) with monopodially branched, herbaceous, creeping rhizomes. Rhizomes (0.5-)1.5-2(-3) mm in diameter bearing a single leaf and usually 2 roots at each node, often somewhat flexuous (Fig. 33B,C) when young and actively growing, becoming dark-brown to black and brittle with age. Roots unbranched. Vegetative shoots (Fig. 33A,B,D) erect, arising at intervals of 1-several nodes, (5-)25-40(-50) cm high; stems becoming wiry, dark-brown to black, about 1(-2) mm in diameter, bearing a tuft of leaves. Internodes of both rhizomes and erect stems in transverse section (Fig. 34A,B) showing 4-12 vascular bundles in the outer cortex. Leaves (Fig. 34C-J) 2-6(-8) per shoot; sheath (Fig. 34H-J) 1-4 cm long, open, with margins narrowly overlapping, ligule about 0.5 mm long, auricles about 1 mm long; blade linear, (10-)20-25(-35) cm long, (0.5-)1-2(-3) mm broad with 3 longitudinal veins (Fig. 34C-J), the 2 lateral ones submarginal, longitudinal air canals (Fig. 34H,I) 5-9 on each side of the midvein, transverse veins (Fig. 34H-J) at regular intervals usually continuous from the midvein to the submarginal veins; apex (Fig. 34C-G) rounded, usually deeply notched, sometimes with fine denticulations. Squamules (Fig. 34K-M) lanceolate and often dentate, two per node. Fertile shoots (Fig. 34N) erect, sympodially branched, each branch with one to a few spathes, resembling the vegetative leaves but borne on flattened stalks 5-10 mm long and sometimes connate to the axis in the lower part; spathe (Fig. 34O) 12-35 mm long, somewhat inflated and usually broader (up to 5 mm) than its blade, which is 5-10 cm long and up to 4 mm broad (frequently deciduous after flowering), spadix (Fig. 34O,P) borne on a flattened stalk 1-3(-5) mm long and bearing 3-6 male (Fig. 34Q-S) and 3-6 female flowers (Fig. 34Q,T); retinacules (Fig. 34O-Q,U) lanceolate, 1-2(-3) mm long, and 0.3-0.5 mm broad, L/B 2.5-4(-6), usually one near each male flower. Seed (Fig. 34V) ellipsoid, 2-3(-4) mm long, testa dark-brown to black, shiny, with very faint longitudinal striations.

Flowering and fruiting: September to February.

Lectotype from Port Phillip, Victoria (F. Mueller, 1866); in MEL, 2905.



Fig. 33. A-D. Heterozostera tasmanica. A. Habit (ADU, A53317) showing tufted vegetative shoots. B. Habit (ADU, A51057 from shallow water) showing young rhizome. C. Habit (ADU, A53014, from deeper water than B) and an older erect vegetative shoot. D. Habit (ADU, A53236 from Chile).

Distribution: Widely distributed around the southern Australian coast including Tasmania, from Dongara, W. Aust. to Jervis Bay, New South Wales. Records from the Sydney region are drift specimens only (Jacobs & Williams 1980, p. 453). Also known from one locality in Chile. *Heterozostera tasmanica* usually occurs subtidally (P1. 16 fig. 4) in shallow coastal waters to about 8 m deep but it has also been found in deeper, clear oceanic water (e.g. Investigator Strait, S. Aust., 31 m deep (*Watson, 13.i.1971; ADU, A38216*).

Selected specimens: Whitfords Beach, W. Aust., 5 m deep (Lipkin, 2.ii.1982; ADU, A52979). Kellidie Bay, Coffin Bay, S. Aust., 3 m deep (Womersley, 5.xii.1975; ADU, A46917). Barker Rocks, Yorke Pen., S. Aust., 0.5 m deep in pools on rock platform (Robertson, 15.xi.1981; ADU, A52725). Stenhouse Bay, S. Aust., 6-7 m deep (Hartwig, 9.iv.1982; ADU, A53014). Aldinga, S. Aust., reef pools (Skinner, 1.vi.1980; ADU, A51057). Kelso, Tamar R. estuary. Tas., uppermost sublittoral, edge of channel (H. Robertson, 12.viii.1982; ADU, A53317). Bakers Beach, just E of Port Sorell inlet, Tas., drift (H. Robertson, 14.xi.1982; ADU, A53817). Pto Aldea, Bahia Tongoy, near Coquimbo, Chile, inshore edge (Phillips, 1.v.1981; ADU, A53236).

A single sterile specimen of H. tasmanica was collected from the coast of Chile in 1864 by Phillipi. It has recently been found growing extensively in the same region (Phillips, Santelices, Bravo & McRoy 1983). A duplicate is in ADU (see Fig. 33D). Only vegetative material has been found but it appears to be the same species as that from southern Australia. This view is supported by a comparison of secondary compounds in the leaves of the Chile material with *Heterozostera* from Australia (McMillan 1983).

Den Hartog (1970) described branching of the rhizome in H. tasmanica as sympodial and used this as a diagnostic character. Tomlinson (1982) states that examination of a large population does not support this and refers to the branching as obscurely monopodial.

The erect vegetative shoots of *H. tasmanica* are usually deciduous in winter. The remaining prostrate system (Fig. 33B) then appears very similar to *Zostera muelleri* (Fig. 37B). It can be readily distinguished by cutting a transverse section through the rhizome and observing the number of lateral vascular bundles (see key to genera above and Figs 34A, 39A).

Genus ZOSTERA Linnaeus 1753: 968. "Garweed", "Eelgrass".

Monoecious; perennials with monopodially branched herbaceous rhizomes. *Rhizomes* with internodes in transverse section showing only 2 lateral vascular bundles in the cortex, one either side of the central vascular strand. *Roots* 2 per node, or arising in two groups of 1-several roots at each node. *Vegetative shoots* very short, bearing 2-6 leaves and arising laterally from the nodes. *Leaves* alternate, distichous; sheath open (in southern Australian species of subgenus *Zosterella*), margins overlapping, ligulate, auriculate; blade linear, deciduous, leaving a senescent sheath; apex variable in shape. *Squamules* in pairs (in southern Australian species). *Fertile shoots* simple or sympodially branched; spathes stalked, resembling vegetative leaves, sometimes somewhat inflated, enclosing the spadices. *Male and female flowers* arranged alternately in 2 longitudinal rows on the spadix; retinacules present (in southern Australian species), usually one near each male flower. *Seed* ovoid to ellipsoid, longitudinally striate and with numerous finer transverse striations.

Type species: Z. marina Linnaeus.

There are about 12 species widely distributed in temperate regions of both hemispheres. Three species occur in southern Australia, generally in intertidal regions on soft substrates.

All southern Australian Zostera species belong to the subgenus Zosterella which is characterised by having an open leaf sheath, and retinacules present on the spadices.

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Pollination in *Zostera* is always hydrophilous and usually takes place *below* the water surface. However pollination *on* the water surface has been recorded (e.g. den Hartog 1970, p. 12) with intertidal populations where pollen drifts to the partially exposed stigmas.

KEY TO SPECIES OF ZOSTERA

- 1. Leaf apex* more or less tridentate, with the central vein ending in a distinct mucro; roots two only at each node 1. Z. mucronata.
- - 2. Leaf apex rounded and usually more or less deeply notched, frequently with some fine denticulations; leaf blade with 3 longitudinal veins, the two lateral ones submarginal. 2. Z. muelleri
 - 2. Leaf apex truncate; leaf blade with (4-)5 longitudinal veins, the lateral ones on either side of the central vein well-spaced from the marginal veins 3. Z. capricorni
- 1. Zostera mucronata den Hartog 1970: 91, fig. 26. Aston 1973: 330. fig. 137b. Green 1981: 5. Jessop 1978: 73.

Zostera muelleri sensu Blackall & Grieve 1954: 8.

PLATE 16 fig. 5; FIGS 35, 36

Perennial (Fig. 35B) with much-branched rhizomes. *Rhizomes* 1–2 mm in diameter, internodes 0.5-1.5(-4) cm long. *Roots* (1-)2(-4) per node. *Vegetative shoots* more or less prostrate with a cluster of leaves at the apex. *Leaves* (Fig. 36A-H) 2–5 per shoot; sheath (Fig. 36A) 0.6-1.5(-5) cm long with margins overlapping, ligule very short, about 0.1(-0.2) mm long, auricles about 0.5 mm long; blade (Fig. 36A-D) linear, usually about 5 cm long (up to 20 cm long when plants permanently submerged), (0.5-)1.5–2(-2.5) mm broad with 3 longitudinal veins, the lateral ones submarginal, joining the midvein, transverse veins somewhat irregular, rarely extending unbroken from the midvein to the submarginal vein; apex (Fig. 36E-H) tridentate with the central tooth a prolongation of the central vein and always prominent in juvenile leaves, with the two lateral teeth sometimes somewhat rounded, occasional fine denticulations sometimes present. *Squamules* (Fig. 36I,J) lanceolate. *Fertile shoots* (Fig. 36K) short, 0.5-1.5 cm long, bearing 1 to a few spadices (i.e. one at each of several successive nodes), spathe 1–2 cm long on a flattened stalk (0.5-)1–3 cm long, spathal blade frequently

Fig. 34. Hetrozostera tasmanica. A. T.S. rhizome showing arrangement of vascular bundles (v.b.). B. T.S. erect stem showing arrangement of vascular bundles (v.b.). C. Juvenile leaf apices (from Baker Beach, Tas.) D. Mature leaf apices (from same plant as C). E. Leaf apices (from Kelso, Tas.). F. Leaf apices (from Barker Rocks, S. Aust.). G. Leaf apices (from Tongoy, Chile). H. Portion of leaf (adaxial view). Junction of blade and sheath (sh.) (opened out) showing ligule (l.), auricles (a.), longitudinal veins (l.v.), transverse veins (t.v.) and longitudinal diaphragms (l.d.) separating longitudinal air canals (a.c.). I. Portion of leaf (adaxial view) showing overlapping sheath margins. J. Portion of leaf (adaxial view). Junction of blade and sheath showing regular transverse veins (t,v). K. Pair of lanceolate squamules. L. Pair of squamules with dentate apices. M. Pair of squamules (sq.) at node, subtending leaf removed. N. Portion of fertile branch with 3 spathes (s.) with flattened stalks (s.s.). Note stigmatic branches (s.b.) projecting from enclosed spadices. O. Spathe (opened out) showing spadix (pulled to one side) with anthers (an.) and carpels (ca.) in position. Note retinacules (r.). P. Spadix with flowers removed showing retinacules $(r_{.})$ and anther connectives $(c_{.})$. O. Portion of spadix showing one female flower of a single carpel (ca.) and one male flower of 2 anthers (an.) next to a retinacule (r). R. Anther dehiscing longitudinally liberating filiform pollen grains. S. Male flower of 2 anthers (an.) with connective (c.). T. Female flower with 2 stigmatic branches. U. Retinacule showing line of attachment. V. Seed. (A-D, K, N-U from ADU, A53817. E from ADU, A53317. F,V from ADU, A52725. G from ADU, A53236. H-J, L,M from ADU, A46917.)

^{*} The shape of the leaf apex is a useful diagnostic character especially in juvenile leaves. It should be assessed from the whole plant and not from only one or two leaves and should be used in conjunction with other characters.





Fig. 35. Zostera mucronata. A. Portion of isotype sheet (vegetative only). B. Fertile plants (ADU, A52728). Note spadices.

falling early; spadix (Fig. 36L) subsessile, often attenuated at the apex, with 4–6 male and 4–6 female flowers; retinacules (Fig. 36M) obliquely suborbicular, frequently shortly mucronate, 1-1.5 mm broad and L/B 0.95–1.2. *Seed* (Fig. 36N) broadly ellipsoid, 1.8–2 mm long, testa brown, shiny, with 16–18 longitudinal striations and numerous finer transverse striations.



Fig. 36. A-N. Zostera mucronata. A. Portion of leaf (adaxial view). Junction of blade and sheath (sh.) (opened out) showing ligule (l.), auricles (a.), longitundinal veins (l.v.), transverse veins (t.v.) and longitudinal diaphragms (l.d.) separating the longitudinal air canals (a.c.). B. Mid-portion of leaf blade showing venation and longitudinal diaphragms (from isotype). C. Mid-portion of leaf blade showing venation and longitudinal diaphragms (from Coodanup, W. Aust.). D. Mid-portion of leaf blade (from Barker Rocks, S. Aust.). E. Leaf apices (from isotype). F. Leaf apices (from Barker Rocks, S. Aust.). G. Juvenile leaf apices (from Coodanup, W. Aust.). H. Juvenile leaf apices (from Port Lincoln, S. Aust.). I. Pair of squamules (sq.) at node (subtending leaf removed). J. Squamules. K. Portion of file plant showing 2 spathes (s.) with flattened stalks (s.s.). Note stigmatic branches (s.b.) projecting from enclosed spadices. L. Spathe opened out, with spadix pulled to one side (male and female flowers removed). Note retinacules (r.) and anther connective (c.). M. Retinacules showing line of attachment. N. Seed showing longitudinal and (in part) transverse striations. (A, I-M from ADU, A53657. B, E from isotype. C, G from ADU, A53394. D, F, N from ADU, A52724. H from ADU, A46929.)

O. Zostera mucronata-Z. muelleri intergrade (ADU, A52794 from Port Gawler, S. Aust.). Leaf apices, intermediate in shape between Z. mucronata and Z. muelleri.

Flowering and fruiting: August to February.

Type from Mandurah, W. Aust., in sandy estuary (G.G. Smith 274, 16.viii.1950); in L, isotype in PERTH.

Distribution: From the Swan River estuary, W. Aust., southwards and eastwards to Spencer Gulf and Gulf St Vincent as far as Port Clinton, S. Aust., in estuaries and on sheltered intertidal sand and mud flats, some plants permanently submerged. *Ruppia tuberosa* and *Lepilaena marina* are frequently found growing in association with Z. mucronata on sheltered intertidal flats around the South Australian coastline, e.g. at Port Clinton, S. Aust. (Pl. 16 fig. 5).

Selected specimens: Mandurah, W. Aust., in sandy estuary (G.G. Smith 274, 16.viii.1950; isotype PERTH). Coodanup Beach, Peel Inlet, W. Aust., 0.5 m deep (Carstairs, 12.ix.1982; ADU, A53394). Tulka, Port Lincoln, S. Aust., mid eulittoral (Womersley, 6.i.1976; ADU, A46929). Barker Rocks, Yorke Peninsula, S. Aust., mid eulittoral flats (Robertson, 15.xi.1981; ADU, A52724). Goldsmith Beach (near Edithburgh), S. Aust., upper sublittoral (Robertson, 14.xi.1981; ADU, A52728). Sultana Point, Edithburgh, S. Aust., intertidal (Owen, 23.xii.1969; ADU, A35723). Port Clinton, S. Aust., mid eulittoral (Robertson, 2.x.1982; ADU, A53657). Muston, American River Inlet, Kangaroo I., S. Aust., 0–0.5 m deep (O'Hazy, 13.iv.1982; ADU, A53008).

When den Hartog (1970, p. 91) described Z. mucronata only sterile material was known (see isotype photo, Fig. 35A). Fertile material which compares well with the type is now available. However, although Z. mucronata sensu stricto is well-defined, many populations in South Australia and Victoria are now known with some leaves bearing a more or less well-developed central mucro and other leaves notched [e.g. Port Gawler, S. Aust., mid eulittoral (Robertson, 16.xii.1981; ADU, A52794) (see Fig. 36O)]. It is not always possible to distinguish between Z. mucronata and Z. muelleri with these intergrades. (See further discussion under Z. muelleri.)

 Zostera muelleri Irmisch ex Ascherson 1867a: 15; 1867b: 168. Aston 1973: 322, figs 136c,d, 137a, 138. den Hartog 1970: 87, figs 24, 25. Jacobs & Williams 1980: 454. Jessop 1978: 73. Sainty & Jacobs 1981: 427. Setchell 1933: 815. Willis 1970: 67.

FIGS 37-39A-Y

Rhizomes 1–2(-3) mm in diameter, internodes 2–3(-5) cm long, in transverse section (Fig. 39A) showing only 2 vascular bundles in the outer cortex, one either side of the central strand, one leaf and 2 only, or 2–6(-10) roots in each of two groups per node. *Vegetative shoots* short, usually 1–2 cm long. *Leaves* 2–4(-5) per shoot; sheath usually about 5 cm long (up to 20 cm long in permanently submerged plants of the robust estuarine form), ligule about 0.1 mm long, auricles to 0.5 mm long; blade linear, usually 5–10 cm long (to 60 cm long when plants permanently submerged, e.g. in Onkaparinga R. estuary, S. Aust.), 1–2(-3) mm broad, longitudinal veins 3, the 2 lateral ones very close to the margin so that the leaf may appear 1-veined to the naked eye, longitudinal air canals 5–8 on each side of the midvein; apex rounded with a shallow or deep notch and frequently small denticulations. *Fertile shoots* short and bearing a single spadix (or a succession of single spadices), or 15–30 cm long (up to 60 cm in some estuarine material) and branched sympodially, bearing many spadices; spadix subsessile. *Male and female flowers* 4–12 of each per spadix; retinacules broadly triangular to suborbicular, (0.5-)1.3–1.5(-1.7) mm broad, L/B 0.7–1.4. *Seed* ellipsoid, 2.2–2.4 mm long, testa yellow-brown or brown, shiny, with 16–20 longitudinal striations and numerous finer transverse striations.

Flowering and fruiting: October to March.

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Fig. 37. A-B. Zostera muelleri sensu stricto. A. Portion of lectotype sheet (fertile). B. Habit, some plants fertile (ADU, A53901 from Kelso, Tas.). Note spadices.

Lectotype from "Australia felix"*(F. Mueller, Nov. 1852); in MEL, 3759.

Distribution: From Goldsmith Beach (near Edithburgh), Yorke Peninsula, S. Aust., eastwards around the southern Australian coast and Tasmania, and northwards to Sussex Inlet on the southern coast of New South Wales. Zostera muelleri (syn. Z. novazelandica Setchell) also occurs in New Zealand (Moore & Edgar 1970, p. 9; Moore & Irwin 1978, p. 202-3).

In southern Australia Z. *muelleri* is found in inlets and estuaries, on mud or sand in the intertidal region on calm water coasts, in lagoons separated by sandbars from the open sea, and other land-locked waters only occasionally in direct contact with the sea.

Characters such as the leaf apex shape, length and breadth of the leaf blade, the number of roots per node and the degree of branching of the fertile shoot can vary considerably. Many plants from southern Australian localities have been maintained in culture for periods of 2-12 months. These have flowered and some produced fruits and the characters given above have remained constant.

The range of material recognised as Z. *muelleri* can conveniently be divided into 2 forms which cover the same geographic region but occupy different ecological niches.

- (a) Zostera muelleri sensu stricto**
- (b) Zostera muelleri estuarine form.

(a) Zostera muelleri sensu stricto (Figs 37, 39A-O). Roots (Fig. 39B) usually only 2 at each node. Leaf blade (Fig. 39C,D) 5-10 cm long, 1-2 mm broad, 5-7 longitudinal air canals on each side of the midvein, transverse veins regular, usually continuous from the midvein to the submarginal vein, submarginal veins reaching almost to the notched leaf apex (Fig. 39E-G) before uniting with the midvein. Squamules (Fig. 39H) lanceolate. Fertile shoots short, bearing 1-few spadices (often only one apparent at a time), spathes (Fig. 39I) on flattened stalks 2-4 cm long, spadix (Fig. 39J,K) subsessile, linear-oblong, about 1(-1.5) cm long, 4-6 male flowers (Fig. 39J,L) and 4-6 female flowers (Fig. 39J,M) per spadix; retinacules (Fig. 39 J,K,N) 1.3-1.7 mm broad, L/B 0.7-1.4. Seed (Fig. 39O) ellipsoid, 2.0-2.1 mm long, testa brown, shiny, with 16-18 longitudinal striations and numerous finer transverse striations.

This form is found in inlets and sheltered bays, on sand or mud in the lower intertidal region on calm-water coasts and is normally emergent during low tide.

Selected specimens: The lectotype and Port Gawler, S. Aust., low eulittoral, tidal mud flats (*Robertson*, 16.xii.1981; ADU, A52804). Swan Bay, Port Phillip Bay, Vic., uppermost sublittoral (*Womersley*, 13.v.1982; ADU, A53087). Swan Bay, Port Phillip Bay, Vic., low eulittoral (*Shepherd*, 4.v.1980; ADU, A51059). Kelso, Tas., low eulittoral (*H. Robertson*, 5.xii.1982 and 23.i.1983; ADU, A53901 and A54000 resp.). Lagoon Bay, Low Head, Tas., low eulittoral on flats (*Womersley*, 6.xi.1982; ADU, A53970).

The lectotype (Fig. 37A) of Z. *muelleri* has short fertile shoots with spadices 1-1.3 cm long and appearing singly and not in groups, spathes short on flattened stalks about 2 cm long. The leaves are narrow with notched apices and there are only two roots per node. Plants from the intertidal region of Port Phillip Bay, Victoria and sheltered areas on the northern coast of Tasmania (Fig. 37B) compare well with the lectotype.

^{* &}quot;In November 1852, Mueller made many collections in the Port Phillip area including near the mouth of the River Yarra, which was part of "Australia felix" (see p. 78). It is this region that is assumed to be the type locality of Z. muelleri.

^{**} i.e. in a narrow, or strict sense.



Fig. 38. A-B. Zostera muelleri estuarine form. A. Habit showing erect fertile branches (ADU, A46712 from Onkaparinga R. estuary, S. Aust.). Note spadix (arrowed). B. Habit, fertile plant (ADU, A52007 from Wallagoot Lake, N.S.W.). Note spadix (arrowed). C. Zostera capricorni (ADU, A52006).

(b) Zostera muelleri estuarine form (Figs 38A,B, 39P-X). Roots (Fig. 39P) arising in two distinct groups of 2-6 (-10) at each node. Leaf blade (Fig. 39Q,R) 10-20(-60) cm long, (1.5-) 2-2.5 (-3) mm broad; 6-8 longitudinal air canals on each side of the midvein, transverse veins somewhat irregular, rarely continuing unbroken from the midvein to the submarginal vein, submarginal veins uniting with the midvein some distance from the notched leaf apex (Fig. 39S,T). Squamules (Fig. 39U) lanceolate. Fertile shoots (Fig. 38A,B) elongate, branched sympodially, bearing several spadices; spathe linear, stalked; spadix (Fig. 39V) linear, about 2.5 (-3) cm long, subsessile; 6-10 (-12) male flowers and 6-10 (-12) female flowers per spadix; retinacules (Fig. 39V,W) 0.5-1 mm broad, L/B 0.7-1.2. Seed (Fig. 39X) narrowly ellipsoid, 2.0-2.4 mm long, testa yellow-brown, shiny with 18-20 longitudinal striations and numerous finer transverse striations.

This form is usually just subtidal and rarely if ever emergent, frequently in estuarine localities, on the edge of channels or in lagoons and other land-locked waters which are only rarely in contact with the open sea.

Selected specimens: Port Gawler, S. Aust., 0.5 m deep in pools on tidal mud flats (Robertson, 16.xii.1981; ADU, A52802). Onkaparinga R. estuary, S. Aust., 0.25 m deep at edge of channel (Thomas, 11.xii.1975; ADU, A46712). Onkaparinga R. estuary, S. Aust., 0.5 m deep (Robertson, 13.x.1981; ADU, A52695). Onkparinga R. estuary, S. Aust., lowest eulittoral (Robertson, 10.xii.1981; ADU, A52783). Camp Noonameena, N. Lagoon, Coorong, S. Aust., drift (Robertson, 18.ix.1982; ADU, A53633). Mallacoota, Vic., in lagoon isolated by sandbar (Womersley, 12.xi.1982; ADU, A53978). Twofold Bay, N.S.W., in sand over mud in inlet open to bay (Jacobs 2410 and Williams, 18.xi.1975; ADU, A52009). Wallagoot Lake, N.S.W., submerged lake margin (Jacobs 2421 & Williams, 18.xi.1975; ADU, A52007).

Fig. 39. A-O. Zostera muelleri sensu stricto. A. T.S. rhizome showing arrangement of vascular bundles (v.b.) B. Portion of rhizome showing 2 roots (rt.) per node. C. Portion of leaf (adaxial view). Junction of blade and sheath (sh.) (opened out) showing ligule (l.), auricles (a.), longitudinal veins (l.v.), transverse veins (t.v.) and longitudinal diaphragms (l.d.) separating longitudinal air canals (a.c.). D. Mid portion of leaf blade showing venation and longitudinal diaphragms. E. Leaf apices (from lectotype). F. Leaf apices (from Swan Bay, Vic.). G. Leaf apices (from Kelso, Tas.). H. Pair of squamules. I. Spathe (s.) with flattened stalk (s.s.), and stigmatic branches (s.b.) projecting from enclosed spadix. J. Spadix (removed from spathe) showing 5 male flowers (anthers, (an.)), 5 female flowers (carpels, (ca.)) and 5 retinacules (r.) in position. K. Spadix (with flowers (an), 5 female flower of one carpel with 2 stigmatic branches. N. Retinacule showing line of attachment. O. Seed showing longitudinal and (in part) transverse striations. (A-D, G-N from ADU, A53901. E from lectotype. F from ADU, A51059. O from ADU, A54000.)

P-X. Zostera muelleri estuarine form. **P.** Portion of rhizome showing roots (*rt.*) arising in two groups at each node. **Q.** Portion of leaf (adaxial view). Junction of blade and sheath (*sh.*) (opened out) showing ligule (*l.*), auricles (*a.*), longitudinal veins (*l.v.*), transverse veins (*t.v.*) and longitudinal diaphragms (*l.d.*) separating longitudinal air canals (*a.c.*). **R.** Mid portion of leaf blade showing venation and longitudinal diaphragms. **S.** Leaf apices (from Onkaparinga R. estuary, S. Aust.). **T.** Leaf apices (from Mallacoota, Vic.). U. Pair of squamules. V. Spadix (with flowers removed) showing retinacules (*r.*) and anther connective (*c.*). W. Retinacule showing lines of attachment. X. Seed showing longitudinal and (in part) transverse striations. (**P.R.S.X** from ADU, A52695. **Q.U** from ADU, A52783. I from ADU, A53978. **V.W** from ADU, A46712.)

Y. Zostera muelleri intergrade between typical and estuarine forms (ADU, A52800 from Port Gawler, S. Aust.). Leaf apices.

 Z_1 - Z_4 Zostera capricorni. Z_1 Mid portion of leaf blade showing longitudinal (*l.v.*) and transverse veins (*t.v.*) and longitudinal diaphragms (*l.d.*) separating longitudinal air canals (*a.c.*). (ADU, A52352). Z_2 - Z_4 Leaf apices (ADU, A52355).



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Numerous intergrades [e.g. Port Gawler, S. Aust., mid eulittoral with mangroves (Robertson, 16.xii.1981; ADU, A52800) (see Fig. 39Y)] occur between Z. muelleri sensu stricto and the robust estuarine form and all of these are here referred to Z. muelleri sensu lato. The central mucro characteristic of Z. mucronata is also a very variable character and numerous intergrades occur between both forms of Z. muelleri and Z. mucronata. If the character of roots arising in two groups at the node is a Z. capricorni character (den Hartog 1970, pp. 64, 81), then many southern Australian populations may be intergrades between Z. capricorni and either Z. muelleri or Z. mucronata.

Between the eastern limit of Z. mucronata and the south-western limit of Z. capricorni, Z. muelleri with all its variations is the generally recognised species, and its range overlaps with Z. mucronata to the west and Z. capricorni to the east. However, within the range of Z. muelleri on the South Australian and Victorian coasts a broad spectrum of integrades occurs and further work is required to elucidate the Z. mucronata-Z. muelleri-Z. capricorni complex.

 Zostera capricorni Ascherson 1876a: 11; 1876b: 59. Aston 1973: 330, fig. 137c. den Hartog 1970: 81, figs. 21, 22. Jacobs & Williams 1980: 454. Jessop 1978: 73. Sainty & Jacobs 1981: 426.

FIGS 38C, 39Z 1.4

Perennial (Fig. 38C) with much-branched rhizomes (0.5-) 1-2 mm thick. Roots arising in 2 distinct groups of 4-8 at each node. Leaf blade linear, 7-25 (-50) cm long, 2.5-5 mm broad, longitudinal veins (Fig. 39Z₁₋₄) usually (4-) 5, with the intermediate veins usually close to the submarginal ones and well-spaced from the midvein, the submarginal veins usually uniting with the intermediate ones some distance from the apex (so that the apex may appear 3-veined), 6-8 longitudinal air canals on each side of the midvein, transverse veins usually not continuous from one longitudinal vein to the next; apex (Fig. 39Z₂₋₄) truncate. Squamules lanceolate. Fertile shoot 10-30 (-50) cm tall, sympodially branched, bearing several spadices; spathe linear, spadix subsessile, with a short mucro; male and female flowers 6-10 each per spadix; retinacules broadly triangular, 1.5-2 mm broad, L/B approximately 1. Seed ellipsoid, brown, about 2 mm long, with fine longitudinal striations and numerous very fine transverse striations.

Lectotype from Moreton Bay, Queensland (Naumann, 10.x.1875); in UC.

Distribution: Widely distributed from the tropical coast of Queensland to New South Wales and as far south as Mallacoota, Vic. There is one record from Cape Willoughby, Kangaroo I., S. Aust. Also on the coasts of Lord Howe I. and North Island, New Zealand. Z. capricorni usually occurs subtidally to about 7 m deep.

Selected specimens: Cape Willoughby, Kangaroo I., S. Aust. (Harswill 1305, Sept. 1885; MEL, 3724). Eden wharf, N.S.W., 0.5 m deep (Jacobs 2413 & Williams, 18.xi.1975; ADU, A52006). Towra Point, Botany Bay, N.S.W. 0-0.5 m deep (Robertson, 23.viii.1981; ADU, A52352). Towra Point, Botany Bay, N.S.W. uppermost sublittoral (Robertson, 23.viii.1981; ADU, A52355).

Z. capricorni is generally more robust than either Z. mucronata or Z. muelleri sensu stricto. Robust plants of the estuarine form of Z. muelleri are very similar in growth habit to Z. capricorni.

Z. capricorni is a tropical or warm temperate species and Cape Willoughby, Kangaroo Island is well beyond its normal range. The specimen, collected in 1885, has been examined and its leaf venation and apex shape certainly place it in Z. capricorni. It is not battered as would be expected if it had drifted a long distance. Unless it bears a misplaced label it would appear to be an interesting disjunct distribution. However, the species has not been re-collected from Kangaroo Island, the closest known population occurring at Mallacoota, Vic., 20 km SW of the N.S.W. border.

7. CHLOROPHYTA

Phylum CHLOROPHYTA Pascher

Thallus microscopic or macroscopic and up to about 60 cm long, free or attached, light to dark green or slightly yellowish green with chlorophylls a and b, β carotene and lutein and other xanthophylls, contained in chloroplasts of varied form but with bands of 2-6 thylakoids and usually with one to several pyrenoids, with starch as the storage reserve. Habit varying from small uninucleate unicells to colonies, filaments, foliose or tubular forms; or of larger multinucleate cells forming unbranched or branched filaments or nets; or coenocytic with no or occasional cross walls, either forming elaborate and variously branched thalli, or consisting of slender filaments entangled or compacted to form macroscopic, branched thalli. Growth intercalary or diffuse, occasionally apical. Cells with one to several chloroplasts, central or parietal, usually numerous and discoid in larger taxa. Nuclear division phragmoplastic or phycoplastic. Cell wall rigid, usually of cellulose microfibrils, in some groups of xylan or mannan, in a few taxa calcified.

Life history haplontic* (i.e. thallus haploid or gametophytic, with meiosis at the first division of the zygote nucleus), diplontic (i.e. thallus diploid with meiosis at gametogenesis) or diplohaplontic with distinct gametophyte and sporophyte generations (isomorphic or heteromorphic).

Reproduction usually by isogametes or anisogametes, occasionally by oogametes, or by amoeboid gametes; and by motile zoospores, aplanospores or akinetes. Motile zooids with two or four apical flagella of equal length (isokont) or a subapical ring of numerous flagella (stephanokontic), without hairs on the flagella.

Algae of the Chlorophyta are usually readily recognised by their colour and morphology. They occur in both fresh and marine waters, in the soil and in moist land situations (e.g. on bark of trees). Marine forms range from motile or non-motile phytoplankton cells to small epiphytic forms, and to larger benthic taxa. Most of the latter are attached to rock, but some grow anchored in mud or epiphytic on seagrasses or other algae.

This account deals only with the attached, benthic or epiphytic Chlorophyta, and does not attempt to cover the planktonic taxa which have not been investigated in South Australian seas. These motile unicells are placed in the Classes Prasinophyceae or Chlorophyceae, and Parke & Dixon (1976) recorded some 17 unicellular genera and 73 species of the former class, and 8 unicellular genera and 55 species of the latter class from Britain. There are probably several taxa in southern Australian waters.

The classification of the Chlorophyta used here is essentially that of Round (1971), which was adopted by MacRaild (1981). Reference should be made to Round and also to Bold & Wynne (1978) for a general discussion of the Chlorophyta and for orders not represented in the southern Australian benthic marine flora. Considerable changes in classification of the Chlorophyta have occurred in recent years, particularly as ultrastructural and biochemical knowledge (i.e. of nuclear division and cell wall structure) has developed, and it will probably be some time before any one classification is generally accepted. Van den Hoek (1981) reviewed the value of morphological, life history and ultrastructural features in the classification of the Chlorophyta, and Tanner (1981) discussed life histories and their variations in the orders of this phylum.

^{*} These terms are distinct from haplobiontic and diplobiontic, which refer to organisms with one or two generations in their life history.

CHLOROPHYTA

As knowledge has developed, there has been a strong tendency to elevate family groups to the rank of orders (e.g. Round 1971). Whereas some years ago the Chlorophyta were considered to include only one class, the Chlorophyceae (e.g. Papenfuss 1955, Bold & Wynne 1978), other authors (e.g. Parke & Dixon 1976) have recognised a second class, the Prasinophyceae. Round (1971) separated the latter group as a phylum, Prasinophyta, and grouped his 33 orders of the Chlorophyta as four classes, of which two (Bryopsidophyceae and Chlorophyceae) have marine representatives. However, van den Hoek (1981, p. 122) considers the class Prasinophyceae not to be justified, and comments on the bases for recognition of orders and classes in the Chlorophyta. Kornmann (1973) has since added the class Codiolophyceae for taxa with a heteromorphic life history involving a unicellular sporophyte and Christensen (1962) recognised several other classes. Stewart & Mattox (1978) placed *Ulva* and its relatives in the Class Ulvophyceae. A catalogue of the class and family names used in the Chlorophyta has been given by Silva (1980).

The account below of the Chlorophyta is based on orders, of which the Ulotrichales would be placed in the Class Codiolophyceae, coenocytic orders (Cladophorales to Caulerpales) in the Bryopsidophyceae, and the remaining uninucleate celled orders in the Chlorophyceae.

The larger benthic Chlorophyta of southern Australian coasts are now generally well known, though other species may well be found, especially in deep water collections. The remarkable *Palmoclathrus* (see below) shows that unusual taxa are still to be discovered. The small, often epiphytic or shell-boring taxa of the Ulotrichales and Chaetophorales are, however, far from adequately known and no doubt other genera will be recorded from our coasts. While the general morphology of most southern Australian Chlorophyta may be known, there are few records (and almost none in detail) of their reproduction and life history. For most widely distributed species (e.g. in the genera *Cladophora, Chaetomorpha,* and *Ulothrix)*, the information on the reproduction of the species is based largely on Northern Hemisphere studies.

KEY TO ORDERS OF CHLOROPHYTA

- 1. Thallus of small uninucleate cells, organised into filaments or foliose; or filaments of large multinucleate cells; or coenocytic and organised into thalli of various forms2

Thallus of uniseriate filaments, simple or branched. Thallus foliose or tubular, one or two cells thick; or of filaments 2 cells broad; or more or less terete, solid and 1-4 cells thick (uniseriate only in young stages)

- 4. Thallus (gametophyte) unbranched, of free filaments to 5 cm high; sporophyte unicellular and microscopic (Codiolum stage)..... ULOTRICHALES

CHLOROPHYTA

- 5. Thallus foliose (not tubular) and one cell thick; *or* filamentous and 1 to a few cells thick, 2–10 mm high, chloroplast central and somewhat stellate; diplontic with gametic meiosis in upper thallus cells or haplontic; oogamous **PRASIOLALES**

 - 6. Thallus filamentous (entangled or not); or of various macro forms; or with whorled organisation; in all cases without complete cross walls in the vegetative thallus...9

Dictyosphaena (Sh HonoclaDala

- 8. Usually isomorphic; pores of zooidangia simple; cell wall of cellulose I microfibrils in crossed sets; chloroplasts numerous, discoid to angular, forming a parietal reticulum, containing bilenticular pyrenoids; cross wall formation independent of nuclear division **CLADOPHORALES**
- 8. Usually heteromorphic, the sporophyte unicellular (*Codiolum* like); pores of zooidangia operculate or simple; cell wall with random microfibrils of cellulose II; chloroplasts continuous, parietal, perforate, containing polypyramidal pyrenoids; cross wall formation following division of many nuclei in plane of cell division

ACROSIPHONIALES

- 9. Thallus not of radial and whorled construction; cysts not formed10
- 11. Thallus simple or branched, composed of densely entwined filaments forming a medulla and a cortex of utricles bearing gametangia laterally; homoplastic, chloroplasts only present; wall containing mannan. CODIALES

ORDER TETRASPORALES Lemmermann

Thallus of small, non-motile cells of chlamydomonine structure, embedded usually without order in a gelatinous matrix, of indefinite or definite form. *Cells* uninucleate, with a single cup or plate-like chloroplast.

Reproduction by fragmentation, by zoospores or by isogametes with zygotic meiosis where known.

An order of largely fresh-water or soil taxa, probably closely related to the Volvocales.
PALMELLACEAE

FAMILY PALMELLACEAE (Endlicher) Kuetzing

Thallus of cells irregularly arranged within the gelatinous matrix; cells without individual stalks, becoming motile in some taxa under certain conditions, without pseudoflagella.

An ill-defined family, as is the type genus *Palmella*. One genus of remarkable form (*Palmoclathrus*) is known from southern Australian coasts and is tentatively placed in this family and order.

Genus PALMOCLATHRUS Womersley 1971b: 299

Thallus erect, with a discoid holdfast producing one to several erect, terete stipes each bearing a solid disc at their upper end, continuing as a cupulate, clathrate membrane. *Cells* immersed without order in the firm gelatinous matrix, uninucleate and with a large cup-shaped chloroplast, without a pyrenoid.

Reproduction unknown.

Type and only species: P. stipitatus Womersley.

Palmoclathrus stipitatus Womersley 1971b: 229, figs 1-6.

PLATE 11; FIG. 40

Thallus (Pl. 11, Fig. 40A) medium to dark green, epilithic with a spreading discoid base 1-4(-6)cm across and 1-8 erect stipes to 8 cm high and 5-10 mm in diameter, simple or occasionally branched and often with annular ridges at their upper end. *Disc* at upper end of each stalk to 2 cm across, 1-2 mm thick and solid, then continuing from its margin as a cup-shaped, perforate membrane (Fig. 40A) to 15 cm across, becoming slightly undulate and with the perforations arising marginally and reaching 5 mm in diameter away from the margin. *Structure* (Fig. 40B,C) of ovoid cells 8-10 μ m across with a single cup-shaped chloroplast without pyrenoid or eyespot, irregularly arranged (denser near the frond surfaces) in a firm gelatinous matrix. *Pigments* typical of the Chlorophyta but with almost equal amounts of chlorophyll b and chlorophyll a.

Reproduction unknown.

Type from Waldegrave I., S. Aust., 22 m deep (Shepherd, 23.x.1970; ADU, A37363).

Distribution: Known from several collections from Waldegrave Island (e.g. Branden, 25.x.1973; ADU, A44197—"Marine Algae of southern Australia" No. 144). D'Estrees Bay, Kangaroo I., S. Aust., drift (*Krafi*, 17.i.1974; ADU, A44606). 9–12 km S. of Port MacDonnell, S. Aust., 45–60 m deep (*R. K. Lewis*, 9.ix.1975, 19.x.1975 and 27.ii.1978; ADU, A46507, A46616 and A46969 respectively). Discovery Bay, Vic., 45 m deep (*Kraft*, 25.i.1977; ADU, A47990).

This remarkable alga is only known from deep water but in such localities may be common. At Waldegrave Island and off Port MacDonnell the stipes are present throughout the year but the clathrate upper parts disintegrate in winter and new ones arise in spring, becoming fully developed in summer. The stipes are thus probably perennial and their annular ridges may indicate the seasonal development of the clathrate membranes.

Palmoclathrus is provisionally placed in the Palmellaceae. It is clearly a much more highly evolved plant than other members of this group.



Fig. 40. Palmoclathrus stipitatus. A. The type sheet. B. Cross section of clathrate upper part. C. Cells in gelatinous matrix, iodine stained. (From Womersley 1971b, Figs 2, 4, 5.)

ULOTRICHACEAE

ORDER ULOTRICHALES Borzi

Thallus of slender, unbranched, uniseriate filaments. *Cells* small, uninucleate; chloroplast single, parietal, band-shaped and often somewhat lobed or slightly reticulate, usually not occupying all of the cell wall, usually with one to a few pyrenoids.

Life history heteromorphic with an erect, usually macroscopic gametophyte producing in vegetative cells biflagellate gametes (isogametes, anisogametes or oogametes) or bi- or quadriflagellate zoo(mito)spores, and a unicellular, microscopic sporophyte (Codiolum stage) producing quadriflagellate zoo(meio)spores.

The order Ulotrichales is often (e.g. Scagel 1966, p. 26; Abbott & Hollenberg 1976, p. 54) considered to include families (e.g. Chaetophoraceae, Ulvaceae) which are here recognised as separate orders, following Round (1971), Kornmann & Sahling (1977) and Bold & Wynne (1978). The only family so far recognised in the southern Australian marine flora is the Ulotrichaceae.

The Codiolum stage has often been recorded as a separate taxon, and C. kuckuckii Skottsberg & Levring ex Levring (1941, p. 604, fig. 1A) was described from the apices of branches of the brown alga Splachnidium rugosum. This latter alga is widespread in subantarctic seas and occurs in south-eastern Australia, but there is no definite record of Codiolum in Splachnidium in Australia. The "record" of Levring (1941, p. 604) was apparently a generalisation from the distribution of Splachnidium.

FAMILY ULOTRICHACEAE Kuetzing

Thallus filamentous, unbranched, basally attached or free-floating. Cells cylindrical, usually short (L/B less than 3); chloroplast single, parietal, band-shaped and usually not completely encircling the cell, with one (to a few) pyrenoids.

Reproduction by biflagellate or quadriflagellate zoospores, aplanospores, and by isogametes or anisogametes.

KEY TO GENERA OF ULOTRICHACEAE

1.	Attachment by a basal rhizoid, cells L/B about 1, filaments of uniform diameter throughout
	most of their length
1.	Attachment by a gelatinous, conical disc, cells L/B (2-)4-8(-10), filaments of increasing
	diameter aboveURONEMA

Genus ULOTHRIX Kuetzing 1833: 517

Thallus of slender unbranched filaments, basally attached by an elongate, rhizoidal cell. Cells short, usually about as long as broad; chloroplast a parietal band usually incompletely encircling the wall and often not reaching both cross walls, with one to a few pyrenoids.

Life history haplontic as far as known, with zygotic meiospores in the Codiolum stage. Reproduction of the gametophytic filamentous thallus by quadriflagellate zoospores and biflagellate isogametes, liberated through a lateral pore in the cell wall from any cell except the basal one.

Lectotype species: U. tenuissimum Kuetzing.

Only one species is currently reported from southern Australia, and its reproduction from living material has not been investigated. Other species probably occur since occasional consistently broader filaments are often present in material of *U. subflaccida*.

Ulothrix subflaccida Wille 1901: 27. Lokhorst 1978: 242, figs 18-19.

U. implexa Kuetzing sensu Womersley 1950: 141.

U. pseudoflacca Wille sensu Womersley 1956: 349.

FIG. 41 A-C

Thallus of numerous, slender, discrete filaments (Fig. 41A, B), each with a basal, elongate, tapering, rhizoidal holdfast cell, uniform in diameter throughout the length of the filament, (8-)9-11(-12) μ m in diameter, not or scarcely incised at cross walls. Cells L/B (0.5-)0.7-1 (-1.3); chloroplast encircling most of the cell (Fig. 41A) and reaching (or almost so) to cross walls, with one pyrenoid; wall thin.

Reproduction unknown in detail for Australian material, though zooids are usually present (Fig. 41C). In Europe (Lokhorst 1978, p. 244) by quadriflagellate zoo(mito)spores, aplanospores and biflagellate isogametes (2-16 per cell), filaments dioecious, and by quadriflagellate zoospores [(1-)2-4(-8) per cell] from the unicellular sporophyte stage.

Lectotype from Dröbak, Norway, in UPSV (isotypes in BM, L (920, 13... 380), LD).

Distribution: Widely distributed in marine and brackish situations of sheltered to moderate wave action, intertidal.

In southern Australia, known from American River inlet, Kangaroo I., S. Aust., on boats at water line, near jetty (*Womersley*, 26.viii.1948; ADU, A 9461; 31.viii.1950; ADU, A15399, and 18.vii.1954; ADU, A19779). Port MacDonnell, S. Aust., mid eulittoral on rocks, inside of breakwater (*Parsons & Womersley*), 5.vi.1982; ADU, A53182). Apollo Bay, Vic. just above bow water-line on boats (*Womersley*, 13.v.1982; ADU, A53176). There is no significant fresh water dilution at these localities.

The American River inlet material has been checked by Dr G.M. Lokhorst as belonging to U. subflaccida.

Genus URONEMA Lagerheim 1887: 517

Thallus of slender, unbranched filaments, each basally attached by a conical to discoid, gelatinous holdfast, filaments usually slightly to markedly increasing in diameter upwards, apical cell usually tapering. Cells mostly two to several times longer than broad, with a single chloroplast occupying most of the cell periphery, with 1-4 pyrenoids.

Life history uncertain.

Reproduction (Printz 1964, p. 34) by biflagellate and quadriflagellate zooids and by aplanospores.

Type species: U. confervicolum Lagerheim.

A genus of about 7 species (Chaudhary 1979), all from fresh water or soil.

Uronema is often regarded as scarcely distinct from Ulothrix (e.g. Fritsch 1935, p. 201) but the basal discoid attachment (not rhizoidal) and the relatively long cells appear to separate it satisfactorily (Mitra 1947; Printz 1964, pp. 6, 34; Lee 1978). In the type species and some others the terminal cell has an acuminate tip or is often somewhat asymmetric, but this is not consistently shown in some species (Mitra 1947, p. 360), nor in the Australian species described below. In some species of Uronema, the filaments are rather short compared to Ulothrix, and this applies to the Australian species.



Uronema marina Womersley sp. nov.

FIG. 41D,E

Thallus of microscopic filaments (Fig. 41D,E) to 200 (-250) μ m high, unbranched, straight to slightly curved, each arising from a basal, gelatinous, conical attachment on *Chaetomorpha* linum or *Pterocladia lucida*, forming a tomentum on the host. *Filaments* increasing in diameter from the base upwards, 4–6 μ m in diameter and L/B 4–6 in the upper cells, not or slightly incised at the cross walls; apical cells (Fig. 41D1) terete with a rounded end, becoming reproductive and soon lost, leaving wall remnants (often with bacteria) on the then apical cell; chloroplast single, occupying most of the cell but usually with invaginations at one or both ends, with a single (rarely two) prominent pyrenoid (Fig. 41 D,E); wall about 1 μ m thick, cross walls 1–2 μ m thick.

Reproduction by zooids (Fig. 41D) formed in the slightly swollen terminal cell (occasionally in the subterminal cell), with a lateral pore; terminal cell lost soon after discharge of zooids.

Diagnosis: Thallus filamenta minuta ad 200 (-250) μ m altus, simplex, rectus vel paulo recurvatus per tomentum gelatinosum conicum, basalem ad Chaetomorpha linum vel Pterocladia lucida affixus. Filamenta ex baso spissescentia, cellulae distales 4-6 μ m diametro et 4-6 plo longiores quam latae, septa parum vel non incisa; cellulae apicales teretes rotundatae primo reproductivae deinde exutae, vestigiis septorum (et saepe bacteriis) in cellula propinquo relictis. Chloroplastus simplex cellulam plerumque complens, una vel utroque extremitate vaginatus, pyrenoideis unis (rariter duobus) prominentibus; paries 1 μ m, et septa 1-2 μ m crassa.

Propagatio ope zoosporarum in cellula terminali paulum tumida (rariter in cellula subterminali) poro laterali formatorum; cellula terminalis exuta est cum zoosporae liberantur.

Type from Kellidie Bay, Coffin Bay, S. Aust., on *Chaetomorpha linum*, lower eulittoral to upper sublittoral (*Womersley*, 22.viii.1967; ADU, A31827).

Distribution: As well as the type, also known from Strickland Bay, Rottnest I., W. Aust., on *Pterocladia lucida*, 1-2 m deep (*Clarke & Engler*, 5.ix.1979; ADU, A51119).

This species is provisionally referred to Uronema, but needs to be investigated from living material.

ORDER CHAETOPHORALES Wille

Thallus of branched filaments of cells, heterotrichous with distinct prostrate basal and erect branch systems but in some genera with either system strongly reduced and in some taxa with unicellular or multicellular colourless hairs. Cells small, uninuncleate; chloroplast single, parietal, often band-shaped or lobed and not occupying all the cell wall, usually with one to a few pyrenoids.

Life history inadequately known, but haplontic and diplohaplontic types apparently occur.

Reproduction by isogametes, anisogametes or oogametes and by biflagellate or quadriflagellate zoospores.

Fig. 41. A-C. Ulothrix subflaccida. A. Upper part of filament (ADU, A15399). B. Base of filament with elongate rhizoidal cell (ADU, A15399). C. Reproductive cells with zooids (ADU, A53176). D,E. Uronema marina. D. Filament with upper cell containing zooids (ADU, A51119). D1. Terminal cell of young filament (ADU, A31827). E. Filament (ADU, A31827). F. Entocladia viridis. Thallus epiphytic on Cladophora rhizoclonioidea (ADU, A52871). G,H. Pilina novae-zelandiae. G. Thallus on Sargassum, with terminal sporangia on short erect filaments (ADU, A32003). H. Part of a long erect filament with lateral sporangia (ADU, A50870).

This order, which has frequently been placed as a family of the Ulotrichales, consists (in the marine environment) mostly of small epiphytes characterised by branched filaments showing distinct heterotrichy. Only two genera have been recorded for southern Australian coasts but others certainly occur, including some shell-boring taxa. The better known marine flora of Britain (Parke & Dixon 1976) includes 16 genera and 23 species, and that of California (Abbott & Hollenberg 1976) 8 genera and 12 species of Chaetophorales.

The two genera so far recorded from southern Australian coasts are placed in separate families, of which the second (Chroolepidaceae) appears to be inadequately characterised.

KEY TO FAMILIES OF CHAETOPHORALES

FAMILY CHAETOPHORACEAE Harvey

Thallus heterotrichous but often with the erect system strongly reduced, with or without hairs. Cells with grass-green pigments; reproductive zooids formed in normal vegetative cells.

A family of numerous genera, mostly small epiphytes or shell-boring algae. Only *Entocladia* is as yet recorded from southern Australia.

Genus ENTOCLADIA Reinke 1879: 476

Thallus minute, epiphytic or largely endophytic on or in the surface of larger algae, consisting of wholly prostrate branched filaments of cells square to rectangular or irregularly shaped in surface view and lying parallel to the host surface; filaments mostly free, sometimes forming pseudoparenchymatous layers in older parts of the thallus. *Cells* uninucleate, chloroplast single, lobed, with 1 (-2) pyrenoids; hairs occasional on some plants.

Life history sexual with isomorphic generations, or asexual only.

Reproduction by cells forming gametangia with biflagellate anisogametes and sporangia with quadriflagellate zoospores.

Type species: E. viridis Reinke.

A cosmopolitan genus with several species, and which O'Kelly & Yarish (1981) consider includes *Ectochaete* (Huber) Wille and *Epicladia* Reinke. Nielson (1979) considers *Entocladia* a synonym of *Acrochaete* Pringsheim since both genera can produce hairs, but O'Kelly & Yarish maintain *Entocladia* as having cells lying on (parallel to) the substrate whereas *Acrochaete* has cells perpendicular to the substrate. Yarish (1976) has shown that hair production is largely a response to low nutrient levels.

Entocladia viridis Reinke. Abbott & Hollenberg 1976: 64, fig. 18. Levring 1946: 216. O'Kelly & Yarish 1981: 32, figs 1-12. South 1974: 913, fig. 7. Womersley 1956: 350.

FIG. 41F

Thallus (Fig. 41F) largely within the wall of various algal hosts, consisting of radiating filaments from a central (older) part which may become pseudoparenchymatous; filaments irregularly branched, mostly separate from each other, individual filaments often extending along the cell walls of elongate hosts (e.g. *Cladophora*). Cells irregular in shape, (4-) 6-7.5 (-9) μ m in diameter, L/B 1-2 in the older part to L/B (1-) 2-3 (-4) in younger extending filaments which often have long and short cells intermixed; chloroplast lobed, with one (-2) pyrenoids.

Pilinia

Reproduction (O'Kelly & Yarish 1981) by biflagellate anisogametes and quadriflagellate zoospores.

Type from Naples, Italy (on *Derbesia* [= *Pedobesia*] *lamourouxii*); in KIEL (not located by O'Kelly & Yarish (1981, p. 33)).

Distribution: Probably cosmopolitan.

From Nora Creina and Rosetta Bay, Victor Harbor, S. Aust. "Sydney" and "Melbourne" (Levring 1946, p. 216), and observed on a variety of algae.

Selected specimens: Rosetta Bay, Victor Harbor, S. Aust., on *Enteromorpha linza*, 1 m deep (*Hone*, 20.vi.1982; ADU, A53313). Nora Creina, S. Aust., on *Cladophora rhizoclonioidea* in shaded pool (*Womersley*, 31.xii.1981; ADU, A52871).

E. viridis is probably a fairly common endophyte in the cell walls of large algae, but very few collections have been designated as such. The Nora Creina specimen agrees well with descriptions of the species from elsewhere.

FAMILY CHROOLEPIDACEAE Rabenhorst

Thallus heterotrichous with prostrate and erect systems usually well developed, without hairs. Cells with chloroplasts usually other than grass-green due to excess of carotenoid pigments (e.g. Trentepohlia, red; Pilinia, yellow-green); reproductive organs usually differentiated from vegetative cells (Papenfuss 1962, p. 9).

This family contains only a few genera and is sometimes considered to include essentially acrial algae such as *Trentepohlia*. Only the marine genus *Pilinia* is recorded from southern Australian seas.

Genus PILINIA Kuetzing 1843: 273; 1854: 20, pl. 91, fig. I

Thallus epilithic or epiphytic, with a basal stratum of radiating filaments, each cell of which produces erect filaments. *Erect filaments* without hairs and of one or two heights; a dense layer of short filaments one to 6 cells long, overtopped by scattered filaments many cells long. *Cells* elongate, chloroplast single, filling most of the cell and often somewhat lobed, with one to a few pyrenoids.

Reproduction by sporangia borne terminally on the short filaments or laterally on the long filaments, sessile or with a single-celled pedicel. Nature of zooids not recorded.

Type species: P. rimosa Kuetzing.

A genus of about nine species (see Gallagher & Humm 1980, p. 536).

The type species is discussed by Papenfuss (1962, p. 9) but a detailed study of material from the type locality (Cuxhaven, Germany) is clearly needed to establish the characters of the genus. Papenfuss considered that *Sporocladopsis* Nasr is a synonym of *Pilinia* and transferred *S. novae-zelandiae* Chapman to this genus. Other species are discussed by Gallagher & Humm (1980).

Pilinia novae-zelandiae (Chapman) Papenfuss & Fan ex Papenfuss 1962: 10. South & Adams 1976: 18.

Sporocladopsis novae-zelandiae Chapman 1949: 496, fig. 4; 1956: 433, fig. 85. Cribb 1956: 183, pl. 1 figs 1-6, pl. 2 fig. 3.

FIG. 41G,H

Thallus (Fig. 41 G,H) epiphytic on cartilaginous larger brown (and occasionally red) algae (e.g. *Ecklonia, Durvillaea, Sargassum*) forming initially small, irregularly circular patches which may later become confluent and form areas several cm across, yellow-green in colour and often drying somewhat brownish. *Basal layer* (Fig. 41G) of closely adjacent, branched, radiating

filaments adherent to the host surface, without rhizoids, with cells $3-4(-5) \mu m$ in diameter and L/B 2-4. *Erect filaments* arising from every cell of the basal filaments, without hairs; shorter filaments at first of one cell bearing a sporangium (Fig. 41 G), later becoming up to 6 cells long, simple or branched, $4-5 \mu m$ in diameter and L/B 1.5-2.5; long filaments (Fig. 41H) 0.5-1.5 mm long, unbranched or with an occasional branch, cells 6-10 μm in diameter and L/B (1.5-)2-3(-4); chloroplast single, filling most of the cell and often somewhat lobed at the ends, with one (rarely two) pyrenoids.

Reproduction with ovoid to elongate-ovoid sporangia (Fig. 41 G,H), borne terminally on the shorter erect filaments or laterally on the longer erect filaments, varying from occasional to dense (radially or often unilaterally arranged), $6-8 \ \mu m$ in diameter and $15-20 \ \mu m$ long. Zooids (8-16) liberated through a terminal pore but of unknown nature.

Type from Bay of Islands, New Zealand; in AK (Chapman).

Distribution: New Zealand.

In southern Australia, from Elliston, S. Aust. to Bridgewater Bay, Vic. and Port Arthur, Tas., on *Ecklonia radiata, Durvillaea potatorum*, and occasionally on *Macrocystis, Scytothalia, Myriodesma* and *Sargassum*.

Selected specimens: Cape Carnot, S. Aust., on Myriodesma harveyanum, sublittoral fringe (Womersley, 8.i.1951; ADU, A15109). Port Elliot, S. Aust., on Ecklonia radiata, drift (Skinner, 7.ix.1976; ADU, A 50870) and on Sargassum, drift (Woelkerling, 6.x.1967; ADU, A 32003). Pennington Bay, Kangaroo I., S. Aust., on Sargassum, sublittoral fringe (Womersley, 20.v.1945; ADU, A 2272). Bridgewater Bay, Vic., on Durvillaea potatorum, upper sublittoral (Womersley, 25.i.1967; ADU, A31769).

Pilinia novae-zelandiae is a not uncommon epiphyte on larger brown algae, but detailed study of both its reproduction and its relationships with the type species are needed. The two distinct types of erect filaments, both bearing sporangia, may be adequate to separate it generically. The record of Beanland & Woelkerling (1982, p. 94) of this species from *Avicennia* pneumatophores in Spencer Gulf applies to a different taxon.

ORDER ULVALES Blackman & Tansley

Thallus tubular, membranous and monostromatic or distromatic, or of biseriate filaments, basally attached or occasionally free floating. Cells small, uninucleate, with a single laminate or cup-chaped parietal chloroplast usually not occupying the whole cell, with one to a few pyrenoids.

Life history diplohaplontic and isomorphic; in some species only one phase present.

Reproduction by biflagellate or quadriflagellate zoospores and by biflagellate isogametes or anisogametes from unisexual or bisexual thalli, or by parthenogametes (Tanner 1981, p. 225)

This order includes the common foliose and tubular green algae of the genera Ulva and Enteromorpha (and other related genera), which are basically diplohaplontic and isomorphic in their life histories though some species apparently have lost one phase of the life history. Heteromorphic taxa (e.g. Monostroma) with a single-celled sporophyte (Codiolum stage) are considered to comprise a separate order but are not as yet recorded from southern Australia, though Chapman (1956, p. 377) records nine species from New Zealand. Prasiola is also sometimes included in the Ulvales (e.g. Bold & Wynne 1978) but is here regarded as belonging to a separate order.

Our knowledge of the species of *Ulva* and *Enteromorpha* on southern Australian coasts if not satisfactory; so far, it is morphologically based and most of the species are considered to be the same as those from Europe. Cultural and life-history studies involving crossing experiments, similar to those of Bliding (1963, 1968) on European species, are essential to give a firm knowledge of the taxa.

ULVACEAE

Chapman (1952; 1956, pp. 396, 398) described two segregate genera of Ulvaceae, *Lobata* which is based on the presence in central axial regions of enlarged cells and *Gemina* which frequently has cells in pairs. As Papenfuss (1960, p. 312) has also noted, the characters of these genera are unsatisfactory since the enlarged cells are only those forming internal rhizoids (as in most species of *Ulva*) while the pairing of cells is seen shortly after cell division. Chapman's figures of cell structure of *G. letterstedtioidea* and *G. linzoidea* are very similar to *U. rigida*.

FAMILY ULVACEAE Lamouroux

Thallus tubular, membranous, or of biseriate filaments, attached or free floating. Cells with parietal, laminate or cup-shaped chloroplasts with 1-4 pyrenoids. Life history diplohaplontic and isomorphic, but some taxa asexual.

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KEY TO GENERA OF ULVACEAE

1. Thallus of uniseriate or usually biseriate filaments, loose-lying as entangled masses PERC	URSARIA
1. Thallus tubular or membranous, usually basally attached	
 Thallus membranous, monostromatic or distromatic Thallus tubular and hollow, at least near the base and margins 	3 4
 Thallus monostromatic throughout Thallus distromatic throughout, often with rhizoids between the cell layers thallus base 	ULVARIA near the ULVA
4. Thallus with a basal, cellular attachment disc, without rhizoids, cells of the than $10\mu m$ across in surface view, chloroplast stellate with a single central statement of the statement of	hallus less 1

Genus PERCURSARIA Bory 1823: 393

Thallus unbranched, filamentous, uniseriate at first but soon becoming biseriate with two rows of rectangular cells fairly regularly arranged, at first attached by a basal disc or by rhizoids but soon becoming loose-lying. Cells uninucleate, chloroplast parietal, laminate, usually occupying only part of the cell, with 1-3 pyrenoids.

Life history diplohaplontic, isomorphic and anisogamous.

Type species: P. percursa (C. Agardh) Rosenvinge.

A genus with one widely distributed species and a second from California (Abbott & Hollenberg 1976, p. 69).

Percursaria percursa (C. Agardh) Rosenvinge. Bliding 1963, 20, figs 5, 6. Davey & Woelkerling 1980: 57. Kornmann 1956: 259, figs 1-7.

FIGS 42A, 43A, B

Thallus (Fig. 42A) of entangled, loose-lying or floating masses of unbranched filaments to several cm long, $24-32\mu$ m broad and $14-18\mu$ m thick, uniseriate at first but mostly biseriate (Fig. 43A) and one cell thick (Fig. 43B), with the cells more or less paired. *Cells* square to slightly rectangular in surface view, $10-12\mu$ m in diameter and $(8-)10-20\mu$ m long; chloroplast usually occupying less than half of the cell with (1-)2-3 pyrenoids.

Reproduction (Bliding 1963). Generations isomorphic, with quadriflagellate zoospores and biflagellate anisogametes; also by fragmentation.

Type from Hofmansgave, Denmark; in Herb. Agardh, LD, 13617.

Distribution: Widely distributed on temperate and tropical coasts, usually in sheltered bays and inlets in the upper intertidal region.

In southern Australia, from Tumby Bay, S. Aust. to Wallager Lake, N.S.W., associated with mangroves or samphires.

Selected specimens: Redcliff Point, Spencer Gulf, S. Aust., mid eulittoral on Avicennia pneumatophores (Beanland, 9.iii.1981; LTB, 12197). Fawthrop Lagoon, Portland, Vic., in shallow water (Womersley, 29.xii.1981; ADU, A52859). Port Fairy, Vic. in shallow pool amongst samphires in a salt-marsh (van den Hoek, 2.ix1981; ADU, A52661—"Marine Algae of southern Australia" No. 215). Hovells Creek, Port Phillip, Vic., mid eulittoral on Avicennia pneumatophores (Woelkerling, 12.viii.1977; LTB, 10205). Wallager Lake, N.S.W. (Cribb 80.11, 6.x.1950; ADU, A21053).

Percursaria is probably widely distributed on southern Australian coasts in shallow pools in sheltered areas such as samphire and mangrove communities.

The southern Australian material agrees well with the species, though the filaments are somewhat slenderer and the cells smaller than the dimensions given by Bliding (1963).

Genus ULVARIA Ruprecht 1851: 410

Thallus membranous, tubular when very young but soon opening out and remaining monostromatic throughout, attached by rhizoids from basal cells. Cells isodiametric to elongate; chloroplast parietal, laminate, filling part or most of the cell, with one to several pyrenoids.

Reproduction. Generations isomorphic, the sporophyte producing quadriflagellate zoo (meio) spores and gametophyte isogametes or anisogametes; *or* by biflagellate zoo (mito) spores from a single generation.

Lectotype species: U. obscura (Kuetzing) Gayral (see Bliding 1968, p. 582).

A genus of some 4 species, separated from *Monostroma* since the latter genus has a multicellular, membranous gametophyte but a single-celled (*"Codiolum* phase") sporophyte, whereas *Ulvaria* is basically isomorphic though one generation may not occur in some species. *U. oxysperma* has been made the type species of *Gayralia* Vinogradova (1969, p. 1354), but is referred to *Ulvaria* by most authors.

KEY TO SPECIES OF ULVARIA

- 1. Thallus about as broad as long, margin often ruffled; growing in intertidal habitats
- habitats
 1. U. oxysperma

 1. Thallus laciniate, forming ribbons many times longer than broad, margin smooth; from deep water habitats
 2. U. shepherdii
- 1. Ulvaria oxysperma (Kuetzing) Bliding 1968: 585, figs 31-34. Kapraun & Flynn 1973: 148, figs 15-17. Womersley 1971a, 113, fig. 1.

Monostroma oxysperma (Kuetzing) Doty 1947: 12. Kornmann 1964: 17.

FIGS 42B, 43C, D.

Thallus (Fig. 42B) light to medium green, delicate but fairly firm, somewhat shiny when partly dried, 2-8 (-12) cm high and usually as much across, irregularly foliose, often with ruffled marginal parts but usually without lobes, usually epilithic, attached by rhizoids from the basal cells (Fig. 43D); thallus 10-15 (-20) μ m thick. *Cells* (Fig. 43 C) of the expanded



Fig. 42. A. Percursaria percursa (ADU, A52661). B. Ulvaria oxysperma (ADU, A31812). C. Ulvaria shepherdii (ADU, A33006). D. Blidingia minima (ADU, A31811). E. Blidingia marginata (ADU, A21065).

blade irregularly polygonal to rounded, $7-15 \,\mu$ m across with gelatinous walls, mostly irregularly arranged but sometimes in groups or in rows; chloroplast filling most of the cell, with 1 (-2) prominent pyrenoids.

Reproduction (Bliding 1968, p. 587) by biflagellate zoospores only, formed in marginal cells of the thallus.

Type from the Baltic Sea; in L (938, 53...82a).

Distribution: Widely distributed on temperate coasts within the mid to upper culittoral, usually under sheltered conditions, and often where salinity varies considerably.

In southern Australia, from Coffin Bay, S. Aust. to Crawfish Rock, Westernport Bay, Vic., Botany Bay, N.S.W. and south-east Tasmania, usually mid eulittoral, in sheltered localities.

Selected specimens: Kellidie Bay, Coffin Bay, S. Aust., mid eulittoral (*Womersley*, 22.viii.1967; ADU, A31874—"Marine Algae of southern Australia" No. 1 b). Proper Bay, Port Lincoln, S. Aust., mid eulittoral (*Womersley*, 21.viii.1967; ADU, A31812—"Marine Algae of southern Australia No. 1a). Noonameena, Coorong, S. Aust. (*Robertson*, 27.viii.1976; ADU, A47260) Crawfish Rock, Westernport Bay, Vic., mid eulittoral (*Womersley*, 29.viii.1971; ADU, A39439). Louisville, Tas., on *Heterozostera* (*Olsen*, 6.ix.1967; ADU, A31965).

Bliding (1968, pp. 585, 590) recognizes three varieties of U. oxysperma but the differences between them appear slight.

In southern Australia, U. oxysperma is found mainly during winter (April to October) in mid eulittoral habitats.

2. Ulvaria shepherdii Womersley 1971a: 115, figs 2, 5-7.

FIGS 42C, 43E-G

Thallus (Fig. 42C) light green, delicate, 6–12 cm high, deeply lacerate into numerous linear to narrowly cuneate, straight to slightly curved, segments 2–15 (-20) mm broad with rounded to truncate ends, arising from a small, semi-prostrate region attached on the lower side by numerous slender rhizoids (Fig. 43 F,G) to 0.5 mm long; thallus 50–75 μ m thick below, decreasing to 30–40 μ m thick above. *Cells* (Fig. 43 E) in surface view polygonal with rounded to narrowly angular ends, tending to form lengthwise rows, 25–50 (-85) μ m long and 10–25 (-35) μ m broad; cells often separated by elongate slits (Fig. 43 E), some leading to laceration of the thallus; in sectional view cells (0.7-) 1–1.5 times as high as broad, walls 4–5 μ m thick; chloroplast filling most of the cell, with 3–5 pyrenoids.

Reproduction unknown.

Type from 12 km S. of Vivonne Bay, Kangaroo I., S. Aust., from craypots 50-70 m deep (*Latz*, 24.xi.1968); in ADU, A33006.

Distribution: Only known from the type and from Pearson I., S. Aust., 22-50 m deep (*Shepherd*, Jan. 1969, several collections in ADU, e.g. 10.i.1969; A34107).

U. shepherdii is provisionally placed in *Ulvaria* until its reproduction can be investigated. It appears to be confined to deep water habitats.

Fig. 43. A,B. Percursaria percursa (ADU, A52661). A. Biseriate filament, face view. B. Side view of filament. C,D. Ulvaria oxysperma (ADU, A31874). C. Cells near thallus margin. D. Lower part of thallus with cells developing attachment rhizoids. E-G. Ulvaria shepherdii (ADU, A33006). E. Cells in upper thallus. F. Lower cells with rhizoids. G. Cross section of thallus near base, with rhizoid producing cells. H,I. Blidingia minima (ADU, A53181). H. Cells in upper thallus. I. Base of thallus. J,K. Blidingia marginata (ADU, A52990). J. Cells in upper thallus. K. Base of thallus.



ULVACEAE

Genus ULVA Linnaeus 1753: 1163, nom. cons.

Thallus flat, simple or laciniate, or much branched with elongate, plane or ruffled branches, attached by a small holdfast formed by rhizoidal extensions from the lower cells which then increase in size. Blade formed of two layers of cells adherent throughout (except in germination stages less than a few mm high). *Cells* with a single chloroplast occupying normally the outer part of the cell, with 1 to 4 pyrenoids.

Life history. Most species diplohaplontic with isomorphic generations.

Reproduction. Usually anisogamous but unrecorded for species in Australia.

Type species: Ulva lactuca Linnaeus.

Ulva is a common, cosmopolitan genus, usually occurring in the lower eulittoral zone and the uppermost sublittoral. Previously, the Australian taxa (apart from U. spathulata) had been lumped into U. lactuca L. (see Womersley 1956, p. 353), but six species can be distinguished on southern Australian coasts, and U. lactuca appears to be one of the less common species. Probably other species than those discussed below occur on southern Australian coasts, especially on the south-west coasts of Western Australia.

The following treatment is based entirely on habit and structure of the thallus, following the criteria used by Bliding (1968). However, it is highly desirable that these taxonomic hypotheses should be tested by cultural and experimental crossing studies.

KEY TO SPECIES OF ULVA

- 3. Thallus usually with several fronds from near the base, without marginal spines; cells in transection of mid and lower parts of thallus L/B (1-) 1.5-2, more or less parallel sided with rounded corners but not tapering outwardly 2. U. australis
- 3. Thallus simple or branched near the base, usually with microscopic spines on areas of intact margin; cells in transection of upper parts of thallus rounded, in mid and lower parts elongate (L/B 2-3 (-5)) and tapering outwardly (to the thallus surface) 3. U. rigida

1. Ulva lactuca Linnaeus. Bliding 1968: 540, figs 1-5. Koeman & van den Hoek 1981: 31, figs 53-77. Papenfuss 1960: 303, figs 1-3, 10. Womersley 1956: 353 (in part only).

FIGS 44A, 45A-C

Thallus (Fig. 44A) grass-green, usually with a single frond from the holdfast, entire or irregularly lobed or divided, to 15 cm long and 1–10 cm across; margin entire, surface smooth. *Cells* in surface view (Fig 45A- C) in short rows becoming more irregular below, isodiametric to slightly elongate, (10-)12–18(-20) μ m across or long above, 20–25 μ m long below; pyrenoids 1–2(-3) per cell. Thallus 40–60 μ m thick in upper parts (Fig. 45A) with cells in sectional view rather square to rectangular, L/B 1.0–1.4 and 18–22 μ m long; 60–85 μ m thick in mid and lower parts (Fig. 45B) with cells in section L/B 1–1.2(-1.4) and 22–26 μ m long, becoming 75–100 (-250) μ m thick near the base with a narrow to moderately broad central mass of rhizoids (Fig. 45C).

Reproduction (Bliding 1968, p. 542). Generations isomorphic, the sporophyte producing quadriflagellate zoo(meio)spores, and the gametophytes unisexual with biflagellate anisogametes which can germinate directly to form the gametophyte again.

Type from the west coast of Sweden; in LINN.

Distribution: Recorded from most oceans; in Europe U. lactuca is a cold temperate to Arctic species, and records from warmer seas need verification.

In southern Australia, known from Christies Beach and St Kilda, S. Aust. and Port Phillip, Vic. and recorded from other scattered localities most of which require verification.

Selected specimens: Christies Beach, S. Aust., 6 m deep near sewer outfall (*Clarke & Engler*, 10.xi.1980 and 11.iii.1981; ADU, A51838 and A52029 respectively). Hobsons Bay, Port Phillip, Vic., 0-0.5 m deep at Power Station outfall (*Watson*, 1.v.1972; ADU, A42338).

U. lactuca appears to be far less common around southern Australia than U. australis, U. rigida and U. taeniata. It is characterized by a single, simple to irregularly divided and relatively thin thallus with an entire margin, and cells which in cross section are almost square (rarely with a length more than 1.5 times their breadth), fairly tightly packed and with rounded corners. These features agree well with Bliding's and Papenfuss' descriptions, although Australian material more frequently has 2(-3) pyrenoids per cell compared to the one in plants from Sweden.

2. Ulva australis Areschoug 1854: 370. J. Agardh 1883: 169. Sonder 1881: 39.

U. laetevirens Areschoug 1854: 370. J. Agardh 1883: 167. De Toni 1889: 114. May 1938: 211.

FIGS 44B, C, 45D-F

Thallus (Fig. 44B, C) dark green below, lighter above, epilithic or on seagrasses (e.g. Amphibolis), 4–20(-30) cm high, with several broad fronds from the holdfast, usually much and irregularly divided and lacerate or lobed, 1–6 cm across, margin entire, surface smooth. Cells in surface view arranged in short rows above, soon becoming irregularly arranged (Fig. 45D,E), isodiametric to elongate, 10–20 (-25) μ m broad and 20–25 (-30) μ m long, basal rhizoid-producing cells larger; pyrenoids 1 (-2) per cell. Thallus 45–60(-70) μ m thick in upper parts (Fig.45D) with cells in sectional view L/B about 1(-1.5) and 18–25 μ m long, 80–110 μ m thick in mid and lower parts (Fig.45E) with cells L/B 1.5–2(-2.5) and 22–40 μ m long, and (120-)200–250(-300) μ m thick near the base (Fig.45F) with a broad central mass of dense rhizoids, with cells L/B 1–1.5 (-2) and 25–40 μ m high.

Reproduction not recorded.

Type from Port Adelaide, South Australia, on Amphibolis antarctica; in S. The type sheet consists of four specimens.

Distribution: Common in southern Australia, on coasts of strong to moderate wave action, just above and below low tide level, from Whitfords Beach (Perth), W. Aust. to Avoca Beach, N.S.W. and around Tasmania.

Selected specimens: Whitfords Rock (Beach), Perth, W. Aust., 4-5 m deep (Lipkin, 6.ii.1982; ADU, A52961). Port Stanvac, S. Aust., 2 m deep on Amphibolis antarctica (Clarke & Engler, 22.x.1980; ADU, A51817). Rosetta Bay, Victor Harbor, S. Aust., uppermost sublittoral (Womersley, 26.x.1980; ADU, A51819). Sorrento, Vic., lower eulittoral on outer coast (Womersley, 13.i.1981; ADU, A51984). Avoca Beach, N.S.W., in lower eulittoral pools (Womersley, 18.i.1981; ADU, A51983).

U. australis was previously (Womersley 1956, p. 354) placed in synonymy with U. lactuca, but accounts of the latter species by Papenfuss (1960, p. 303, figs 1-3, 10) based largely on the type specimen, and by Bliding (1968, p. 540, figs 1-4) show that the southern Australian plant is specifically distinct. U. australis differs in habit, with several irregularly divided fronds from the base, in cell arrangement (irregular except in upper parts), in thallus thickness (greater, especially in mid and basal parts, where U. lactuca is about 40 μ m and 100 μ m thick respectively, c.f. Bliding) and in cell size where U. australis cell dimensions considerably exceed those given by Bliding for U. lactuca, both for surface view and also for sectional dimensions. The base of U. australis is more strongly developed with a much thicker central rhizoidal region than is usual in U. lactuca. J. Agardh (1883, p. 169) placed U. australis tentatively under U. rigida, and while in thickness and cell dimensions it is similar to this species, it does not have the microscopic, marginal spines of U. rigida and the cells of U. australis are more angular and do not taper outwardly in transection of the thallus.

Phycoseris ulva Sonder (1845: 49; 1846: 153) from W. Aust. (*Preiss*) may be the same as Ulva australis but the Preiss specimen in MEL (608403) does not fully agree with Sonder's description and other Preiss material should be examined.

Ulva laetevirens Areschoug, from Port Phillip, Vic., comprises two specimens in Herb. Areschoug, S; one, with a single, large, expanded and lacerate frond, has been selected as lectotype. The cells do not show the characteristics of *U. rigida* and the lectotype appears to be a large, single frond with the cell dimensions and proportions of *U. australis. U. laetevirens* was recorded from around New Zealand by Chapman (1956, p. 393).

U. australis occurs under strong to moderate water movement, whereas U. lactuca in Sweden and also as recognized in southern Australia is found in more sheltered waters. Some of the above differences might be expected between plants in rough-water and sheltered habitats, and it is highly desirable that crossing experiments be carried out between these species.

3. Ulva rigida C. Agardh 1823: 410. Bliding 1968: 546, figs 6-9. Koeman & van den Hoek 1981: 37, figs 78-107. Papenfuss 1960: 305, fig. 4.

FIGS 44D, 45G-J

Thallus (Fig. 44D) grass-green, lighter above, usually epilithic, sometimes epiphytic (e.g. on Posidonia), 10-30(-40) cm high and across, usually with a single frond from the holdfast, plane to irregularly divided or lacerate above, often perforate; intact margin in some places with slight to prominent microscopic, multicellular spines (Fig. 45G), occasionally almost entire, surface smooth. Cells in surface view in rows in both directions, more irregular below, isodiametric to slightly elongate, (8-)12-18(-25) μ m across in both upper and lower parts, with 1-2 pyrenoids (Fig. 45I, J). Thallus 35-55 μ m thick in upper parts with cells in transection rounded to avoid (Fig. 45H) and 12-18 μ m high; 80-100 μ m thick in mid parts with cells L/B 2-3, 25-35 (-40) μ m high, and usually tapering from their base (centrally in thallus) to their outer end (Fig. 45I); thallus just above rhizoidal region 100-200 μ m thick, 120-200 μ m thick near the base with cells L/B 2.5-4(-5) and 40-50 μ m long, and tapering outwardly, and with a central mass of dense rhizoids.



Fig. 44. A. Ulva lactuca (ADU, A42338). B. Ulva australis, on Amphibolis (ADU, A51817). C. Ulva australis (ADU, A51819). D. Ulva rigida (ADU, A51821).

Reproduction (Bliding 1968, p. 550) isomorphic with the sporophyte producing quadriflagellate zoo(meio)spores and the gametophytes unisexual with biflagellate anisogametes.

Type from Cadiz, Spain; in LD (Herb. Agardh, 14294).

Distribution: Widely distributed in temperate (especially warm) seas.

In southern Australia, from Hardwicke Bay, Yorke Pen., S. Aust. to Swan Bay, Vic. (probably more widely distributed), usually in sheltered to moderate wave action habitats.

Selected specimens: Hardwicke Bay, York Pen., S. Aust., in lower eulittoral pools (Womersley, 9.xi.1980; ADU, A51844). Port Stanvac, S. Aust., eulittoral pool on ramp (Engler & Clarke, 21.x.1980; ADU, A51816). Rosetta Bay, Victor Harbor, S. Aust., uppermost sublittoral (Womersley, 19.vii.1980; ADU, A51253—"Marine Algae of southern Australia" No. 216). Yilki, Victor Harbor, S. Aust., near-shore pool area (Womersley, 26.x.1980; ADU A51821).

U. rigida is characterized by the irregularly divided thallus without elongate ruffled branches, a margin with microscopic spines where it is intact (often near the base, sometimes above, and usually only evident on parts of the thallus), cells in the upper thallus rather rounded in transection and those in older parts elongate and tapering from the centre to the outside in transection.

Specimens with the above characteristics agree well with Bliding's concept of U. rigida, and this is one of the more easily recognized species of Ulva on the cell features. However, the description and illustration of the type specimen by Papenfuss (1960, p. 305, fig. 4) do not show the elongate, outwardly tapering cells of older parts of the thallus and further checking of the type specimen is needed to establish whether these features are present or not.

4. Ulva spathulata Papenfuss 1960: 209, pl. 3, fig. 15.

Letterstedtia petiolata J. Agardh 1883: 176. Chapman 1956: 384, fig. 27, pl. 24 in part. De Toni 1889: 139.

Ulva petiolata (J. Agardh) Womersley 1956: 354.

FIGS 46A, 47A-C

Thallus (Fig. 46A) medium green, epiphytic (on *Amphibolis?*) or epilithic, 5–10 cm high, divided into numerous fronds from just above a relatively massive holdfast 2–5 mm across; fronds with narrow (1–2(-3) mm broad) and long (2–4 cm) lower parts, simple or branched, with expanded, often lobed, spathulate terminal parts 1–2(-3) cm long and 0.5–1(-1.5) cm broad, intact margin entire, surface smooth. *Cells* in surface view of upper and mid parts (Fig. 47A) in rows in both directions (more irregular below), isodiametric to elongate, 10–20 μ m across, each with 1–2 pyrenoids. Thallus 70–80 μ m thick in upper spathulate parts (Fig. 47A) with cells in transection (Fig. 47A) L/B 1–1.5, rounded to angular, 15–20 μ m high; "petiolar" part (110-) 150–300 μ m thick in upper parts (Fig. 47C) with cells 10–20 μ m across in surface view, L/B 2–3 and 30–50 μ m high in transection; 300–500 μ m thick near base, with an internal layer of rhizoids usually 200–350 μ m thick below and which develops just below the spathulate terminal parts.

Reproduction unknown.

Lectotype from Port Phillip, Vic.; in Herb. Agardh, LD, 14551.

Distribution: The type locality, and from Ward I. and Point Sinclair in S. Aust., and Port Jackson and Lake Illawarra in N.S.W. Papenfuss (1960, p. 309) examined specimens from Fremantle, W. Aust. and New Zealand which he referred to this species. Chapman recorded it from throughout New Zealand.

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Fig. 45. A-C. Ulva lactuca (ADU, A52029). A. Surface and cross section views of young thallus. B. Ditto, of mid thallus. C. Ditto, rhizoidal region near base. D-F. Ulva australis (ADU, A51819). D. Surface and cross section views of young thallus. E. Ditto, of mid thallus. F. Cross section view of rhizoidal region near base. G-J. Ulva rigida (ADU, A51816). G. Thallus margin with spines. H. Cross section view of young thallus. I. Surface and cross section views of mid thallus. J. Surface view of rhizoidal region near base.

Selected specimens: Point Sinclair, S. Aust., reef surface (low eulittoral) (*Womersley*, 26.i.1951 and 8.ii.1954; ADU, A15224 and A19623 respectively). Ward I., Investigator Group, S. Aust., 25-30 m deep (*Shepherd*, 31.iii.1982; ADU, A53126).

The type sheet in LD bears 4 specimens of which the two lower ones agree well with J. Agardh's type description. The lower left specimen is designated as lectotype and the lower right (14550) is probably from the same plant. The large upper specimen (14549) is probably a different species (possibly U. rigida or U. australis) of different form, and is the only specimen which appears to be attached to the stem of Amphibolis.

U. spathulata appears to be distinctive in form, with the elongate petiolar part resulting from loss of the sides of the spathulate terminal part as this develops. However, some plants of U. australis tend to this form and the differences need further assessment. It is desirable that the development of the adult form should be followed in culture and the field.

Chapman's specimens from New Zealand need re-investigation.

 Ulva fasciata Delile 1813: 297, pl. 58, fig. 5. Dangeard 1958: 23, figs 5-8. Gayral 1963: 79. Kapraun 1970: 210, figs 1,2 41-43. Saifullah & Nizamuddin 1977: 522, pl. 1C, figs 5-7. Taylor 1960: 66, pl. 1, fig. 4.

FIGS 46B, 47D-G

Thallus (Fig. 46B) grass-green to brownish-green on drying, 20-45 cm high, with a small discoid holdfast, divided shortly above the base into numerous, simple or branched, relatively flat and smooth, elongate-lanceolate branches, each slightly to distinctly constricted basally, broadest (1-2(-4) cm) a few cm above the base and then tapering fairly evenly to a slender tip 1-4 mm broad; margin relatively smooth to slightly irregular or with occasional coarse spinous projections; surface even, in some branches with a lighter-coloured, broad central region in dried specimens. *Cells* in surface view arranged in slight, often curved rows or irregularly, isodiametric to elongate and (8-)10-13(-15) μ m across in central and upper parts of branches (Fig. 47D), (10-)12-17 μ m across in lower rhizoidal parts where rhizoid-producing cells are rounded and 16-25 μ m across (Fig. 47D); pyrenoids (1-)2-3 per cell. Thallus (70-)90-115 (-140) μ m thick in mid and upper parts (Fig. 47D,E) with cells L/B about 2 and (25-)30-45 (-50) μ m long (Fig. 47E); 100-140 μ m thick in lower parts with cells L/B 1-2 and 30-45 (-50) μ m long; and 150-250 μ m thick with cells L/B 3-4 and 35-50 μ m long where rhizoids develop and become densely aggregated as a central mass up to 100 μ m thick (Fig. 47G).

Reproduction. Gametes isogamous, also developing parthenogenetically (Kajimura 1973, p. 31).

Type from Alexandria, Egypt; in MPU.

Distribution: Widely distributed in warmer seas though probably some references to this species are doubtful.

Only known in southern Australia from Wanna (Port Lincoln), S. Aust. (Womersley, 19.ii.1959; ADU, A22338, A22437) and West Lakes (Adelaide), S. Aust. (MacFarlane, 10.xi.1980; ADU, A51836). Also from Turimetta Head, N.S.W. (King, 20.x.1976; UNSW 13873; ADU, A53995).

The collection from Wanna agrees remarkably well in morphology and cell structure with the illustrations and description of *U. fasciata* by Dangeard, based on material from Morocco. The species was recorded from southern New Zealand by Chapman (1956, p. 396).



Fig. 46. A. Ulva spathulata (ADU, A15224). B. Ulva fasciata (ADU, A22338). C. Ulva taentata (ADU, A24416).



Fig. 47. A-C. Ulva spathulata (ADU, A15224). A. Surface and cross section views of upper spathulate part. B. Surface view of petiolar region. C. Cross section of petiolar region. D-G. Ulva fasciata (ADU, A22437). D. Surface view of young part near tip. E. Cross section of mid part of thallus. F. Surface view of thallus just above rhizoidal region. G. Cross section of thallus in rhizoidal region. H-M. Ulva taeniata (ADU, A24416). H. Margin with spines. I. Cross section of thallus near margin. J. Surface of mid part of upper thallus. K. Cross section view in central part of upper thallus. L. Surface view of rhizoidal region. M. Cross section view of rhizoidal region.

Ulva taeniata (Setchell) Setchell & Gardner 1920a: 286, pl. 28; 1920b: 273, pl. 23. Abbott & Hollenberg 1976: 87, fig. 43. Chapman 1956: 387, fig. 31,I. Smith 1944: 48, pl. 3 figs 1-3.

U. fasciata f. taeniata Setchell ex Collins 1903: 10.

FIGS 46C, 47H-M

Thallus (Fig. 46C) light to medium green when living, drying darker, (10-)20-80(-175) cm long and 2-3(-5) cm broad, with a small discoid holdfast producing one to several elongate blades from shortly above the base; blades simple or occasionally branched, broadest near or somewhat above the base then tapering gradually to the tip, the sides moderately to strongly ruffled, often twisted usually with small, marginal few-celled spines (Fig. 47H). Cells in surface view arranged in short rows (Fig. 47J) or irregularly, more or less isodiametric and (7-) 10-15 μ m across in central and upper parts of the thallus, becoming 20-25 μ m across in the rhizoidal region near the base (Fig. 47L); pyrenoids 1-2 per cell, 2-3 in basal cells. Thallus in mid and upper parts 45-70 μ m thick near the margins (Fig. 47I) with cells L/B 1-2 and 20-25 μ m long; 70-125 μ m thick centrally (Fig. 47K) with cells L/B (1-)2-2.5(-3) and 25-38 μ m long; rhizoids confined to basal few mm of thallus which is then 110-160 μ m thick, cells L/B (1-)1-2(-2.5) and 35-45 μ m long, with a relatively thin central layer of rhizoids (Fig. 47M).

Reproduction. Gametes isogamous (Abbott & Hollenberg 1976, p. 87); not reported for Australian plants.

Type from Monterey, California, U.S.A.; in UC.

Distribution: Central California. New Zealand.

In southern Australia, from Elliston, S. Aust. (probably further west, possibly to Cottesloe, W. Aust.) to Walkerville, Vic. and around Tasmania, generally on rough-water rock platforms at about low tide level. The longest thalli develop where water streams over the platforms at low tide.

Selected specimens: Cottesloe, W. Aust., on reefs (Smith, Jan. 1944; ADU, A5670)—needs confirmation. Elliston, S. Aust., 4 m deep near Salmon Point (Shepherd, 22.x.1970; ADU, A37514). Yilki, Victor Harbor, S. Aust., near-shore pools (Womersley, 26.x.1980; ADU, A51822). Robe, S. Aust., upper sublittoral pools, slipway reef (Womersley, 24.viii.1960; ADU, A24416). Lauderdale, Tas. (Kingsbury, 5.ii.1980; HO, 41350).

The southern Australian specimens agree well in form and cell structure with this Californian species, which appears closely related to *U. stenophylla* Setchell & Gardner (1920a, p. 282, pl. 26 fig. 2, pl. 29). The latter species was described as without pyrenoids, but Chihara (1969, p. 858) found a pyrenoid in each cell of the type. Both Setchell & Gardner (1920b, pp. 262, 271, 273) and Abbott & Hollenberg (1976, pp. 78, 87) separate *U. taeniata* as having divided fronds from near the base and *U. stenophylla* as having simple fronds. Southern Australian specimens are usually divided near their base into 2 to several fronds and are therefore referred to *U. taeniata*, which (as a forma) is also an earlier name than *U. stenophylla*.

Juvenile forms without elongate ruffled branches are similar in habit and structure to U. *australis* and the relationships of such forms, and of U. *taeniata* and U. *australis*, on Australian coasts need further study.

Genus BLIDINGIA Kylin 1947: 181

Thallus of several to many tubular, erect fronds, simple or branched, arising from a prostrate, multicellular attachment disc, without distinct rhizoids. Cells of thallus small, mostly less than 10 μ m across; chloroplast near the outer end of the cells, lobed and usually stellate, with a single, central pyrenoid.

Life history and reproduction (Bliding 1963, p. 23) by quadriflagellate zoospores only. Sexual reproduction unknown.

Type species: B. minima (Naegeli ex Kuetzing) Kylin.

A genus of three species, widely distributed and usually intertidal, distinguished from *Enteromorpha* by the germination of the zoospores (where in most species the cell contents move to the upper cell at the first division), by the basal multicellular holdfast without rhizoids (though the cells are usually elongate), by the stellate chloroplast with a single central pyrenoid, and by the small size of the cells.

KEY TO SPECIES OF BLIDINGIA

- 1. Cells of tubular thallus arranged without order
 1. B. minima

 1. Cells of tubular thallus mostly arranged in distinct rows
 2. B. marginata
- Blidingia minima (Naegeli ex Kuetzing) Kylin 1947: 181. Abbott & Hollenberg 1976: 72, fig. 24. Bliding 1963: 23, fig. 7. Dangeard 1961: 193, figs 1,2, pls IA, IIC, D, III A-I, N-P. Scagel 1966: 42, pl. 21 C-E. Womersley 1956: 350.

Enteromorpha nana (Sommerfelt) Bliding. Chapman 1956: 412, figs 57-61.

FIGS 42D, 43H, I

Thallus (Fig. 42D) pale to medium green, usually on rock in the mid or upper eulittoral, 0.5-5 cm high and 200-1 000 μ m broad, simple or proliferous from near the base, arising from a multicellular pad-like holdfast of cells (Fig. 431) which often become elongate but not rhizoidal. *Cells* irregularly arranged throughout the thallus, angular to rounded and isodiametric, 5-8 μ m across (Fig. 43H). Chloroplast filling most of the cell and often slightly stellate, with a single central, prominent pyrenoid.

Reproduction by quadriflagellate zoo(mito)spores (Bliding 1963, p. 24).

Type from Helgoland, Germany; in L (938.69...168).

Distribution: Widely distributed in temperate regions, usually in the mid eulittoral.

In southern Australia from Proper Bay, Port Lincoln, S. Aust. to Botany Bay, N.S.W., on solid substrate in calm situations; probably more widespread.

Selected specimens: Proper Bay, Port Lincoln, S. Aust., mid eulittoral on rocks (Womersley, 21.viii.1967; ADU, A31811). American River inlet, Kangaroo I., S. Aust., mid eulittoral on jetty steps (Womersley, 17.viii.1948; ADU, A8540). Port MacDonnell, S. Aust., mid eulittoral on inside of breakwater (Womersley, 5.vi.1982; ADU, A53181).

Blidingia minima grows at the highest intertidal level of any of the enteromorphoid algae and is apparently confined to winter months.

2. Blidingia marginata (J. Agardh) P. Dangeard 1958: 59; 1961: 195, pls IB, IIA,B, III J-M. Bliding 1963: 32, figs 12, 13.

Enteromorpha marginata J. Agardh. Hamel 1930: 152, fig. 46A. E. nana var. marginata (J. Agardh) Chapman 1956: 416, fig. 63. Blidingia minima sensu Womersley 1953: 36.

shungia minima sensa wontersicy 1755. 50.

FIGS 42E, 43J,K

Thallus (Fig. 42E) grass-green, usually growing on basal stems of samphires or in shaded intertidal situations, 0.2-2 (-5) cm high and (50-) 100-300 (-1 000) μ m broad, simple or occasionally branched, arising from a multicellular pad-like holdfast of isodiametric to elongate cells (Fig. 43K). *Cells* arranged in lengthwise rows throughout the thallus (Fig. 43J), angular to rounded and mostly isodiametric, 6-8 (-9) μ m across. Chloroplast filling the cell or slightly stellate, with a single, central, prominent pyrenoid.

Reproduction by quadriflagellate zoo(mito)spores (Bliding 1963, p. 34).

Lectotype from Nice, France; in Herb. Agardh, LD (14161).

Distribution: Europe, Eastern N. America, New Zealand, in the mid to upper eulittoral zone in calm water samphire or *Juncus* communities.

In southern Australia, known from the Recherche Archipelago, W. Aust., Streaky Bay, Ardrossan and Port Adelaide and the I.C.I. saltfields, Port Adelaide, S. Aust.

Selected specimens: Coombe I., Recherche Arch., W. Aust., in shallow pools (Willis, 21.xi.1950; ADU, A15844). Ardrossan, S. Aust., mid eulittoral (Womersley, 7.iv.1950; ADU, A16080). Port Adelaide, S. Aust., mid eulittoral on mangroves, east side (Womersley, 14.vi.1957; ADU, A21065). I.C.I. saltfields, Port Adelaide, S. Aust., on stems of Sarcocornia, upper eulittoral (Gibbs-Clema, 16.xii.1981; ADU, A52990).

B. marginata is readily distinguished from *B. minima* in having the cells in well defined rows throughout the thallus. It is likely to be more widespread than indicated above, and probably confined to the lower stems of samphires and mangroves or other shaded situations.

Genus ENTEROMORPHA Link 1820: 5, nom. cons.

Thallus of simple to much branched, tubular (sometimes compressed) fronds, arising from a holdfast formed of internal rhizoidal extensions from cells near the base, occasionally loose-lying; zooids germinating first to a uniseriate filament which soon becomes tubular with a wall one cell thick, surrounding a narrow to broad cavity. Cells usually over 10 μ m across or long, arranged in rows or un-ordered; chloroplast laminate or parietal, sometimes lobed, occupying part or most of the outer part of the cell, with one to several pyrenoids.

Reproduction: generations isomorphic, or with sporophyte or gametophyte only, by biflagellate anisogametes (sometimes apogamous) and quadriflagellate (or biflagellate) zoospores.

Lectotype species: E. intestinalis (Linnaeus) Link.

A genus of numerous species, many of which are widely distributed in temperate and tropical oceans and often variable in form. The southern Australian species described below are based largely on the work of Bliding (1963) and on specimens (in ADU) of Bliding from the west coast of Sweden of several of the common species. Bliding clarified the European species, relegating many old names to synonymy, and he also described a number of new species, as has Dangeard (1958). These new species are usually based in part on cross-fertilisation experiments and morphological differences do not always clearly separate them. Some authors (e.g. Chapman 1956 for New Zealand) have described large numbers of species of *Enteromorpha*, with numerous sub-specific categories, but it is often impossible to satisfactorily relate such taxa to Bliding's concepts. Accordingly the account below refers the southern Australian taxa to the older, widely distributed, species as recognised by Bliding and should be regarded as provisional only. Detailed studies on their life-history, reproduction and interfertility, similar to those of Bliding, and also ecological studies, are needed to clarify their relationships. Notes are appended on a few species previously recorded from southern Australia but which probably do not occur here.

Enteromorpha as a genus is easily recognised by its tubular fronds and moderately large cells, and is most closely related to *Blidingia* (see under the latter for comparisons). Study of well preserved or (preferably) living material for morphological features is highly desirable, and features of taxonomic importance are:—the form of the thallus; whether the cells lie in distinct rows (of many cells) or whether they become un-ordered as seen in surface view; the size of the mature cells (not just after division) and their shape; the form of the chloroplast; and the number and relative size of the pyrenoids, usually as seen in surface view of the cells.

The distinctiveness of cell rows is often variable and needs careful assessment since most species can have short rows where active division has occurred. In some cases this is in lower parts of the thallus, in others (e.g. *E. compressa*) it may be in upper, broader parts. Further, species with normally a single pyrenoid per cell will have two just prior to cell division, and if material was collected at an active division stage, the proportion of cells with two pyrenoids will be greater; also, in cells elongate transversely to the thallus, pyrenoids in the inner part of the cell may be hidden from surface view.

Branching in some species is very variable and must be used with caution. It has not proved possible to separate the southern Australian species on branching features as has Kapraun (1970, p. 211) for species on the coast of Texas.

ULVACEAE

KEY TO SPECIES OF ENTEROMORPHA

- 3. Thallus simple (cells un-ordered) or usually branched, terete or compressed (but not with layers adherent); cells in rows or un-ordered, each with one to a few pyrenoids4
 - 4. Thallus usually branched, often proliferous; cells small to mid-sized (mostly 10-16 μm long), usually square to rectangular in surface view and in distinct longitudinal rows (less so in transverse rows); chloroplast parietal, with one large pyrenoid (20-60% of the cell width)
 4. E. prolifera
- 5. Thallus usually branched; cells mid-sized to large, usually arranged in distinct longitudinal and often in transverse rows throughout the thallus; chloroplast parietal or lateral, usually with 2-5 pyrenoids
- - 6. Thallus usually much branched; cells large, in longitudinal rows and often in transverse rows in younger parts, angular to rounded; chloroplast often lateral and lobed or dentate, leaving much of each cell clear, with (2-)3-5 pyrenoids ... 6. E. clathrata

- 1. Enteromorpha ralfsii Harvey 1850, pl. 282. Bliding 1963; 43, fig. 18.

FIGS 48A, 49A,B

Thallus (Fig. 48A) light to dark green, unbranched (rarely with short proliferations), forming entangled, loose-lying masses on mud in the mid to upper culittoral in mangrove or samphire communities; filaments of similar diameter throughout though differing considerably



Fig. 48. A. Enteromorpha ralfsii (ADU, A52642). B. Enteromorpha paradoxa (ADU, A22574). C. Enteromorpha linza (ADU, A53344). D. Enteromorpha prolifera (ADU, A14129). E. Enteromorpha flexuosa (ADU, A43697).

in different collections (Fig. 49A,B), $(35-)60-200(-250) \mu m$ thick, cavity narrow to several times as broad as cell thickness. *Cells* (Fig. 49A,B) in distinct longitudinal rows (with 3-8(-15) rows in surface view), square to rectangular, $14-20(-24) \mu m$ long and $8-14 \mu m$ broad with L/B 1-2; chloroplast filling most of the cell, with (2-)3-5 pyrenoids per cell.

Reproduction (Bliding 1963, p. 45) by quadriflagellate zoospores only.

Type from Bangor, N. Wales; lost (see Bliding 1963, p. 45).

Distribution: Britain, Europe, recorded by Chapman (1956, p. 423) from New Zealand.

In southern Australia, known from Garden I., Port Adelaide, S. Aust., mid eulittoral on mud and in depressions under mangroves (*Womersley*, 1.X.1981; ADU, A54642—"Marine Algae of southern Australia" No. 218) and from the I.C.I. saltfields, Port Adelaide, S. Aust., upper eulittoral (*Gibbs-Clema*, 2.vi.1982; ADU, A53180).

E. ralfsii is a distinctive species with its unbranched, narrow filaments of similar diameter throughout (though often differing considerably in different collections), with cells in distinct rows, and 2-5 pyrenoids per cell. The related species *E. torta* (Mertens) Reinbold, which has smaller cells and only a single pyrenoid per cell, has not been recorded from Australia.

2. Enteromorpha paradoxa (Dillwyn) Kuetzing 1845: 247; 1856, pl. 35, 1.

E. plumosa Kuetzing 1843: 300, pl. 30.

E. flexuosa sub sp. paradoxa (Dillwyn) Bliding 1963: 79, fig. 42 (Typus II).

FIGS 48B, 49C,D

Thallus (Fig. 48B) light green, very slender and flaccid, much branched and vaguely spreading, basally attached but often loose-lying in calm situations, 2–20 cm long; younger branches 20–40 μ m in diameter, bearing alternately or sometimes oppositely, numerous uniseriate branchlets (Fig. 49C) mostly 0.5–1 mm long and 10–20(-25) μ m in diameter, (4-)10–40 cells long; older axes (Fig. 49D) 50–200 μ m in diameter, central cavity narrow. *Cells* (Fig. 49C,D) in longitudinal rows and often in transverse rows, but frequently displaced, square to rectangular or polygonal in surface view, 15–40 μ m long and 10–25 μ m broad (L/B 1–2) in uniseriate branches, 40–50 μ m long and 30–40 μ m broad in lesser branches, becoming 40–70 μ m long and 30–50 μ m broad in lower axes; chloroplast parietal, not covering all of the cell wall, with numerous [4–10(-14)] small pyrenoids (Fig. 49D).

Reproduction (Bliding 1963, p. 80): generations isomorphic, gametophytes dioecious and anisogamous.

Type from Bangor, Wales.

Distribution: Probably cosmopolitan, at least in temperate seas.

In southern Australia, known from Port Lincoln, Outer Harbour and the Coorong, and American River inlet, Kangaroo I., S. Aust., where it is common in *Posidonia* beds. Probably present in most very sheltered inlets.

Selected specimens: Port Lincoln, S. Aust., on tidal flats (Womersley, 23.ii.1959; ADU, A22574). Pelican lagoon, American River inlet, Kangaroo I., S. Aust., low eulittoral (Womersley, 12.i.1950; ADU, A12933). American River inlet, Kangaroo I., S. Aust., 2–3 m deep opposite Muston (Kraft, Johnson & Wickes, 16.iv.1973; ADU, A43736).

Fig. 49. A,B. Enteromorpha ralfsii. A. Part of slender filament (ADU, A52642). B. Part of broader filament (ADU, A53180). C,D. Enteromorpha paradoxa (ADU, A43736). C. Young part of thallus. D. Older part of thallus. E-G. Enteromorpha linza (ADU, A53312). E. Surface view of cells. F. Cross section of young thallus margin. G. Cross section of older thallus margin. H. Enteromorpha prolifera (ADU, A21045). Surface view of cells.

Enteromorpha



E. paradoxa is common in very sheltered habitats and characterised by its very slender, much branched thallus with numerous uniseriate laterals. The cells in lower branches become considerably larger than in other species and usually contain numerous (6-14) small pyrenoids. This corresponds to Bliding's Typus II of subspecies *paradoxa*.

On southern Australian coasts, this taxon appears to be specifically distinct and it seems preferable to recognise it as a species rather than a subspecies of E. flexuosa as Bliding does.

3. Enteromorpha linza (Linnaeus) J. Agardh. Bliding 1939: 139, figs 4-7; 1963: 127, figs 79-81. Phillips & Clayton 1983: 11, figs 1-8. Womersley 1956: 353.

FIGS 48C, 49E-G

Thallus (Fig. 48C) medium green, surface smooth and "silky", simple, margin smooth to slightly flounced, basally attached by a small holdfast and broadening usually rapidly to a flat, cuneate to elongate blade, 2-10(-20) cm high and 2-8(-10) cm broad; stipe short, tubular; blade almost completely compressed apart from a narrow marginal cavity (Fig. 49F, G), with the two layers separated by mucilage and moderately adherent (Fig. 49F). Cells in longitudinal and often in transverse rows (Fig. 49E), often curved around growth centres, square to rectangular in surface view, (13-)16-22 μ m long and 10-16 μ m broad; chloroplast laminate, with a single prominent pyrenoid.

Reproduction by quadriflagellate zoo (mito) spores and occasionally by biflagellate zooids (Phillips & Clayton 1983, p. 15)

Type from Europe; lost.

Distribution: Widely reported in temperate seas.

In southern Australia known definitely from the localities listed below, with doubtful records from Tasmania and N.S.W.

Selected specimens: St Kilda, S. Aust., 1.5 m deep on *Posidonia (Lewis,* 23.viii.1972; ADU, A42719). Rosetta Bay, Victor Harbor, S. Aust., 0-1 m deep (*Hone,* 20.vi.1982; ADU, A53312 and 4.viii.1982; ADU, A53344). Port Phillip, Vic. (see Phillips & Clayton 1983).

Phillips & Clayton (1983) have shown that *E. linza* is often common in and near Port Phillip, Vic. and while not as common as some species of *Enteromorpha*, it is probably frequent in bays and on coasts with moderate water movement. However, many species in herbaria named as *E. linza* are complanate forms of *E. compressa*.

E. linza is distinguished by its unbranched, smooth ("silky") thallus, the fairly close adherence of the two layers with only the very margins saccate and the prominent rows of fairly large cells, each with a fairly large pyrenoid.

4. Enteromorpha prolifera (Muller) J. Agardh. Bliding 1963: 45, figs 19-23. Kapraun 1970: 214, figs 15, 16, 57-59. Womersley 1956: 353.

FIGS 48D, 49H

Thallus (Fig. 48D) light to medium green, erect from a small holdfast and often flaccid, terete or compressed, mostly 5-15 cm high and 0.5-2 cm broad, usually with frequent, proliferous branches but sometimes almost simple. *Cells* (Fig. 49H) usually arranged in longitudinal rows, often partly disrupted above, and to some extent in transverse rows, typically angular and four sided in upper thallus, 10-14 (-16) μ m long and 8-12 (-14) μ m broad, more rounded and larger in the stipe (to 25 μ m long); chloroplast occupying most of the cell, with a single, relatively large pyrenoid occupying 20-60% of the cell width (Fig. 49H).

Reproduction (Bliding 1963, p. 46): generations isomorphic, gametophytes dioecious, anisogamous.

Type from Lolland, Denmark; lost. Bliding (1963, p. 52) discusses the nomenclature of E.

prolifera and considers Herb. Agardh, LD, 13862 should be the "lectotype" of C. Agardh's understanding of the species.

Distribution: Widely distributed in temperate seas.

In southern Australia, known from the localities listed below, but probably more widespread.

Selected specimens: Onkaparinga R. estuary, 100 m from mouth, 30 cm deep (Inns & Thomas, 16.viii.1973; ADU, A43910). Altona, Vic., mid eulittoral on tidal flats (Maclennan, 7.ix.1950; ADU, A14129). Stewarts Bay, Port Arthur, Tas., 3-6 m deep (Cribb 149.21, 21.vi.1951; ADU, A21045).

E. prolifera is characterised by the regular longitudinal rows of relatively small cells which are usually angular, square or shortly rectangular, and contain a single large pyrenoid. The above specimens agree well with one of Bliding's from Sweden but are little branched. The species clearly needs further study on Australian coasts.

5. Enteromorpha flexuosa (Wulfen ex Roth) J. Agardh. Bliding 1963; 73, figs 38-41. Womersley 1956: 353.

FIGS 48E, 51A

Thallus (Fig. 48E) medium green, erect but flaccid, proliferous from near the base, 3-6 cm high and 2-8 mm broad. Cells (Fig. 51A) in longitudinal rows throughout most of the thallus and in many parts also in transverse rows, angular and square to rectangular, (10-) 14-18 μ m long and 8-12 μ m broad; chloroplast parietal, usually with 2-3 pyrenoids per cell.

Reproduction (Bliding 1963, p. 74): generations isomorphic; gametophytes dioecious and anisogamous, with apomictic development of gametes.

Type from Duino (near Trieste), Adriatic Sea; in WU (Bliding 1963, p. 74).

Distribution: Cosmopolitan?

One specimen only is referred to this species, from St Kilda, S. Aust., 1 m deep on *Posidonia australis (Johnson*, 25.v.1973; ADU, A43697). It may well be more widespread.

E. flexuosa is a branched or proliferous species characterised by having the cells in longitudinal and also in transverse rows throughout the thallus, and 2 or 3 pyrenoids in most cells. Further study of the taxon in southern Australia is clearly needed.

6. Enteromorpha clathrata (Roth) Greville. Bliding 1963: 107, figs 64-68. Kapraun 1970: 212, figs 5, 6, 60-62. Womersley 1956: 352.

FIGS 50A, 51B,C

Thallus (Fig. 50A) light to medium green, erect but often flaccid, 2-8 (-20) cm high, basally attached or becoming loose-lying, usually much and irregularly branched but often with almost simple branches from near the base, branches usually 1-3 (-5) mm broad, sometimes very slender but mostly pluriseriate. Cells (Fig. 51B) mostly in longitudinal rows but not in prominent transverse rows, square to rectangular or often rounded in surface view, 12-16 (-20) μ m long and (5-) 10-16 μ m broad; chloroplast often occupying only part of the cell in surface view and lobed or dentate, with 2-4 (-6) pyrenoids (Fig. 51C).

Reproduction (Bliding 1963, p. 108): generations isomorphic, gametophytes dioecious and slightly anisogamous; apomictic development of gametes can occur.

Type from the Baltic Sea; lost.

Distribution: Cosmopolitan.

In southern Australia, found throughout in most situations.

Selected specimens: Point Sinclair, S. Aust., mid eulittoral (Womersley, 7.ii.1954; ADU, A19584). American River inlet, Kangaroo I., S. Aust., on red buoy (Womersley, 29.vii.1947 and 17.viii.1954; ADU, A5771 and A19775 resp.). Pelican Point, Coorong, S. Aust., lagoon edge (Robertson, 26.viii.1976; ADU, A47275).

E. clathrata is a common species in calm to moderate water movement, characterised by the usually much branched thallus, cells of medium size and in longitudinal rows, and 2-4 pyrenoids per cell.

It is likely that more than one species is represented in material currently referred to E. *clathrata*, since some appear to have only one pyrenoid in many of the cells. Further studies of the "*clathrata* complex" are needed.

7. Enteromorpha compressa (Linnaeus) Greville. Bliding 1948: 128, figs 6-9, 10e-h; 1963: 132, figs 82-84. Womersley 1956: 352.

FIGS 50B, C, 51D-F

Thallus (Fig. 50B, C, 51D) medium green, 2–20(-40) cm high, erect and basally attached, usually much branched from near the base and often from above, occasionally with few basal branches only; branches broadening above, either remaining terete and 3–10(-20) mm in diameter, or commonly becoming compressed and 0.5–3(-6) cm broad, with the cell layers adjacent but not attached and the margins remaining saccate and in some forms becoming ruffled. *Cells* (Fig. 51E, F) un-ordered at least in upper stipe and lower blade, but above with mixture of un-ordered areas and patches where rows of cells have developed by localised divisions; cells polygonal to rounded, 10–14(-16) μ m across, square to rectangular when in rows; chloroplast laminate, filling most of the cell in surface view, with a single pyrenoid (two in larger cells prior to division).

Reproduction (Bliding 1963, p. 132): generations isomorphic, gametophytes dioecious, anisogamous.

Type from Hoburgen, Baltic Sea; lost (see Bliding 1963, p. 132).

Distribution: Cosmopolitan.

Throughout southern Australia, often common in shallow water and recorded to 25 m deep.

Selected specimens: Topgallant I., off Eyre Pen., S. Aust., 20-25 m deep (Shepherd, 8.xi.1980; ADU, A51882). Boston I., Port Lincoln, S. Aust., upper sublittorial (Womersley, 14.v.1968; ADU, A32508). American River inlet, Kangaroo I., S. Aust., on red buoy (Womersley, 17.viii.1954; ADU, A19774). Rosetta Bay, Victor Harbor, S. Aust., uppermost sublittoral (Womersley, 19.vii.1980; ADU, A51252—"Marine Algae of southern Australia" No. 217, and A51248—"Marine Algae of southern Australia" No. 188, as *E. linza*). Of the above specimens, A51252 has slender terete branches while others are compressed, usually (scarcely in A51882) with ruffled margins (A51248).

Two forms of *E. compressa* occur on southern Australian coasts. One (Fig. 50C) has a much branched thallus from near the base and some branches above, remaining terete and less than 1 cm broad. The other (Figs 50B, 51D) has relatively few branches from near the base and is unbranched above and strongly compressed, usually 0.5-3 cm broad, with the margins becoming strongly ruffled.

The latter form, when with very few branches from near the base, has been incorrectly placed under E. *linza* (e.g. "Marine Algae of southern Australia" No. 188). The thallus does not have prominent rows of cells throughout as does E. *linza*, the cells are smaller than in the latter species and the thallus is coarser and less delicate than the "silky" thallus of E. *linza*.

С



Fig. 50. A. Enteromorpha clathrata (ADU, A19775). B. Enteromorpha compressa, compressed and ruffled form (ADU, A51248). C. Enteromorpha compressa, terete form (ADU, A51252). D. Enteromorpha intestinalis (ADU, A10136).

ULVACEAE

Bliding (1948) separated *E. compressa* and *E. intestinalis* essentially on the basis that the former is branched and the latter unbranched. This separation needs caution in herbarium specimens where individual fronds may have been separated from the base, but nearly all the southern Australian specimens referred to *E. compressa* do have branches from near the base. Bliding (1963) also considered that *E. compressa* has cell rows in parts of the upper thallus whereas *E. intestinalis* does not. In this respect also, most southern Australian material agrees with *E. compressa*.



Fig. 51. A. Enteromorpha flexuosa (ADU, A43697). Surface view of cells. B,C. Enteromorpha clathrata (ADU, A19775). B. Surface view of cells. C. Chloroplast and pyrenoids of a single cell. D-F. Enteromorpha compressa (ADU, A51248). D. Branch of compressed, ruffled form. E. Surface view of cells of terete form (ADU, A51252). F. Surface view of cells of compressed form (A51248). G,H. Enteromorpha intestinalis (ADU, A52030). G. Surface view of cells. H. Cross section of part of thallus.

Enteromorpha

8. Enteromorpha intestinalis (Linnaeus) Link. Bliding 1948: 123, figs 2-4, 10a-d; 1963: 139, figs 87, 88.

FIGS 50D, 51G,H

Thallus (Fig. 50D) medium to dark green, erect and basally attached, 2–15 cm high, unbranched, terete and broadening above to 4–6 mm. *Cells* (Fig. 51G, H) un-ordered throughout the thallus, polygonal to rounded, $10-14(-18) \mu m$ long by (8-) $10-14 \mu m$ broad; chloroplast laminate with one (rarely two) pyrenoids.

Reproduction (Bliding 1963, p. 141): generations isomorphic, gametophytes dioecious, anisogamous.

Type locality uncertain; type probably lost.

Distribution: Cosmopolitan?

In southern Australia, from Christies Beach, S. Aust., 7 m deep on sewer outfall (*Engler & Clarke*, 11.iii.1981; ADU, A52030) and Taroona, Hobart, Tas., upper eulittoral pools (*Womersley*, 13.i.1949; ADU, A10136).

E. intestinalis is regarded by Bliding (1948; 1963, p. 139) as differing from *E. compressa* in being unbranched (except for mention of occasional proliferous brackish water specimens regarded as abnormal—see also Reed & Russell 1978) and in having the cells un-ordered throughout the thallus. On these characters, very few southern Australian specimens can be referred to *E. intestinalis* and the species clearly needs more detailed study. Of the above two specimens, A52030 is morphologically and structurally similar to var. *asexualis* Bliding (with transversely elongate cells, and thick internal membrane—Fig. 51H) and A10136 is referred to *E. intestinalis* with some doubt. The latter is unbranched but more than one frond arise from a single holdfast. Bliding in 1950 also identified a specimen from the coast at Middle River, Kangaroo I., S. Aust., in rock pools (*Womersley*, 8.i.1946; ADU, A3456) as *E. intestinalis*, but the specimens in ADU show a few basal branches and also some cell rows in the upper frond and appear better referred to *E. compressa*.

NOTES ON OTHER SPECIES (recorded in Womersley 1956, pp. 351-353).

E. acanthophora Kuetzing. As noted previously Australian specimens referred to this species are now placed under *E. clathrata*.

E. ahlneriana Bliding. This species was recorded since Bliding considered it "probably represented amongst specimens from American River inlet, Kangaroo Island." It is closely related to *E. prolifera*, differing in reproducing only by asexual zoospores. *E. ahlneriana* awaits confirmation as a southern Australian species.

E. bulbosa (Suhr) Montagne. The southern Australian specimens are now referred to E. clathrata.

ORDER PRASIOLALES Fritsch

Thallus foliose and monostromatic, or more or less terete and solid, commencing as a uniseriate filament but soon becoming 2-4 (-6) cells thick, basally attached by rhizoids. Cells small, uninucleate, in foliose taxa often arranged in square to rectangular groups separated by thicker walls, with a single somewhat stellate chloroplast containing a central pyrenoid.

Life history diplontic, with meiosis occurring in upper thallus cells prior to gamete formation; or haplontic with zygotic meiosis.

Reproduction by the contents of upper cells being liberated as non-motile mitospores and by oogamy, with eggs and sperms liberated from groups of cells in the upper thallus following meiosis.
The Prasiolales (Schizogoniales of some authors) are sometimes ranked as a family of the Ulvales (e.g. Bold & Wynne 1978, p. 177) but the life history and reproduction (see Tanner 1981, p. 220), as well as their morphology and cell structure, separate them clearly as an order. The order includes a single family, Prasiolaceae (Rabenhorst) Borzi.

Two genera, *Prasiola* and *Rosenvingiella*, are currently placed in the family, and several authors (e.g. Bravo 1965, Edwards 1975) have suggested that the latter may be only a growth form of *Prasiola*. However, southern Australian collections are of one genus or the other, apparently with no admixture, and Kornmann & Sahling (1974), Hooper & South (1977, p. 385), and Hanic (1979) have presented evidence that they are distinct genera.

Both genera occur at a high intertidal to well above tidal level, often associated with bird colonies.

KEY TO GENERA OF PRASIOLACEAE

- 1. Thallus foliose, usually 2-10 mm high, monostromatic 1. PRASIOLA

Genus PRASIOLA (C. Agardh) Meneghini 1838: 360

Thallus usually under 1 (-2) cm high, foliose, monostromatic, basally attached by rhizoids and often stipitate, usually with cells arranged in square to rectangular blocks and often in smaller groups of four; chloroplast stellate to laminate, with a central pyrenoid.

Reproduction by non-motile mitospores, and by oogametes formed following division of haploid cells derived by meiosis from upper thallus cells.

Type species: Not designated.

A genus of about 12 species (Knebel 1936), freshwater and marine, often growing above high tide level. The monostromatic, foliose blades, with cells regularly arranged in groups (from fours to large blocks) distinguish the genus.

KEY TO SPECIES OF PRASIOLA

- Prasiola stipitata Suhr in Jessen. Edwards 1975: 291, Friedmann 1959: 571, pls 1-4; 1969: 203. Hamel 1930: 17, fig. 4. Kornmann & Sahling 1977: 82, fig. 40. Taylor 1957: 75, pl. 1 figs 4-7.

FIG. 52A-C

Thallus (Fig. 52A) dark green, in masses on rock within bird colonies, individual thalli single to clustered in small tufts, (1-)2-4 mm high, with a basal holdfast and slender stipe expanding gradually or suddenly to a lanceolate, flabellate or irregularly reniform blade, with the margin often ruffled. Growth from elongate marginal cells (Fig. 52B), with cell divisions resulting in blocks of cells (Fig. 52C), with the cells in lines in both directions. Cells square to oblong in surface view, 5-10 μ m long and 3-6 μ m broad, often in groups of four; chloroplast somewhat stellate (though often occupying most of the cell) with a central pyrenoid.

Reproduction (Friedmann 1959) as for the genus.

Type from Hibernia (Ireland).

Distribution: Cold temperate N. Atlantic on both European and N. American coasts, from the upper intertidal region and above, often associated with bird colonies; Chile (Levring 1960, p. 10); New Zealand (Chapman 1956, p. 432, fig. 84).

In southern Australia, known from Lawrence Rock, Portland, Vic., approximately 30 m from sea (*Beauglehole*, 13.i.1954; ADU, A20486). Granite I., Corner Inlet (Port Welshpool), Vic., in bird colony (*Gillham*, 27.i.1959; ADU, A22606). Three Sisters I., Ulverstone, Tas., in gull colony (*Gillham*, 28.ii.1959; ADU, A22607).

The above specimens, though only 1-4 mm in height, agree well in habit and cell details with the N. Atlantic *P. stipitata*, which has also been recorded from Chile and New Zealand.

 Prasiola crispa (Lightfoot) Meneghini. Chapman 1956: 431. Gain 1912: 178. Knebel 1936: 13, figs 2-10. Newton 1931: 79. Wille 1902: 209, pl. 3 figs 1-20, pl. 4.

P. antarctica Kuetzing. Chapman 1956: 431, fig. 82. Svedelius 1900: 289, fig. 2b,c, pl. 16, figs 4,5.

FIG. 52D-F

Thallus (Fig. 52D) medium to dark brownish-green, on rock well above high tide level, individual thalli single, 2-5(-20) mm across or high, usually partly vesicular or cupulate and crisped, occasionally expanding as a relatively flat sheet, attached by a few rhizoids or slight holdfast, or free, not stipitate. Growth marginal and diffuse, margin smooth to irregular, with ill-defined blocks of cells. Cells (Fig. 52E,F) isodiametric to elongate, 3.5-7(-10) μ m across or long in surface view, often in weakly defined groups of four or more; chloroplast somewhat stellate with a central pyrenoid.

Reproduction not recorded (?).

Type from Scotland?; in BM (ex K)?

Distribution: N. Europe, Antarctic and subantarctic.

In southern Australia, known from south-east Tasmania only: Lady Bay, Southport, Tas., on rocks in bird roosting area, 3-4 m above high tide in spray zone (*Curtis*, 6.xii.1958; HO 57886; ADU, A53835 and *Womersley & Parsons*, 28.x.1982; ADU, A53837—"Marine Algae of southern Australia" No. 231). Recherche Bay, Tas., supralittoral on rocks in bird roosting area (*Womersley*, 28.x.1982; ADU, A53836).

These Tasmanian collections agree well in form and cell arrangement with *P. crispa*, which is generally accepted to include the Antarctic *P. antarctica*. It differs in form and lack of a stipitate base from *P. stipitata*, and usually consists of small, crisped plants densely aggregated on rocks where birds roost, subject to salt spray only under storm conditions. The Curtis collection, however, shows that flat sheets to 2 cm long and as much across can develop.

Genus ROSENVINGIELLA Silva 1957: 41

Thallus forming entangled mats, filiform, often irregularly constricted when older, uniseriate when young and becoming several cells thick, solid, attached by rhizoids; chloroplast stellate to laminate, with a central pyrenoid.

Reproduction. Probably by non-motile spores liberated from cells and also by gametes (Edwards 1975).

Type species: R. polyrhiza (Rosenvinge) Silva.

Rosenvingiella polyrhiza (Rosenvinge) Silva 1957: 41. Kornmann & Sahling 1974: 107, figs 5-10.

Gayella polyrhiza Rosenvinge 1893: 937, figs 45, 46. Hamel 1930: 18, fig. 5. Setchell & Gardner 1920b: 280. Womersley 1956: 355.

FIG. 52G,H

Thallus (Fig. 52G,H) light to medium green, unbranched, forming tangled masses several cm across, on soil or rock in bird colonies above high tide level; filiform and solid, uniseriate initially (12–25 μ m in diameter) and becoming irregular in thickness (30–40 μ m in diameter) depending on degree of cell division, with occasional single or often paired rhizoids (Fig. 52G). *Cells* L/B 0.2–0.5 in uniseriate parts, variable in size in older parts and often in groups of two or four (Fig. 52H), isodiametric to elongate transverse to the filament, mostly 4–6 μ m long in surface view, with a stellate to laminate chloroplast containing a central pyrenoid (Fig. 52H).

Reproduction (Edwards 1975) probably by non-motile spores and gametes; unknown for southern Australian plants.

Type from Goothalb, Greenland; in C.

Distribution: Cold temperate N. Atlantic, associated with sea bird colonies; Alaska ? (Scagel 1966, p. 70).

In southern Australia, known from Shag Rock, Pelican Lagoon, American R. inlet, Kangaroo I., S. Aust., supralittoral (*Womersley*, 27.vii.1947 and 10.i.1948; ADU, A5769 and A6729 resp.), Pennington Bay, Kangaroo I., S. Aust., supralittoral (*Womersley*, 28.vii.1947 and 23.viii.1948; ADU, A5795 and A9466 resp.), and probably (uniseriate only) Redbanks, Kangaroo I., S. Aust., upper eulittoral (*Womersley*, 25.viii.1950; ADU, A15350).

The southern Australian collections agree well with original material of Rosenvinge and with descriptions of the species.

ORDER CLADOPHORALES Haeckel

Thallus filamentous, branched or unbranched, with filaments free or laterally attached forming a complanate net, with fairly regularly placed cross walls separating multinucleate cells; cell division apical or intercalary, cross walls formed by ingrowth from the periphery, independent of nuclear divisions; chloroplasts numerous, parietal, densely packed or united into a reticulum, individual chloroplasts discoid to lenticular, many with a bilenticular pyrenoid; cell wall of crossed microfibrils of cellulose I.

Life history isomorphic, the gametophyte producing biflagellate isogametes (rarely anisogametes) and the sporophyte quadriflagellate zoo(meio)spores or biflagellate zoo(mito)spores; or by parthenogametes.

This order is marked by their large (except *Rhizoclonium*) but fairly evenly sized cells (in contrast to some Siphonocladales) with each cell containing a few (in *Rhizoclonium*) to many (*Cladophora, Chaetomorpha*) nuclei. In attached species such as those of *Cladophora* and *Chaetomorpha*, the basal cell(s) are often considerably longer than upper cells, and length of cells above the base, or along loose-lying filaments, can vary depending on when cell division has occurred.

In the family Anadyomenaceae, characterised by net formation, the cells are usually relatively small, containing only a few nuclei.

Fig. 52. A-C. Prasiola stipitata. A. Holdfast with several stipitate blades (ADU, A20486). B. Cells near margin (ADU, A22607). C. Cells within margin of thallus (ADU, A22607). D-F. Prasiola crispa (ADU, A53837). D. Habit, with slight basal attachment. E. Cells near margin. F. Cells in older part of thallus. G,H. Rosenvingiella polyrhiza (ADU, A5769). G. Largely uniseriate filament with rhizoids. H. Older multiseriate part of thallus.



KEY TO FAMILIES OF CLADOPHORALES

- 1. Thallus of unbranched or branched filaments, not laterally united to form a net
- 1. Thallus of filaments united laterally to form a net lying largely in one plane ANADYOMENACEAE

FAMILY CLADOPHORACEAE Haeckel

Thallus erect or prostrate, attached or free-living, of free uniseriate filaments, branched or unbranched, with apical and usually few to many intercalary divisions resulting in most genera in cells of more or less similar length (though often basally longer in erect species) but of irregular length in *Cladophoropsis*; branching when present usually from the upper ends of cells; attaching rhizoids from the lower poles of basal or suprabasal cells. Chloroplasts numerous and densely packed or forming a reticulum, some chloroplasts containing a bilenticular pyrenoid.

Life history isomorphic.

Reproduction by biflagellate gametes and from sporophyte by quadriflagellate or biflagellate zoospores; in some species asexual only.

Species of Cladophoraceae are common on most southern Australian coasts, usually in shallow water or the lower eulittoral. Most are easily recognised as members of this family but the slender, small-celled species of *Rhizoclonium* may be confused with the uninucleate celled, unbranched, filaments of *Ulothrix* (which differs in chloroplast structure and is basally attached). Entangled species of *Cladophora* may be confused with *Cladophoropsis*, which has relatively few and more irregularly placed cross walls and does not have basal cross walls to the laterals.

KEY TO GENERA OF CLADOPHORACEAE

- - 2. Filaments slender, less than 60 μ m in diameter, with (or occasionally without) short, rhizoidal laterals; loose-lying, forming entangled mats or strands RHIZOCLONIUM

Genus RHIZOCLONIUM Kuetzing 1843: 261

Thallus of slender (10-45 μ m in diameter) filaments forming entangled masses, unbranched apart from occasional to frequent, short, lateral rhizoidal branches. Cells cylindrical, L/B usually 1-8, with 1-4 nuclei and a parietal, reticulate (loose to dense) chloroplast with few to several pyrenoids.

Reproduction by biflagellate isogametes and quadriflagellate zoospores, diplohaplontic with isomorphic generations (not recorded for Australian material).

Type species: R. jürgensii Kuetzing (= *R. riparium* (Roth) Harvey 1849: pl. 238). See Koster 1955, p. 341.

The Australian species of *Rhizoclonium* need detailed revision, from living field material and culture studies. They are not uncommon in mangrove communities and other shaded, intertidal habitats in calm bays and inlets, forming mats or felts on the substrate or on the lower parts of mangroves. Four species are recognised below, but others may well occur. *R. riparium* and *R. implexum* are usually recognised as distinct species but some authors (e.g. Nienhuis 1974) include the latter under *R. riparium*.

Some species of *Rhizoclonium* have been placed in *Lola* Hamel & Hamel by Chapman (1956, p. 463) and Zaneveld (1966, p. 47). *Lola* is based on *R. lubricum* Setchell & Gardner and is distinguished by its sexual reproduction by anisogametes. The nature of the gametes of other species appears not to have been described and *Lola* is used by Chapman (1956, p. 462) as a borderline genus between *Chaetomorpha* and *Rhizoclonium*. It seems best, as most authors have done, not to recognise *Lola* but place the slenderer species (often with lateral rhizoids) in *Rhizoclonium* and broader species (without such rhizoids) in *Chaetomorpha*.

KEY TO SPECIES OF *RHIZOCLONIUM*

1.	Cells of filaments	usually L/B	2 or greater	, rhizoids absent or	occasional	2
1.	Cells of filaments	usually L/B	less than 2,	rhizoids occasional	to frequent	3

- Filaments straight to irregularly curved, rhizoids irregularly placed, filament diameter 16-22 μm
 R. riparium
- Filaments regularly curved between rhizoids at more or less regular intervals, filament diameter 24-32 μm
 R. curvatum
- Rhizoclonium implexum (Dillwyn) Kuetzing. Abbott & Hollenberg 1976: 92, fig. 45. Cribb 1965: 264. Koster 1955: 343, fig. 2. Scagel 1966: 73, pl. 33A,B. *R. kochianum* Kuetzing. Bliding 1957: 271, figs 1, 2.

FIG. 53A

Thallus light green, forming thin mats or strands of entangled filaments to 10 cm long in eulittoral, usually shaded, calm-water habitats (e.g. on sandy mud or mangroves). Filaments (Fig. 53A) unbranched, usually without but rarely with occasional lateral rhizoids of 1-2 cells,

occasionally with filament ends tapering into a rhizoid. Cells (14-)16-22(-24) μ m in diameter, L/B (2-)3-5(-6), wall about 2 μ m thick, 2-4 nuclei per cell; chloroplast reticulate with several to numerous pyrenoids.

Reproduction not reported for Australian plants. Elsewhere, by biflagellate isogametes and quadriflagellate zoospores.

Type from Bantry, Eire (Hutchins); in BM (ex K).

Distribution: Cosmopolitan.

In southern Australia, known from Venus Bay, S. Aust., lower eulittoral (*Womersley*, 13.ii.1954; ADU, A19481). Kellidie Bay, Coffin Bay, S. Aust., low eulittoral (*Womersley*, 22.viii.1967; ADU, A31821). Port Wakefield, S. Aust., mid eulittoral in samphires (*Womersley*, 26.iii.1950; ADU, A13021). Thompson Creek, St Kilda, S. Aust., upper eulittoral on Sarcocornia (*Gibbs-Clema*, 25.iii.1982; ADU, A52995). Cockle Bank, American River inlet, Kangaroo I., S. Aust., uppermost sublittoral (*Womersley*, 6.i.1948; ADU, A8400). Portland Bay, Vic., low eulittoral (*Muir*, Jan. 1950; ADU, A15789). Probably widespread in sheltered localities along southern Australia. Beanland & Woelkerling (1982, p. 100) have recorded *R. implexum* from several localities in Spencer Gulf.

Koster (1955) investigated type and other material of R. *implexum* and included R. *kochianum* as a synonym. R. *implexum* appears to be distinct from R. *riparium* though sometimes (e.g. Nienhuis 1974) included under the latter.

Rhizoclonium tortuosum (Dillwyn) Kuetzing. Chapman 1939: 20. Setchell & Gardner 1920b: 185.

Conferva tortuosa Dillwyn 1809, pl. 46. Harvey 1846: pl. 54A, R. riparium f.validum Foslie. Koster 1955: 351.

FIG. 53B, C

Thallus light to medium green, forming mats of entangled filaments in shaded, upper eulittoral, calm-water habitats. Filaments (Fig. 53C) unbranched, in some cases without but in other material with lateral, 1-5 celled, rhizoids (Fig. 53B). Cells (23-)25-40(-45) μ m in diameter, L/B (1.5-)2-3(-4), wall 3-5(-8) μ m thick; chloroplast moderately to densely reticulate with numerous pyrenoids.

Reproduction unknown for Australian (or European?) plants.

Type from Yarmouth, England; in BM (see Chapman 1939, p. 21).

Distribution: Europe, Britain, N. America, New Zealand; probably widely distributed.

In southern Australia, known from Picnic Point, American R. inlet, Kangaroo I., S. Aust., upper eulittoral *(Womersley,* 30.viii.1950; ADU, A15398) and from Thompson Creek, St Kilda, S. Aust., upper eulittoral on lower stems of *Sarcocornia (Gibbs-Clema,* 25.iii.1982; ADU, A52994). The first of these collections has fairly frequent rhizoids 3–5 cells long, while the second is without rhizoids. They are referred to *R. tortuosum* on cell dimensions but require further study.

R. tortuosum is sometimes included under *R. riparium*, which is then considered to be variable in cell diameter (e.g. Koster 1955, p. 351; Scagel 1966, p. 74). The southern Australian specimens appear distinct from the slenderer *R. riparium* or *R. implexum*.

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Fig. 53. A. Rhizoclonium implexum (ADU, A52995). B,C. Rhizoclonium tortuosum. B. Filament with rhizoidal branch (ADU, A15398). C. Filament (ADU, A52994). D. Rhizoclonium riparium (ADU, A52913). E,F. Rhizoclonium curvatum (ADU, A52647). E. Arcuate filament with rhizoids. F. Part of filament with rhizoid.

 Rhizoclonium riparium (Roth) Harvey 1849: pl. 238, Abbott & Hollenberg 1976: 92, fig. 46. Bliding 1957: 274, fig. 3. Davey & Woelkerling 1980: 57. Kornmann & Sahling 1977: 47, fig. 18A-F. Koster 1955: 335, fig. 1. Nienhuis 1974: 172. Scagel 1966: 74, pl. 32A-E.

FIG. 53D

Thallus light to medium green, forming thin mats or strands of entangled filaments to 5(-10) cm long in eulittoral, usually shaded, calm water habitats (e.g on sandy mud or mangroves). Filaments (Fig. 53D) simple, irregularly curved or twisted, with occasional to fairly frequent lateral rhizoids of 1-2(-5) cells, irregularly placed. Cells 16-22 μ m in diameter, L/B 1-1.5(-2), wall about 2 μ m thick, 1-4 nuclei per cell; chloroplast densely reticulate with several pyrenoids.

Reproduction not reported for Australian plants. Elsewhere by biflagellate isogametes and quadriflagellate or biflagellate zoospores (Nienhuis 1974).

Type from Norderney, Germany (*Mertens*); holotype destroyed but lectotype in BM (ex K) (see Koster 1955, p. 336).

Distribution: Cosmopolitan.

In southern Australia known from Proper Bay, Port Lincoln, S. Aust. upper eulittoral, shaded (*Womersley*, 7.i.1951; ADU, A15065). Port Clinton, S. Aust., mid eulittoral on *Avicennia* pneumatophores (*Womersley*, 18.ix.1981; ADU, A52913). Pelican Lagoon, American R. inlet, Kangaroo I., S. Aust., upper eulittoral in shade (*Womersley*, 19.i.1950; ADU, A12923). Long Bay, Port Arthur, Tas., upper eulittoral (*Cribb*, 22.i.1951; ADU, A16012). Probably fairly general in sheltered habitats along the coast. Beanland & Woelkerling (1982, p. 100) have recorded *R. riparium* from numerous localities in Spencer Gulf, S. Aust., but their range of filament diameters is considerably greater than accepted here.

4. Rhizoclonium curvatum Chapman 1956: 468, fig. 127.

FIG. 53E,F

Thallus medium green, forming mats or felts of entangled filaments in eulittoral, shaded, calm water habitats. Filaments (Fig. 53E,F) simple, forming slight to distinct curves separated by fairly frequent 1-3(-5) celled rhizoids, forming a regularly positioned Y at the junction, and often with several emitted from the same side of the filament. Cells 24-32 μ m in diameter, L/B (0.7-)1-1.5(-2), wall 2-3(-4) μ m thick, 1-4 nuclei per cell; chloroplast dense with several pyrenoids.

Type from Manakau Harbour (by Puketutu I.), New Zealand; in AK.

Distribution: Apparently only known from the type collection in New Zealand.

In southern Australia, known from Outer Harbour (Port Adelaide), S. Aust., mid eulittoral on piles (*Womersley*, 22.vi.1953; ADU, A18828—"Marine Algae of southern Australia" No. 8, previously as *R. riparium*) and Garden I., Port Adelaide, S. Aust., mid eulittoral on mangroves (*Womersley & van den Hoek*, 1.x.1981; ADU, A52647—"Marine Algae of southern Australia" No. 8a, and *Womersley*, 9.iii.1982; ADU, A52983).

The Australian specimens agree well with Chapman's description and illustration. The species seems distinct in the curved segments of the filaments separated by fairly regularly spaced rhizoids which arise often on one side of the filaments and form a distinct Y at their junction. Known records from both New Zealand and South Australia are from harbour areas.

Genus CHAETOMORPHA Kuetzing 1845: 203

Thallus of erect tufts or loose-lying filaments; unbranched; erect species mostly with the elongate basal cells producing attaching rhizoids, loose-lying species usually without basal cells. *Filaments* of erect species usually increasing in diameter upwards, those of loose-lying species of fairly uniform diameter; cell divisions intercalary. *Cells* with reticulate chloroplasts, with pyrenoids; nuclei numerous per cell; cell wall lamellate, often thick.

Reproduction: generations isomorphic, in most species with the gametophyte producing isogametes and the sporophyte quadriflagellate or biflagellate zoospores. New filaments arise from the basal rhizoids of some erect species and fragmentation occurs in loose-lying species.

Type species: Ch. melagonium (Weber & Mohr) Kuetzing.

A genus of 20-30 species, widely distributed.

KEY TO SPECIES OF CHAETOMORPHA

1. Filaments single or usually clumped, each attached by an elongate basal cell; filaments usually increasing in diameter above 2
1. Filaments loose-lying and usually entangled, usually without any basal cells, of fairly uniform diameter throughout
 Filaments 1-4(-5) mm in diameter in mature parts
 Basal cells less than 1 mm long, filaments usually less than 150 μm in diameter near the basal cell, increasing in diameter upwards to 250-600 μm
4. Filaments over 200 μ m in diameter54. Filaments 70-120 μ m in diameter7
5. Cells mostly L/B about 1, rarely greater4. Ch. linum5. Cells mostly L/B 2-46
 6. Filaments fairly straight and flaccid, colour light green becoming yellow- green
 Filaments (65-)80-100(-105) μm in diameter, cells L/B 1-2, thick-walled and cells not collapsing on drying
1. Chaetomorpha coliformis (Montagne) Kuetzing 1849: 380; 1853: 20, pl. 62 fig. 2. Womersley 1956: 356.
<i>Conferva coliformis</i> Montagne 1842: 16; 1845: 5. <i>Chaetomorpha darwinii</i> (Hooker) Kuetzing 1849: 380. Chapman 1956: 458. Kornmann 1969b: 335. Womersley 1956: 356.

Conferva clavata var. darwinii Hooker 1847: 493, pl. 192 fig. 1.

PLATE 13 fig. 1; FIGS 54A, 55A-G

Thallus (Pl. 13 fig. 1; Fig. 54A) light to deep green, erect, usually epiphytic (on Amphibolis, Heterozostera, Halopteris, Cladostephus, Ballia and other algae) with filaments single but often densely clustered on the host, forming spreading tufts commonly 10-40(-60) cm long. Filaments increasing in diameter upwards and becoming moniliform (Fig. 55C), arising from an elongate basal cell (1-)3-7 mm long (Fig. 55A, D), attached by a lobed, fimbriate holdfast but without

descending rhizoids. Cells near base 0.5-1 mm in diameter and L/B (1-) 2-3(-8); mid cells (Fig. 55B) 1.5-2.5 mm in diameter and L/B 0.5-1(-1.5), 1.5-3(-4) in calmer water forms (Fig. 55E); upper cells 2-4(-5) mm in diameter and L/B 1-1.5(-2); mid and upper cells usually markedly constricted at cross walls, subspherical (Fig. 55C,G). Cells turgid when living, collapsing on drying; wall 4-8(-10) μ m thick, chloroplasts fairly densely reticulate with numerous pyrenoids.

Reproduction: generations isomorphic, the gametophyte producing bi-flagellate isogametes and the sporophytes quadriflagellate zoo (meio) spores, discharged through scattered pores (Fig. 55C).

Type incorrectly reported from Toud I., Torres Strait (now Warrior Islet, $9^{\circ}48'S$, $142^{\circ}57'E$), in PC (see below); probably from Tasmania.

Distribution: From Venus Bay, Eyre Peninsula, S. Aust. to Walkerville, Vic., and around Tasmania. New Zealand, South America.

Ch. coliformis occurs on rough-water and moderate coasts, from just below low tide level to 3-4 m deep; it is often common in rock pools and occurs on rock and a variety of hosts.

Selected specimens: Victor Harbor, S. Aust., 3-4 m deep on *Cladostephus (Hone, 20.iii.1982; ADU, A52991)*. Robe, S. Aust., upper sublittoral pools (*Womersley, 20.xii.1953; ADU, A19109)*. Port MacDonnell, S. Aust., drift on *Heterozostera (Womersley, 15.v.1982; ADU, A53158)*. Port Arthur, Tas. (*Perrin & Lucas, Feb. 1931, ADU, A47081)*. Triabunna, Tas. (*Cribb, 18. iii. 1950; ADU, A16055)*. Coles Bay, Great Oyster Bay, Tas., upper sublittoral on *Heterozostera (Womersley, 4.xi.1982; ADU, A53828—"Marine Algae of southern Australia" No. 230)*.

It is regrettable that the well known epithet *darwinii* has to be replaced by the older *coliformis*, but there is little doubt that the type specimen of the latter is the common taxon of south-east Australian coasts and New Zealand, and that the type was mis-labelled as to locality. The Durville expedition of 1838-40 visited Tasmania and then New Zealand before sailing north to Toud I. (now Warrior Islet) in Torres Strait. No large-celled *Chaetomorpha* is known from northern Queensland (pers. comm. Drs A. B. Cribb and I. R. Price). Other apparently mis-labelled species of the Durville expedition have been recorded by Womersley (1979, p. 501).

The type of *Ch. coliformis* in PC has been examined. It is epiphytic on *Heterozostera tasmanica* (of which sections show a central and 6-7 peripheral outer vascular strands, plus fibre strands), and has relatively long cells in mid parts. It is very similar to forms from partly sheltered situations (such as ADU, A53828 from Coles Bay, Tas. and ADU, A53158 from Port MacDonnell, S. Aust.) which have long cells due to lack of cell divisions. This is a similar habitat to localities near Hobart, where the Durville expedition landed. Chapman (1956, p. 459) described three varieties from New Zealand, none of which deserve recognition.

The very large cells of *Ch. coliformis* have been used for physiological studies on ion movements across the cell membranes (e.g. Raven & Smith 1980).

 Chaetomorpha aerea (Dillwyn) Kuetzing 1849: 379. Hamel 1930: 123, fig. 38A-D. Harvey 1847a: pl. 99B. Kornmann 1972: 10, figs 9-13. Kornmann & Sahling 1977: 36, fig. 12A,B. Valet 1960: 81, figs 1-3d. Womersley 1956: 355.

FIGS 54B, 55H-J

Thallus (Fig. 54B) medium to dark green, erect, epilithic (or epiphytic on Posidonia), with numerous closely associated, unbranched filaments, each attached by an elongate basal cell 100–900 μ m long with a lobed base (Fig. 55H) and descending rhizoids. Filaments increasing in diameter upwards (Fig. 55I,J). Cells 100–150 μ m in diameter and L/B 1–2(-3) near the base, usually 200–250 μ m in diameter and L/B (0.5-)1–1.5(-3) in upper parts and in long and well developed filaments 500–600(-700) μ m in diameter and L/B 0.5–1(-2); filaments slightly



Fig. 54. A. Chaetomorpha coliformis (ADU, A53158). B. Chaetomorpha aerea (ADU, A52987). C. Chaetomorpha melagonium (ADU, A24699). D. Chaetomorpha linum (ADU, A53201).

to markedly constricted at cross walls; cell length noticeably dependent on time since cell division; wall 2-4 μ m thick; chloroplasts densely reticulate with numerous pyrenoids.

Reproduction: biflagellate and quadriflagellate zooids observed in Australian plants; in Europe, by biflagellate zoospores only (Kornmann 1972, p. 16).

Type from Cromer, England; in BM (ex K).

Distribution: Cosmopolitan.

In Australia, from North Beach, Perth, W. Aust. (and probably further north) around southern Australia and Tasmania to Queensland.

Selected specimens: Cape Leeuwin, W. Aust., upper sublittoral (Gordon, 16.xi.1968; ADU, A34206). Port Noarlunga, S. Aust., lower eulittoral (Womersley, 13.iii.1982; ADU, A52987). Port MacDonnell, S. Aust., low eulittoral (Womersley, 19.viii.1953; ADU, A19034). Ulverstone, Tas., drift (Gordon, 18.i.1966; ADU, A29983).

Ch. aerea occurs mainly in the lower eulittoral and upper sublittoral zones or in rock pools, under moderate to strong water movement, and often where sand accumulates around rocks; occasionally it is epiphytic on *Posidonia*.

3. Chaetomorpha melagonium (Weber & Mohr) Kuetzing. Hamel 1930: 123, fig. 38F-H. Harvey 1847a: pl. 99A. Taylor 1957: 80.

FIGS 54C, 55K,L

Thallus (Fig. 54C) dark green, epilithic, with tufts of several erect, rigid filaments 2-3 cm long, attached by a spreading, lobed, discoid holdfast (Fig. 55K) and also rhizoids from elongate basal cells which are (1.5-)2-3(-4)mm long, clavate and $300-500 \,\mu$ m in diameter at their upper ends. Filaments only slightly increasing in diameter upwards (Fig. 55L). *Cells* 400-600 μ m in diameter and L/B 1.5-2 below, and 400-800(-1000) μ m in diameter and L/B 1-1.5(-2) above; cells not to moderately incised at cross walls, wall 30-50 μ m thick, chloroplasts densely reticulate with numerous pyrenoids.

Reproduction unknown for Australian plants; in Europe, by biflagellate and quadriflagellate zoospores (Kornmann 1972, p. 18).

Type from Sweden (locality unknown).

Distribution: N. Europe and temperate N. Atlantic Ocean.

In southern Australia, known from Belinda Beach, N. side of Middle I., Recherche Arch., W. Aust., in sand near shore on rock platform (*Trudgen* 818, 17.xi.1973; ADU, A51675), and Flat Rock Bay, S. coast of Yorke Pen., S. Aust., lower eulittoral (*Shepley*, 30.i.1961; ADU, A24699).

The above two collections are referred to the northern hemisphere *Ch. melagonium* provisionally. They agree well with this species in dimensions of the filaments and basal cells but are shorter and more tufted than plants from northern Europe. They occurred in similar habitats to *Ch. aerea* but are distinctly more robust with longer basal cells than this species. Detailed studies of living material are necessary to clarify these records.

Chapman (1956, p. 460, fig. 116C) described from New Zealand a var. *novae-zelandiae* of *Ch. melagonium*, but the brief description does not agree well with the above Australian plants.

Fig. 55. A-C. Chaetomorpha coliformis (ADU, A52991). A. Base of filament. B. Mid part of filament with recent divisions. C. Upper part of filament, with zooid discharge pores. D-G. Chaetomorpha coliformis (ADU, A53158). D. Base of filament. E. Mid part of filament. F. Upper part of filament. G. Uppermost cells of filament. H-J. Chaetomorpha aerea (ADU, A52987). H. Base of filament. I. Mid part of filament. J. Upper part of filament. K,L. Chaetomorpha melagonium (ADU, A24699). K. Base of filament. L. Upper part of filament.



Chaetomorpha linum (Müller) Kuetzing 1843: 204. Kornmann 1969a: 223; 1972: 2, figs 1-4. Valet 1960; 83, fig. 3b. Womersley 1956: 357.

PLATE 13 fig. 2; FIGS 54D, 57A

Thallus (Pl. 13 fig. 2; Fig. 54D) medium to dark green, fairly rigid, loose-lying as entangled masses or long strands of single, curved, filaments amongst other algae in sheltered habitats of the lower eulittoral or uppermost sublittoral. Filaments without attachment cells, of similar diameter throughout (Fig. 57A). *Cells* (200-)240-400 μ m in diameter and L/B (0.5-)0.7-1(-1.5), not or only very slightly incised at the cross walls; wall 5-10 μ m thick. Chloroplasts moderately to densely reticulate and lobed, with numerous pyrenoids.

Reproduction not reported for Australian material. In Europe, with gametophytic and sporophytic phases (Kornmann 1972).

Type from Lolland, Denmark (probably lost).

Distribution: Widespread.

In southern Australia, from Walpole Inlet and probably the west cost of W. Aust. to Nelson Lagoon, Vic. and probably further east, in calm water bays and lagoons.

Selected specimens: Kellidie Bay, Coffin Bay, S. Aust., 3 m deep (Womersley, 5.xii.1975; ADU, A46807) and low eulittoral (Womersley, 22.viii.1967; ADU, A31820—"Marine Algae of southern Australia" No. 2). Port Adelaide, S. Aust., 10-20 cm deep on pontoons (Womersley, 10.iii.1982; ADU, A52981). Port MacDonnell, S. Aust., drift in harbour (Womersley, 15.v.1982; ADU, A53159—"Marine Algae of southern Australia" No. 2a). Nelson lagoon, Vic. (Beauglehole, 10.v.1959; ADU, A24672).

Some authors (e.g. Christensen 1957) place Ch. linum as a synonym of Ch. aerea, but others (e.g. Blair, Mathieson & Cheney 1982, p. 171) consider them to be distinct species.

5. Chaetomorpha billardierii Kuetzing 1847: 166; 1849; 379; 1853: 19, pl. 39 fig. 3. Womersley 1956: 355.

FIGS 56A, 57B,C

Thallus (Fig. 56A) light green, becoming yellow-green, loose-lying in extensive entangled masses (up to several metres across) of fairly straight filaments, in sheltered lower eulittoral to upper sublittoral habitats. Filaments without attachment cells, of similar diameter throughout (Fig. 57B,C). Cells (200-)220-350(-450) μ m in diameter and L/B (1-)1.5-3(-4), not or only very slightly incised at the cross walls; wall 3-8(-20) μ m thick, in some species thickened especially at the cross walls; chloroplasts openly reticulate with numerous pyrenoids; nuclei numerous. Reproduction unknown.

Type from "Novae Hollandiae" (King Georges Sound, W. Aust. or southern Tasmania—probably the latter); in L (937, 158...402).

Distribution: From Esperance, W. Aust. to the north coast of Kangaroo I., S. Aust. and around Tas., in calm-water situations. Probably this species is fairly generally distributed in suitable localities along southern Australia.

Selected specimens: Esperence, W. Aust., drift (*Firman*, Dec. 1951; ADU, A18936). Venus Bay, S. Aust., upper sublittoral (*Womersley*, 17.i.1951; ADU, A13745). Head of American R. inlet, Kangaroo I., S. Aust., lower eulittoral (*Womersley*, 24.i.1948; ADU, A6766). Pelican Lagoon, American R. inlet, Kangaroo I., S. Aust., lower eulittoral (*Womersley*, 28. viii. 1948; ADU, A8639). Great Taylor Bay, Bruny I., Tas., 1-2 m deep (*Shepherd*, 14.ii.1972; ADU, A42134).

Ch. billardierii shows some variation in filament diameter in different collections (e.g. Fig. 57B,C) but is separated from *Ch. linum* by its distinctly longer cells and from *Ch. valida* by its fairly straight, flaccid and light green to yellow filaments. The comment (Womersley, 1956, p. 356) that the filaments show occasional branches was apparently based on a contaminant.



Fig. 56. A. Chaetomorpha billardierii (ADU, A8639). B. Chaetomorpha valida (ADU, A5668). C. Chaetomorpha capillaris (ADU, A12783). D. Chaetomorpha indica (ADU, A13756).

6. Chaetomorpha valida (Hooker & Harvey) Kuetzing 1849: 379. Womersley 1956: 357. Conferva valida Hooker & Harvey 1847: 416. Harvey 1855b: 263.

FIGS 56B, 57D

Thallus (Fig. 56B) dark green, loose-lying and forming entangled masses to 15 cm across and 1-5 cm thick, of curved, often crisped, rigid filaments, in the uppermost sublittoral of sheltered habitats. Filaments without attachment cells and of similar diameter throughout (Fig. 57D). Cells (300-)350-400 μ m in diameter and L/B (1.5-)2-3(-4)(3-5 according to Hooker & Harvey), not or slightly incised at the cross walls; lateral walls 30-60 μ m thick, cross walls 8-15 μ m thick; chloroplasts densely reticulate to discoid and closely aggregated, with numerous pyrenoids; nuclei numerous.

Reproduction unknown.

Type from Georgetown, Tas. (Gunn 1345); in BM (ex K).

Distribution: From Venus Bay, S. Aust. to Port Phillip, Vic., and Port Arthur, Tas., usually on tidal flats in sheltered localities.

Stewart I., New Zealand (Harvey 1855b, p. 263).

Selected specimens: Venus Bay, S. Aust., upper sublittoral (Womersley, 17.i.1951; ADU, A13647). Rabbit I., Pelican Lagoon, American R. inlet, Kangaroo I., S. Aust., upper sublittoral (Womersley, 31.v.1947; ADU, A5668). Port Arthur, Tas. (Cribb, 31.iii.1950; ADU, A16050).

Ch. valida and *Ch. billardierii* are closely related species and study of living material of both is needed. They appear to differ in the former having rigid, crisped filaments, usually dark green, whereas the latter has fairly straight, more flaccid, and light green filaments which become yellow-green in emergent masses. There may also be differences in wall thickness and chloroplast structure.

Some of these differences may depend on the habitat and physiological state of the thallus, but scattered plants of *Ch. valida* have been collected from within extensive areas of *Ch. billardierii* at American River inlet on Kangaroo Island, where they appear to be distinct taxa.

Ch. billardierii Kuetzing 1847 was apparently published in March and Conferva valida Hooker & Harvey 1847 in August, so if these names are united then Kuetzing's name has priority.

 Chaetomorpha capillaris (Kuetzing) Boergesen 1925: 45, fig. 13. Davey & Woelkerling 1980: 57. Feldmann 1937: 208, fig. 17. Valet 1960: 85, fig. 4. Womersley 1956: 356.

FIGS 56C, 57E,F

Thallus (Fig. 56C) medium green, loose-lying in shade on tidal flats, forming loose, woolly, entangled masses with few if any attachment cells. Filaments unbranched, of similar diameter throughout (Fig. 57E,F). Cells (70-) 85-100 (-105) μ m in diameter and L/B 1-2, not collapsing on drying; walls $8-12 \mu$ m thick; chloroplasts densely reticulate with numerous pyrenoids.

Reproduction unknown.

Type from Nice, France, in L (937, 155...45).

Distribution: Mediterranean and North Atlantic.

In southern Australia, recorded from Blanche Harbour, N. Spencer Gulf, S. Aust., on *Avicennia* pneumatophores (Beanland & Woelkerling 1982, p. 94); American R. inlet, Kangaroo

Fig. 57. Parts of filaments of A. Chaetomorpha linum (ADU, A52981). B,C. Chaetomorpha billardierii. B. (ADU, A13745). C. (ADU, A6766). D. Chaetomorpha valida (ADU, A5668). E,F. Chaetomorpha capillaris (ADU, A12783). G. Chaetomorpha indica (ADU, A13756).

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I., S. Aust., from under samphires in the mid and upper eulittoral; from Westernport Bay, Vic. (Davey & Woelkerling 1980, p. 57; and from Lake Reeve, Gippsland, Vic. (Ducker, Brown & Calder 1977, p. 35). Probably more widely distributed.

Selected specimen: Pelican Lagoon, American R. inlet, Kangaroo I., S. Aust., upper eulittoral under samphires (*Womersley*, 19.i.1950; ADU, A12783).

The association of the names *Ch. capillaris* and *Ch. tortuosa* was discussed by Womersley (1956, p. 356). The American River inlet specimens agree well with Kuetzing's type in diameter and general morphology and with the descriptions of Boergesen and Feldmann, but their reproduction has not been studied. *Ch. capillaris* is sometimes referred to *Lola* Hamel & Hamel, and Cribb (1965, p. 262) refers it to *Rhizoclonium*. However, Cribb's material is slenderer with much longer cells and occasional lateral rhizoids; it probably is a *Rhizoclonium* and not the same as the southern Australian taxon referred to *Ch. capillaris*.

8. Chaetomorpha indica (Kuetzing) Kuetzing 1849: 376. Womersley 1956: 357.

FIGS 56D, 57G

Thallus (Fig. 56D) light to medium green, loose-lying as masses of long strands (to 15 cm long) or entangled with other algae, in the uppermost sublittoral. Filaments unbranched, apparently without attachment cells, of similar diameter throughout (Fig. 57G). Cells (100-) 105-130 (-150) μ m in diameter and L/B (1-) 1.5-2.5, often collapsing on drying; wall 3-7 μ m thick; chloroplasts openly to fairly densely reticulate, with numerous pyrenoids; nuclei numerous. Reproduction unknown.

Type from Tranquebar, India; in L (936, 249...72).

Distribution: India. Queensland.

In southern Australia, known from Walpole Inlet, W. Aust., Coffin Bay and Robe, S. Aust., and Swan Bay, Port Phillip, Vic. Also recorded from Port Adelaide, S. Aust. by Tate and Tasmania (?) by Lucas (see Womersley 1956, p. 357). Probably more widely distributed in sheltered waters.

Selected specimens: Coffin Bay, S. Aust., upper sublittoral on flats (*Womersley*, 10.i.1951; ADU, A13756). Boat Lake, Robe, S. Aust., loose-lying, intertidal (*Womersley*, 28.ii.1983; ADU, A54005).

In contrast to *Ch. capillaris* which occurs in mid to upper eulittoral situations, *Ch. indica* seems to be a shallow water and floating or loose-lying upper sublittoral species. The size and proportions of the cells seems to separate these two species satisfactorily, but other names may prove to be synonyms of *Ch. indica* (e.g. *Ch. brachygona*—see Womersley 1956, p. 357).

Genus APJOHNIA Harvey 1855a: 335

Thallus dendroid, with an erect, stipitate basal segment attached by rhizoids and increasing in diameter above, bearing apically a row, cluster or irregular whorl of similar branches, followed by several similar branch systems. *Branch segments* consisting of single or subdivided coenocytic segments with ultimate branchlets single or usually opposite; bases of all except juvenile segments with several annular constrictions; segments multinucleate, walls of cellulose microfibrils; cross walls complete, formed by ingrowth from the periphery; chloroplasts numerous, discoid, each containing a pyrenoid.

Reproduction by motile zooids.

Type species: A. laetevirens Harvey 1855a: 335.

A genus of two species, the type from southern Australia, and *A. scoparia* (Kuetzing) Valet (1976) from New Caledonia.

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Apjohnia was earlier placed in the Siphonocladales but is considered by Papenfuss & Chihara (1975) and van den Hoek (1963) to belong to the Cladophorales. The absence of any net formation indicates that it is best placed in the Cladophoraceae, where its size and branching pattern distinguish it from *Cladophora*.



Fig. 58. A. Apjohnia laetevirens (ADU, A27299). B. Cladophoropsis herpestica (ADU, A13612). C. Cladophoropsis magna (Type).

Apjohnia laetevirens Harvey 1855a: 335; 1858: pl. 5. Dawes 1969: 77. Lucas 1936: 30, fig. 12. Papenfuss & Chihara 1975: 311-315, figs 4-11. Womersley 1956: 376.

FIGS 58A, 59A,B

Thallus (Fig. 58A) to 25 cm high, dendroid, with a single (or often clustered) stipitate basal segment 1–6 cm long and 1–4 mm in diameter attached by branched, sparsely septate rhizoids, and producing at its apex a row of 2–5 branches often lying in one plane (Fig. 59A) or an irregular cluster or whorl of 3–9 elongate, linear or slightly expanded upwards, segments 0.5-2 cm long and 0.5-1.5 (–2) mm in diameter. This pattern is repeated two to several times with the subterminal segments producing usually three and later five segments, the central one being produced first, followed by more or less equally developed lateral branches. Segments with prominent annular constrictions (Fig. 59A) confined to the lower quarter to half on upper segments; segments with complete end walls, vacuolar acicular calcium oxalate crystals present; bases of older segments often cutting off 2–8 small hapteroid cells (Fig. 59B) which come to lie between the segments and extend rhizoidal processes downward and largely within the wall of the lower segment; cell wall lamellate, tough, $10-20 \mu$ m thick in younger segments, up to 50 μ m thick below; chloroplasts discoid, closely packed, each with a prominent pyrenoid.

Reproduction by biflagellate zooids, liberated through lateral pores following reticulation of the protoplasm, has been observed.

Type from Phillip I., Victoria; in TCD.

Distribution: From Green Head $(30^{\circ}04'S)$ in W. Aust., around southern Australia to Collaroy, N.S.W. Deal I. and King I., Bass Str. Often common in deep, shaded pools on rock platforms, and recorded to 16 m deep.

Selected specimens: Robe, S. Aust., upper sublittoral pools (*Womersley*, 18.i.1967; ADU, A27299). Flinders, Vic., upper sublittoral (*Womersley*, 18.i.1967; ADU, A31802). East Cove, Deal 1., Bass Strait (*Shepherd & Lewis*, 5.v.1974; ADU, A45246).

A. laetevirens is a most distinctive alga, with much larger coenceytic segments than other algae of the Cladophorales. Its dimensions and branching pattern separate it satisfactorily from *Cladophora*. The other species, A. scoparia from New Caledonia, differs in habit, branching and the frequent presence of more than one cell between laterals.

Young plants of A. lactevirens, comprising a tuft of elongate, clavate basal segments only, are not uncommon.

Genus CLADOPHOROPSIS Boergesen 1905: 288. Papenfuss 1950: 208.

Thallus filamentous, irregularly branched, forming dense mats, cushions or tufts of entangled filaments, often with emergent, erect filaments above; usually with the lower filaments and in some species with nearly all filaments producing a descending rhizoid from the basal pole of cells, below which a lateral occurs in open connection (no basal cross wall) with the lower cell. *Cells* of very variable length, shortest where laterals are clustered, and very long above; chloroplast parietal, reticulate, with numerous pyrenoids; numerous nuclei per cell.

Reproduction unknown.

Fig. 59. A,B. Apjohnia laetevirens (ADU, A27299). A. A branch with series of basally annulate segments. B. Lower cells with annular constrictions and hapteroid cells. C. Cladophoropsis herpestica (ADU, A13612). Filaments with descending rhizoids and open connection to lateral branches. D. Cladophoropsis magna (Type). A cluster of filaments showing branches in open connection to lower cells. E-G. Cladophora rhizoclonioidea (Holotype). E. Habit. F. A group of entangled filaments. G. An old regenerating filament with young lateral branches.



Type species: C. membranacea (C. Agardh) Boergesen 1905: 288, figs 8-13.

A genus of some 20 species, much in need of monographic treatment on a world basis. Two species occur in southern Australia, and C. membranacea also occurs on the N.S.W. and Queensland coasts.

Cladophoropsis is similar to species of Cladophora Section Repentes (especially C. coelothrix) but differs in that cross walls are not present at the base of lateral branches, so that the branch is in open connection with the parent cell. In most species of Cladophoropsis, a descending rhizoid develops from the basal pole of the upper cell, just above the cross wall. The cells in Cladophoropsis are usually quite irregular in length, with some up to a few times as long as broad where laterals are clustered, but others many times longer than broad. In some species of section Repentes of Cladophora, the basal wall of laterals may be delayed in its formation, and rhizoids are usually present from the basal pole of cells at the base of the thallus, but Cladophoropsis appears to be satisfactorily separated from Cladophora at a generic level even though closely related.

Cladophoropsis was first placed in the Cladophoraceae by Boergesen, but later (Boergesen 1913, p. 42) transferred to the Valoniaceae. Boergesen considered that the cells were formed by segregative division as in Siphonocladus, but this has not been convincingly demonstrated and van den Hoek (1982, p. 33) considers that if segregative division does occur in Cladophoropsis then it is not the rule. However, formation of cross walls by ingrowth from the periphery (as normal for Cladophora) has also not been documented in Cladophoropsis.

It seems best to follow van den Hoek in regarding *Cladophoropsis* as a close relation of *Cladophora*.

KEY TO SPECIES OF *CLADOPHOROPSIS*

- 1. Cladophoropsis herpestica (Montagne) Howe 1914: 31. Chapman 1956: 470 (fig. 130, incorrect). Womersley 1956: 377.

FIGS 58B, 59C

Thallus (Fig. 58B) dark green, forming firm, compact cushions up to 15 cm across and (0.5-)1-1.5 cm thick, with basally entangled filaments and the upper filaments erect or sloping but crowded. Filaments (Fig. 59C) 240-340 (-370) μ m in diameter, with lateral branches from below a cross wall and usually a long, descending rhizoid from the basal pole of the upper cell; laterals arising well separated or 2-4 clustered from relatively short cells (L/B (1-)2-5); upper cells very long; wall 20-40 μ m thick; chloroplast reticulate, with numerous pyrenoids. Reproduction unknown.

Type from the Bay of Islands, New Zealand; in Herb. Montagne, PC.

Distribution: New Zealand. Chile? (Santelices & Abbott 1978, p. 215), Thailand (Egerod 1971, p. 123, figs 1-9), New Caledonia? (Valet 1968a, p. 39).

In southern Australia, from Point Peron and Hopetoun, W. Aust., from the Head of the Great Australian Bight to Elliston, S. Aust., and from Encounter Bay, S. Aust. and Queensland. Generally in shaded areas just above or below low tide level under moderate water movement.

Selected specimens: Mangles Bay, Point Peron, W. Aust., sublittoral on reef nodules (Smith 107, Nov. 1946; ADU, A50595). Head of the Great Australian Bight, S. Aust., lower eulittoral, shaded (Womersley, 4.ii.1954; ADU, A19148). Elliston, S. Aust., lower eulittoral, shaded (Womersley, 15.i.1951; ADU, A13612—"Marine Algae of southern Australia" No. 3). Encounter Bay, S. Aust. (Cleland; ADU, A1575).

The southern Australian specimens agree well with specimens from the Bay of Islands, New Zealand, and appear to be confined to the slightly warmer central and western coasts of southern Australia.

2. Cladophoropsis magna Womersley 1955: 390, fig. 7; 1956: 377.

FIGS 58C, 59D

Thallus (Fig. 58C) light to medium green, forming large and fairly loose filamentous masses up to 50 cm across and 7 cm thick, with lower filaments entangled and upper filaments mostly erect. Filaments (Fig. 59D) (400-)500-700 μ m in diameter where branches (often clustered) arise, with one (rarely two) laterals from each cell (L/B mostly (2-)3-5), upper and lateral branches 170-350 μ m in diameter in their lower parts and increasing to near their apices (500-700 μ m in diameter); cross walls infrequent, cells usually very long above; descending rhizoids not observed; wall (6-)10-15 μ m thick; chloroplast reticulate, with numerous pyrenoids.

Type from Smoky Bay, Eyre Pen., S. Aust.; in ADU, A13651—"Marine Algae of southern Australia" No. 4.

Distribution: Only known from the type and from nearby Denial Bay, S. Aust. (in MEL, 3011). The type was a large mass in the drift and probably came from the sublittoral zone.

C. magna, though known from only one main collection, appears distinct in habit and dimensions from other species. Rhizoids are not apparent in the type collection but may well occur on the lowermost filaments.

Genus CLADOPHORA Kuetzing 1843: 262, nom. cons.

by C. van den Hoek and H.B.S. Womersley.

Thallus of erect or prostrate filaments, occasionally loose-lying, sparsely to profusely branched often from every cell above; attached species with basal cells adherent by a discoid holdfast or by descending rhizoids arising from the basal poles of cells. *Filaments* usually decreasing in diameter upwards; cell division apical and/or intercalary. *Cells* relatively large, multinucleate; chloroplasts numerous, small and angular, many with a bilenticular pyrenoid, usually forming a parietal reticulum or closed layer.

Reproduction: generations isomorphic, the gametophyte producing biflagellate isogametes and the sporophyte quadriflagellate zoo(meio)spores or biflagellate zoo(mito)spores; in some species, sporophyte only present; or by thallus fragmentation.

Type species: Cl. oligoclona (Kuetzing) Kuetzing.

A large and common genus. The European species (van den Hoek 1963) and those on Atlantic North Amercian coasts (van den Hoek 1982) have been revised and monographed, but the species from other parts of the world await detailed study.

Criteria used in separation and definition of the species of *Cladophora* have been discussed by van den Hoek (1963, pp. 15-19; 1982, pp. 10-19).

They include the following:

1. The *organisation* of the thallus, whether *acropetal* with cell divisions confined, or largely so, to the apical cells, or *irregular* with lower cell divisions resulting in irregularly scattered branches and branchlets.

- 2. The *insertion* of branches, whether *apical* with an inclined cross wall which may become almost horizontal with age resulting in a pseudodichotomy, or *lateral* with a vertical or steeply inclined cross wall which never becomes subhorizontal. Associated with this is the *angle of ramification* which is often variable but may be characterisitic.
- 3. The distinctness of main axes, the diameter of apical cells, ultimate branch cells (excluding the apical cell) and main axis cells, their length to breadth (L/B) ratios, and the relative increase in diameter from apical cells to main axes.
- 4. The curvature of ultimate branch systems, which vary from straight to fastigiate tufts to falcate or refract.
- 5. The maximum number of branches per node and the density of branches.
- 6. The *form of the apical cells*, whether cylindrical or tapering and the nature of their tip, and also of lower cells, whether cylindrical, swollen or clavate.
- 7. The thickness of cell walls, which increases with age, and stiffness of the plant.
- 8. The mode of attachment, which is usually by multicellular rhizoids but may be discoid.
- 9. The colour of the plant and density of the chloroplasts.
- 10. Macroscopic habit and height of the thallus.
- 11. The type of *life history* (usually isomorphic), the nature and form of the zooidangia, and the mode of aggregation of the zooids before release.

KEY TO SPECIES OF CLADOPHORA

- 3. Cells near the base clavate but short; lateral branches often subterminal, opposite or serial on lower cells; cell walls thick and lamellate, giving the thallus a stiff texture; habit ball-like, free-floating at least when mature..Section Aegagropila 2. Cl. aegagropiloidea

Cladophora

CLADOPHORACEAE

Thallus erect, basal and lower cells many times longer than apical cells and often slightly clavate; no or few intercalary divisions in lower cells....Section Longiarticulatae....6
 Thallus erect, usually densely tufted, basal and lower cells not markedly longer than upper cells; intercalary divisions present in lower cells, often also in upper cells.....8

 6. Thallus dark green, drying dark brown-green; apical cells mostly over 100 μm (70-220 μm)in diameter, lower cells usually with annular constrictions and producing descending rhizoids also with annular constrictions
 Apical cells 15-35 μm in diameter, basal cell usually single
 8. Thallus with pseudo-dichotomous main axes ending in acropetal, often falcate or refracto-falcate branch systems with dominant apical growth; intercalary divisions relatively few, increasing basipetally, without frequent intercalation of branches of different ages
9. Apical cells $170-300 \mu\text{m}$ in diameter, lower cells up to $350 \mu\text{m}$ in diameter
9. Apical cells mostly less than $150 \ \mu m$ in diameter, lower cells less than $250 \ \mu m$ in diameter 10
 Apical cells (80-)100-120(-160) μm in diameter, lower thallus cells (140-)180-220 (-250) μm in maximum diameter. Apical cells mostly less than 90 μm in diameter, lower thallus cells usually less than 200 μm in maximum diameter.
11. Apical cells 40-70(-80) μ m in diameter; maximum number of branches per node 2(-3); thallus usually tuffed; lower filaments (100-)135-160(-180) μ m in maximum diameter and usually 2-3 times the diameter of apical cells
 Diameter of the predominantly cylindrical apical cells (15-) 20-30 μm 11. Cl. dalmatica Diameter of the more or less tapering apical cells (25-) 30-50 (-70) μm; pale plants of saltmarsh pools and lagoons narrower (apical cells approx. 25-30 μm) Cl. vagabunda
13. Apical cells usually tapering, 60-120 µm in diameter at their base, lower filaments usually over 200µm in diameter, cells short (L/B 1-5)
 13. Cl. hutchinsioides 13. Apical cells cylindrical or tapering, less than 65 (-80) μm in diameter, lower filaments less than 150 μm in diameter

 14. Upper parts of main filaments unbranched over long stretches or with short or long series of tapering branchlets of differing lengths; apical cells 20-30 μm in diameter L/B 1.5-4; main filaments 45-70 μm in diameter, L/B 1-214. Cl. montagneand 14. Upper parts of main filaments usually with densely tufted branch systems, withou long series of unbranched cells though short series without branches often occubelow apical cells or in lower parts
15. Apical cells mostly cylindrical with rounded tips, 16-32 μm in diameter, L/B 2-6.5 increasing to 40-80 μm in diameter in lower main filaments (with L/B 2-3)
15. Apical cells mostly more than 30 μm in diameter; lower main filaments more than 80 μm in diameter
 16. Thallus in dense tufts or turfs, basally unbranched or little branched and peripherally more or less penicillate; apical cells cylindrical with slightly tapering tips, 50-80 μm in diameter (-90 μm in zooidangia), increasing to 80-130 μm in lower main filaments diameter of thickest parts of main filaments 1.5-2.5 times that of apical cells
17. Apical cells more or less tapering, $30-55 \mu\text{m}$ in diameter, L/B 3-10, increasing to $130-170 \mu\text{m}$ in diameter in lower main filaments; axes bearing long, often uni lateral, rows of closely arranged, more or less appressed, branches of varying length 17. Cl. sericed
lateral, rows of closely arranged, more or less appressed, branches of varying length

1. Cl. rhizoclonioidea van den Hoek & Womersley sp. nov.

FIGS 59E-G, 60A

Thallus (Fig. 60A) medium to dark green, forming indefinite hair-like masses of more or less curving, intertwined filaments (Fig. 59E), often entangled with other, larger algae; filaments long, unbranched or with scattered curved branchlets (Fig. 59F), regenerating thick-walled akinete filaments with more numerous laterals (Fig. 59G). Growth by frequent intercalary divisions; angle of branching usually wide (about 90°), with scattered cells bearing one lateral; insertion of branches usually with vertical to steeply inclined walls, partly subterminal (Fig. 59F). Apical cells slightly tapering with rounded tips. A tendency for inversion of polarity results sometimes in the outgrowth of branches from opposite cell poles within one and the same akinete filament. Rhizoids were not observed; the entangled growth habit seems to ensure attachment to other algae.

Apical cells 24-30 μ m in diameter, L/B 2-4, increasing only slightly to main filaments with cells 40-50 μ m in diameter and L/B 2.5-7; ratio of main filament cell to apical cell diameters 1.3-2; the scattered akinete-filaments 50-120 μ m in diameter with L/B 2-5; cell walls relatively thin, 1-2 μ m in actively growing parts to 5-15 μ m in akinetes (Fig. 59G).

Reproduction unknown, possibly by fragmentation of akinete filaments.

Diagnosis: Thallus laete-sive atroviridis, fasciculos indefinitos pilosos formans, ex filamentis e ramosis sive pauce ramosis plus minusve crispatis contortuplicatis ramulos dispersos curvatos ferentibus compositus. Organisatio irregularis. Increscentia praecipue divisionibus intercalaribus. Rami lateraliter et saepe subterminaliter ad angulum latum (c. 90°) inserti. E cellula axiali unus ramus oriri potest. Cellulae apicales leviter attenuatae apicibus rotundatis diametro 24-30 μ m, long./diam. 2.5-7. Filamenta akinetorum incrassata usque ad 50-120 μ m, late. Crassities parietum c. 1-2 μ m, usque ad c. 5-15 μ m in akinetibus.

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CLADOPHORACEAE

Cladophora

Type from Nora Creina, S.Aust., drift on Seirococcus in pool (Womersley, 31.xii, 1981).

Holotype: ADU, A52833. Isotype in GRO.

Distribution: Apart from the type, known from Georgetown, Tas. (Perrin, April, 1932; HO, 44866; herb. Sonder in MEL, 597510 and 597511).

Cl. rhizoclonioidea is distinguished by its curved filaments and *Rhizoclonium*-like habit, and by its scattered branches with lateral insertion. It much resembles the European freshwater species *Cl. rivularis* (L.) van den Hoek (1963, p. 113).



Fig. 60. A. Cladophora rhizoclonioidea (Holotype). B. Cladophora aegagropiloidea (Holotype). C. Cladophora coelothrix (ADU, A22470). D. Cladophora subsimplex (ADU, A52857).

2. Cladophora aegagropiloidea van den Hoek & Womersley sp. nov.

FIGS 60B, 61A,B.

Thallus (Fig. 60B) light to medium green, forming free-floating or unattached balls 1-3 cm in diameter with filaments radiating from the central or lower part; filaments densely branched with laterals from every cell except often for the 1-4 (-10) upper (outermost) cells (Fig. 61A). Growth vaguely acropetal to irregular, with mainly apical but also intercalary divisions; angle of branching usually narrow $(30-45^{\circ})$, with most cells bearing 1 (-2, rarely 3), laterals; insertion of branches usually slightly to markedly subterminal (especially below) with vertical to steeply inclined basal walls (Fig. 61A) which may be a short distance from the parent cell; older cells often bearing opposite, serially or irregularly arranged laterals; cells with walls somewhat irregular to undulate, not linear, lower cells clavate, often bearing descending rhizoids from their basal poles (Fig. 61B). Apical cells cylindrical with rounded tips. A tendency for inversion of polarity results in the outgrowth of branches from opposite cell poles within one and the same axis (Fig. 61A1).

Apical cells 30-40(-48) μ m in diameter, L/B (4-)6-15, increasing only slightly to lower cells 30-72(-112) μ m in diameter and L/B 2.5-7; ratio of lower cell to apical cell diameters 1-2(-3); cell walls relatively thick, 5-15 μ m in main filaments.

Reproduction unknown, but the balls increase by fragmentation.

Diagnosis: Thallus pallide sive laete-viridis, sphaericus, diametro 1-3 cm, libere natans, ex filamentis ramosis radiantibus compositus. Increscentia praceipue divisionibus apicalibus. Organisatio indistincte acropetalis, sive irregularis. Rami lateraliter et subterminaliter ad angulum acutum $(30^\circ - 45^\circ)$ inserti. E cellula axiali unus duo tres rami oppositi seriati sive irregulariter inserti oriri possunt. E cellularum nonnularum polo basali atque apicali rami oriri possunt (inversio polaritatis). Cullulae apicales cylindraceae apicibus rotundatis diametro 30-40 (-48) μ m, long./diam. (4-)6-15. Cellulae versus thalli basin clavatae, diametro 30-72 (-112) μ m, long./diam. 2.5-7. Crassities parietum in filamentis principalibus c. 5-15 μ m.

Type from the Bay of Shoals, Kangaroo I., S. Aust., drift (*Womersley*, 13.i.1950); in ADU, A12607—"Marine Algae of southern Australia" No. 219.

Distribution: Only known from the type locality.

This species was found on the one occasion, with vast numbers of balls floating or washed ashore in the calm-water, shallow (3-5 m deep) Bay of Shoals on Kangaroo Island. It was not seen attached, but the extensive beds of the sea-grass *Posidonia* in the bay were not checked for *Cladophora* on the leaves. The locality has not been visited more recently.

The Bay of Shoals is typically marine with no significant fresh-water input. *Cl. aegagropiloidea* thus differs in its habitat from the closely related fresh-water *Cl. aegagropila* (L.) Rabenhorst (see van den Hoek 1963, p. 51) and it is also a slenderer species, especially in the lower filaments.

3. Cladophora coelothrix Kuetzing 1843: 272. van den Hoek 1963: 40, figs 55-78; 1982: 47, figs 11-29.

Cl. repens (J. Agardh) Harvey 1849: pl. 236. Womersley 1956: 359.

FIGS 60C, 61C,D

Thallus (Fig. 60C) medium to dark green, drying brownish, forming dense turfs or cushions to several cm across and to 4 cm high, composed of a basal tangle of branched, often curved, stolon-like filaments giving rise to ascending, more or less erect, branch-systems (Fig. 61C).

Fig. 61. A,B. Cladophora aegagropiloidea (Type, ADU, A12607). A. Upper branch system. A¹. Part of thallus showing reversion of polarity. B. Lower thallus. C,D. Cladophora coelothrix (ADU, A22470). Branch systems with rhizoids. E-I. Cladophora subsimplex (E-H, ADU, A30024; I, ADU, A52662). E. Branching pattern. F. Upper branch system. G. Apical cell. H. Lower branches with rhizoids. I. Fertile upper branches.



Growth largely by divisions of conspicuous apical cells, but intercalary cells may divide into shorter cells; feebly to distinctly acropetal at the apices, densely and irregularly branched with many cells (especially lower ones but often also those near the apices) producing a descending rhizoid from their basal poles (Fig. 61C,D), and which attach to the substrate or other filaments with a terminal coralloid holdfast; lateral branches mostly wide-angled (45° or more) arising singly (occasionally two) at or just below a cross wall, with the new wall remaining steeply inclined to the parent cell.

Apical cells 60-140 μ m in diameter, L/B 3-16, cylindrical with rounded ends; mid and lower thallus cells 70-220 μ m in diameter, L/B 2-11; ratio of lower cell to apical cell diameters (0.6-)1-1.5(-2.5); cell walls thin in younger cells (2-4 μ m), mostly 4-8 μ m thick below and up to 20 μ m thick in old cells.

Reproduction by zooids developing in normal vegetative cells at or near apices of outer filaments of the cushions.

Type from Livorno, Italy (Meneghini); in L (937, 278 ... 392).

Distribution: Warm temperate to tropical Atlantic coasts of Europe, Africa and America; probably widespread in tropical and warm temperate waters.

In southern Australia, from Fremantle, W. Aust. around southern Australia (not Tasmania) to Moreton Bay, Qld., common in shaded areas or pools near low tide level on rough-water coasts but extending into sheltered areas.

Selected specimens: Point Sinclair, S. Aust., upper sublittoral, in gulch, shaded (*Womersley*, 9.ii.1954; ADU, A19606). Wittelbee Point, near Ceduna, S. Aust., low eulittoral pool (*Womersley*, 21.i.1951; ADU, A15166). Venus Bay, S. Aust., upper sublittoral reef pools (*Womersley*, 17.i.1951; ADU, A15172). Wanna, S. Aust., low eulittoral (*Womersley*, 14.ii.1959; ADU, A22470). Louth Bay, S. Aust., upper sublittoral (*Womersley*, 5.i.1951; ADU, A15182). Pennington Bay, Kangaroo I., S. Aust., drift (*Womersley*, 13.iv.1947; ADU, A4498).

Cl. coelothrix is distinguished by its habit, long cylindrical apical cells, irregular branching, dimensions, and by the presence of rhizoids from the basal poles of many of the cells. In the eastern part of its range, plants are coarser with thicker filaments (mostly $140-220 \,\mu$ m) than in the western part where softer plants have filaments mostly $80-100 \,\mu$ m in diameter.

4. Cladophora subsimplex Kuetzing 1849: 411. Womersley 1956: 361.

Cl. simpliciuscula Hooker & Harvey 1845: 295.

Non Cl. simpliciuscula Kuetzing 1843: 262 (see van den Hoek 1963: 113).

Cl. delicatula Montagne sensu Womersley 1950: 143; 1956: 360.

Cl. stuartii Harvey 1859b: 340; 1863, synop.: 60. De Toni 1889: 313. Womersley 1956: 359.

FIGS 60D, 61E-I

Thallus (Fig. 60D) pale to dark green, forming small mats or cushions or entangled curly masses, a few cm across and 1-4(-10) cm high, composed of a basal tangle of branched, often curved, stolon-like filaments giving rise to erect filaments (Fig. 61E), occurring often among turf algae near low tide level, epilithic and epiphytic. *Growth* predominantly by frequent intercalary divisions producing filaments of relatively short cells; the erect filaments (Fig. 61F) in well developed plants extend 5-10 cm beyond the basal mat, and may be unbranched or bear mostly unilateral rows of branchlets or, in some cases, clusters of laterals from several adjacent cells; lateral branches mostly wide-angled (more than 45°), single or rarely two (exceptionally 3) from a parent cell with the basal wall usually steeply inclined but sometimes becoming almost horizontal; cell wall moderately thick; lower cells (Fig. 61H) frequently producing a descending rhizoid from their basal poles, attaching to the substrate or other filaments by coralloid holdfasts.

Apical cells (20-) 30-50 (-60) μ m in diameter, L/B 2-6 (-8), tapering at least in their upper third and prominently so near their apices (Fig. 61G); mid cells 20-80 μ m in diameter, L/B 2-5 (-8); lower cells 50-80 (-100) μ m in diameter, L/B (1-) 2-6 (-7); ratio of lower cell to apical cell diameters 1-2; cell walls prominently lamellate, 4-6 μ m thick above, 8-12 μ m thick below.

Reproduction by zooids formed in terminal chains of swollen zooidangia (Fig. 611), each $60-100 \ \mu m$ in diameter and L/B 1-1.5 (-2).

Type from Hermite I., Cape Horn, Fuegia (Hooker); in BM (ex K).

Distribution: Cape Horn, Falkland Is, New Zealand.

In southern Australia, from Cape du Couedic, Kangaroo I., S. Aust. to Kiama, N.S.W. and south-east Tasmania. *Cl. subsimplex* grows on mid eulittoral wave-washed ledges, in rock pools, and down into the uppermost sublittoral of wave-exposed shores in the algal turf. The colour is mostly medium to dark green, but in summer plants may be bleached to pale green.

Selected specimens: Cape du Couedic, Kangaroo I., S. Aust., lower eulittoral (Womersley, 17.i.1950; ADU, A12674). Cape Lannes, S. Aust., on wave-washed mid eulittoral ledges (van den Hoek, 6.ix.1981; ADU, A52370). Stinky Bay, Nora Creina, S. Aust., mid eulittoral on wave-washed ledges (van den Hoek 81/9a, 5.ix.1981; ADU, A52691). Port MacDonnell, S. Aust., entangled with drift algae, mainly Corallina (van den Hoek 81/10, 3.ix.1981; ADU, A52667). Bridgewater Bay, Vic., upper sublittoral to low eulittoral turf (van den Hoek 81/8, 3.ix.1981; ADU, A52664). Bridgewater Bay, Vic., mid eulittoral wave-washed ledges, on Corallina (Womersley, 29.xii. 1981; ADU, A52657). Apollo Bay, Vic., low eulittoral with Hormosira (van den Hoek 81/13, 2.ix.1981; ADU, A52651—"Marine Algae of southern Australia" No. 220; and amongst Xiphophora, ADU, A52662). Near Orford, Tas., in rock pool (Cribb 170. 3, 23.i.1952; ADU, A21035). Safety Cove, Port Arthur, Tas., lower and mid eulittoral (Skinner, 21.ii.1978; ADU, A49240); lower eulittoral (Gordon, 13.i.1966; ADU, A30024).

Cl. subsimplex is a distinctive species, resembling *Cl. coelothrix* in habit (though smaller) and in the presence of frequent rhizoids, but differing in dimensions, in having much shorter cells, in the tapering apical cells, and in the terminal chains of short zooidangia. Specimens with long, curved, unbranched or little branched filaments may resemble *Rhizoclonium riparium* in habit but the filaments are much greater in diameter.

The type of *Cl. stuartii* in TCD represents the long, erect branches without the entangled base, but agrees well with *Cl. subsimplex*.

5. Cladophora prolifera (Roth) Kuetzing. van den Hoek 1963: 208, figs. 677-682, 686; 1982: 166, figs 318-327.

Cl. rugulosa Martens. Womersley 1956: 359.

FIGS 62A, 63A,B

Thallus (Fig. 62A) dark green, drying dark brown-green, sometimes light brown-green in lower eulittoral plants, forming dense spreading tufts to 15 cm high, with many stipes from a matted rhizoidal holdfast; filaments branched from almost every cell (Fig. 63A). Growth entirely acropetal with lateral branches arising usually from the subapical cell, and with one or commonly two (and then opposite) or occasionally three to five laterals (at acute angles) from each parent cell (Fig. 63A); cross walls at first steeply inclined to parent cell, less so in older parts. Basal and lower cells of stipes and older branches each producing a descending rhizoid which may branch and with annular constrictions; lower thallus cells often with annular constrictions over the lower 0.2-0.5 of their length (Fig. 63B).

Apical cells cylindrical with rounded to slightly tapering tips, (70-) 100-220 μ m in diameter, L/B 3-13; ultimate branch cells (70-) 100-220 μ m in diameter, L/B 2.5-13; basal stipe cells slightly clavate, 350-420 μ m in maximum diameter, L/B 5-22, sometimes tapering into a rhizoid; ratio of basal cell to apical cell diameters 1.5-3 (-5 in plants with narrow apical cells); cell walls relatively thin near apex (3-6 μ m), below 10-12 μ m thick and 20-30 μ m thick near base.

Reproduction (van den Hoek 1963, p. 209) by zoospores only, produced in upper cells following intercalary cell division.

Type from the Mediterranean; lost. *Neotype* from Trieste, Adriatic Sea, in L, 937, 264 ... 23 (see van den Hoek 1963, p. 208).

Distribution: Warm temperate Europe, Mediterranean, African and American tropics, Solomon Is, New Zealand.

In southern Australia, from Rottnest I., W. Aust. to Sorrento, Vic., as occasional occurrences in shallow pools on rough-water platforms and in the sublittoral.

Selected specimens: Esperance, W. Aust., upper sublittoral pools (Woelkerling, 21.ix.1968; ADU, A33944). Off St Kilda, S. Aust., 5 m deep (Lewis, 4.ix.1972; ADU, A42743). Granite I., Victor Harbor, S. Aust., drift near causeway (Womersley 16.iv.1976; ADU, A47202). Queenscliff, Vic., sublittoral on Amphibolis (SCUBA divers, 3.ix.1981; ADU, A52665). Koonya Bay, Mornington Pen., Vic., rear reef pool, shaded (Womersley, 15.i.1974; ADU, A44661—"Marine Algae of southern Australia" No. 221).

Cl. prolifera is a distinctive and widely distributed species, though not known from many localities in southern Australia; where it does occur (e.g. at Sorrento) it may be common. The form, dimensions, descending rhizoids and annular constrictions on lower cells make this an easily recognised species.

6. Cladophora bainesii Mueller & Harvey ex Harvey 1859a: pl. 112. Womersley 1956: 358.

FIGS 62B, 63C

Thallus (Fig. 62B) light to medium green, erect, (3-) 8–25 cm high, with one (or several) erect stipes basally attached by branched rhizoids; filaments gently tapering and much branched above every 1–2 (-4) cells, forming delicate, fastigiate tufts. Growth acropetal (intercalary divisions apparently absent in lower parts), with lateral branches first arising 2–6 cells from the apices (Fig. 63C) with ultimately 1–3 (-4) erect laterals (at acute angles) from each parent cell; cross walls at first oblique to parent cell, soon becoming almost horizontal.

Apical cells 14-25 (-35) μ m in diameter, L/B 7-24, linear to the tapering, obtuse to mucronate apices; ultimate branch cells 15-35 μ m in diameter, L/B 6-17; basal cells (150-) 200-300 (-600) μ m in maximum diameter, L/B (10-) 20-70; ratio of basal cell to apical cell diameters 7-10 (-30); walls 2-4 μ m thick above, relatively thick below (8-15 μ m), especially adjacent to cross walls.

Reproduction: upper cells are transformed into zooidangia by more or less frequent intercalary divisions. Each zooidangium opens by one apical pore, and the empty zooidangium is shed by means of a characteristic basal abscission ring in the sporangial wall. Quadriflagellate zoospores were observed once.

Lectotype from Port Phillip, Vic. (Harvey, Alg. Aust. Exsicc.579F); in Herb. Harvey, TCD; isolectotype in MEL, 597498.

Distribution: From Redcliff, Spencer Gulf, and Vivonne Bay, Kangaroo I., S. Aust. to Port Phillip, Vic. and around Tasmania.

Selected specimens: 5 km off Port Noarlunga, Gulf St Vincent, S. Aust., 21-24 m deep, (Ottaway, 3 and 8.xii.1980; ADU, A52111 and A52103 resp.). Port Phillip, Vic. (Mueller; ADU, A19730). Low Head, Tas. (Perrin, 1926: ADU, A47080). River Derwent (Est.), Tas., 15 m deep (Rodway, 4.xii.1909; HO 44880).

This seems to be a deep-water species.

Cl. bainesii is a distinctive species of Section Longiarticulatae Hamel (van den Hoek 1963, p. 208). It is slenderer than any other species of this group, and most closely related to

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Fig. 62. A. Cladophora prolifera (ADU, A52665). **B.** Cladophora bainesii (ADU, A42650). **C.** Cladophora feredayi, tufts (ADU, A32691). **D.** Cladophora feredayi, separated stipes (ADU, A52712).

the more robust *Cl. feredayi*, which is of similar habit but has apical cells $40-120 \mu m$ in diameter and generally broader lower and basal cells.

7. Cladophora feredayi Harvey 1858: pl. 47. van den Hoek 1963: 221, figs. 700, 701, 706. Womersley 1956: 358.

FIGS 62C, D, 63D, E

Thallus (Fig. 62C,D) light to medium green, erect, 3-25 (-35) cm high with a single or usually densely clustered erect stipes, with the basal cell attached by branched rhizoids; filaments tapering gradually, much branched above usually at almost every cell, forming fastigate tufts. Growth acropetal (intercalary divisions absent or only very few in lower cells), with lateral branches first arising 1-5 cells below the apical cell, with ultimately 1-5 erect laterals (at acute angles) from each parent cell; cross walls at first oblique to parent cell, soon becoming almost horizontal.

Apical cells (Fig. 63D) (35-) 40-120 (-135) μ m in diameter, L/B 6-25, linear to the tapering, obtuse to mucronate, apex; ultimate branch cells 40-170 μ m in diameter, L/B (3-) 6-14; basal stipe cells 350-600 (-800) μ m in maximum diameter, L/B 10-45; ratio of basal cell to apical cell diameters 5-12; walls thick, expecially in lower cells (25-60 μ m), lamellate.

Reproduction: Upper cells are transformed into zooidangia (Fig. 63E) by more or less frequent intercalary divisions, with a basal abscission ring.

Lectotype from Georgetown, Tas. (Harvey, Alg. Aust. Exsicc. 584J); in Herb. Harvey, TCD.

Distribution: From Cottesloe, W. Aust. around southern Australia to Port Jackson, N.S.W. and around Tasmania.

New Zealand. Madeira. Adriatic.

Selected specimens: Cottesloe, W. Aust. (Smith. Dec. 1944; ADU, A2074). 1 km S.E. of Wanna, S. Aust., 0-1 m deep (Johansen, 2.xi.1981; ADU, A52712). Barker Rocks, S. Aust., 1 m deep (van den Hoek 81/65, 20.ix.1981; ADU, A52627). Port Elliot, S. Aust., drift (Womersley, 17.x.1948; ADU, A9330). Robe, S. Aust., reef pools, shaded (Womersley, 9.ix.1968; ADU, A32691). Norman Bay, Wilsons Prom., Vic. (Ducker, 14.xi.1962; MELU, 212). Currie R., Tas. (Perrin & Lucas, Jan. 1936; HO,44867). Tinderbox Bay, S.E. Tas., 1 m deep (Ferris, 2.ix.1979; ADU, A51713). Derwent R. (Est.), Tas. (Rodway, Sept. 1909; HO,44876, 44883/4). Bluestone Bay, N. Freycinet Pen., Tas., 6-10 m deep (Brown, McGeary & Womersley, 4.xi.1982; ADU, A54152).

Cl. feredayi differs from *Cl. bainesii* in its more robust thallus with broader filaments; numerous stipes usually occur clustered together.

Variation within the specimens here referred to *Cl. feredayi* is very wide and largely overlaps with that of the widespread species *Cl. pellucida* (Hudson) Kuetzing, with which it is possibly conspecific. The apical cells vary greatly in diameter, with those of many specimens (e.g. ADU, A2074, A52627, HO, 44867 and 44876) within the range of 40–70 (-85) μ m, while those of others (e.g. ADU, A32691 and A51713) are mostly 70–120 μ m in diameter. However, the apical cells of A54152 are (65-) 75–110 (-140) μ m in diameter, those of A9330 are (45-) 60–80 (-90) μ m and those of A52712 are (45-) 50–80 (-120) μ m. In all cases the form of the plant is very similar, and the authors consider these all belong to one species which varies with age, rapidity of growth and probably with ecological situation.

 Cladophora valonioides Sonder 1845: 49: 1846: 149. Harvey 1859a: pl. 78. Lucas 1936: 27, fig. 10. Womersley 1956: 360.

FIGS 64A, 65A,B

Thallus (Fig. 64A) light to medium green, 3-18 (-25) cm high, singly or as clustered tufts of several plants, attached by rhizoids from the basal and adjacent cells; epilithic or epiphytic;



Fig. 63. A,B. Cladophora prolifera (ADU, A52665). A. Upper branch system. B. Lower branch system with descending rhizoids and annular constrictions. C. Cladophora bainesii (Type in TCD). Upper branch system. D,E. Cladophora feredayi (D, ADU, A24413; E, ADU, A52627). D. Upper branch system. E. Reproductive cell with basal abscission ring.
filaments tapering only slightly, much branched above from almost every cell, forming fastigiate to spreading tufts, filaments straight or slightly incurved (Fig. 65A). Growth acropetal and mainly apical above, with intercalary divisions in lower cells thus separating the lower laterals by 2-6 cells (Fig. 65A); laterals first arising 1-3 cells from apex, ultimately with each parent cell bearing 1-3 (-4) laterals of varying length, often to some extent unilaterally arranged and at acute to 45° angles (Fig. 65A). Cross walls arising and remaining oblique to parent cell, or later becoming almost horizontal.

Apical cells (Fig. 65B) 170-300 μ m in diameter, L/B 2-7, cylindrical with rounded ends; ultimate branch cells 170-280 μ m in diameter, L/B 2-6; basal cells 300-365 μ m in maximum diameter, L/B 2.5-14; ratio of lower cell to apical cell diameters 1-2; walls moderately thick, (4-) 6-8 μ m in apical cells, 20-30 μ m in mid thallus and 40-80 μ m in lower cells, lamellate.

Reproduction by apical or sub-apical cells developing into slightly swollen or clavate zooidangia.

Type from W. Australia, probably near Perth (*Preiss*); Holotype in MEL, 597564. Isotypes in Herb. Harvey, TCD (3 specimens) and MEL, 597565.

Distribution: From Champion Bay, W. Aust. to Guichen Bay, S. Aust., on rough-water rock platforms and extending to 25 m deep. This appears to be essentially a western species though common on the south coast of Kangaroo I.

Selected specimens: Near Perth, W. Aust. type material (MEL, TCD). Swan R., Perth, W. Aust., Alg. Aust. Exsicc. 587 (Herb. Harvey, TCD). Whitfords Beach, Perth, W. Aust., 4 m deep (Cook, 20.viii.1979; ADU, A50564). Ward I., W. of Flinders I., S. Aust., 18–23 m deep (Shepherd, 3.iii.1980; ADU, A50892). Elliston, S. Aust., reef surface (Womersley, 14.i.1951; ADU, A15128). Pearson I., S. Aust., 25 m deep (Shepherd, 28.iii.1982; ADU, A53016). Pennington Bay, Kangaroo I., S. Aust., drift (Womersley, 4.i.1948; ADU, A6592).

Cl. valonioides is a distinctive species of Section Glomeratae, being considerably greater in apical cell dimensions than other species (see van den Hoek 1963, p. 30; 1982, p. 128). The closest Australian species is Cl. lehmanniana, which has apical cells usually less than 150 μ m in diameter.

9. Cladophora lehmanniana (Lindenberg) Kuetzing 1843: 268. van den Hoek 1963: 122, figs 392-408.

FIGS 64B, 65C,D

Thallus (Fig. 64B) light to medium green, single or in clusters, forming pompons when small and fastigiate tufts when large, 2-15 (-30) cm high with the pseudodichotomous axes arising from a base of matted rhizoids from the lowest cells; epilithic or epiphytic; filaments tapering only slightly, much branched from almost every cell above with straight to falcate or refract and often unilaterally arranged branchlets (Fig. 65C). Growth acropetal and mainly apical above, with intercalary divisions in the mid and lower thallus cells thus separating the laterals by 2-8 cells but with few branches arising below intercalary cross walls; each parent cell bearing 1-2 (-3) laterals mostly at an angle of 45° or more, sometimes less; basal cross walls of laterals oblique to parent cell, later often becoming almost horizontal.

Apical cells (80-) 100-120 (-160) μ m in diameter, L/B 3-8, cylindrical, sometimes slightly inflated, with rounded apices; ultimate branch cells (85-) 100-120 μ m in diameter, L/B 2-6; lower thallus cells (140-) 180-220 (-250) μ m in maximum diameter, L/B 2-7; ratio of lower cell to apical cell diameters 1.5-2.5; cell walls thin to moderately thick (10-15 μ m) near the base.

Reproduction by somewhat inflated apical or subapical cells forming zooidangia; (Fig. 65D); in Europe by quadriflagellate zoospores (van den Hoek 1963, p. 124).

Type from Helgoland; isotypes in L (937, 281 . . . 47) and LD (9341-9343).

Distribution: Warm temperate Atlantic and Mediterranean coasts of Europe (van den Hoek 1963, p. 125).



Fig. 64. A. Cladophora valonioides (ADU, A53016). B. Cladophora lehmanniana (ADU, A34858). C. Cladophora laetevirens (ADU, A22489). D. Cladophora dalmatica (ADU, A52561). E. Cladophora vagahunda (ADU, A52692).

In southern Australia, from Geraldton, W. Aust. to Walkerville, Vic., and around Tasmania, in pools and shallow water under moderate water movement.

Selected specimens: Entrance to Kellidie Bay, Coffin Bay, S. Aust., very low eulittoral (*Womersley*, 22.viii.1967; ADU, A31818). Cape Carnot, S. Aust., low eulittoral (*Womersley*, 8.i.1951; ADU, A13802). Barker Rocks, Yorke Pen., S. Aust., upper sublittoral on *Cladostephus* (van den Hoek 81/65, 20.ix.1981; ADU, A52670). Pondalowie Bay, Yorke Pen., S. Aust., mid eulittoral on wave-washed ledges (van den Hoek 81/58, 19.ix.1981; ADU, A52616). Pondalowie Bay, Yorke Pen., S. Aust., shallow sublittoral rocks within sheltered inner bay (*Lipkin*, 19.ix.1981; ADU, A52617). Robe, S. Aust., upper sublittoral pools in bay (*Womersley*, 11.xii.1969; ADU, A34858—"Marine Algae of southern Australia" No. 222). Apollo Bay, Vic., low eulittoral pools, on *Cladostephus* (*Womersley*, 26.i.1964; ADU, A28054). Penquin, Tas., mid eulittoral (*Curtis*, 20.i.1954; HO, 44870). Orford, Tas., mid eulittoral pools (*Kingsbury*, 14.ii.1980; HO, 41515).

Cl. lehmanniana is closely related to the more robust Cl. valonioides (apical cells over 150 μ m in diameter) and to the less robust Cl. laetevirens (apical cells mostly less than 80 μ m in diameter). These three species have similar thallus organisation and development but are distinct on cell dimensions.

10. Cladophora laetevirens (Dillwyn) Kuetzing 1843: 267. Harvey 1848: pl. 190. van den Hoek 1963: 128, figs 409-429, 433, 440; 1982: 127, figs 238-261.

FIGS 64C, 65E

Thallus (Fig. 64C) light to medium green, forming dense tufts 2-10 cm high with pseudodichotomous axes from a small group of rhizoids from cells in the basal region; epilithic; filaments tapering only slightly, branched from almost every cell above with often somewhat falcate and unilateral branchlets. Growth acropetal and mainly apical above, with intercalary divisions in the mid and lower thallus cells thus separating the laterals by 2-6 cells (Fig. 65E) but with new laterals often arising below intercalated cross walls; each parent cell bearing 1-2 (-3) laterals mostly at about 45°; basal cross wall of young laterals usually oblique to parent cell, later becoming almost horizontal.

Apical cells 40-70 (-80) μ m in diameter, L/B 4-11, cylindrical to slightly broader in upper half, apically rounded; ultimate branch cells 40-75 μ m in diameter, L/B 4-7; lower thallus cells (100-) 120-160 (-180) μ m in maximum diameter, L/B 2-8 (-10); ratio of lower cell to apical cell diameters 2-3; cell walls moderately thin (2-4 μ m) in apical cells, thicker below (6-10 μ m).

Reproduction by apical and subapical cells forming zooidangia; in Europe by biflagellate gametes and quadriflagellate zoospores (van den Hoek 1963, p. 130).

Type from near Swansea, South Wales, U.K., in BM (ex K)—see van den Hoek (1963, p. 129).

Distribution: Widely distributed along tropical to warm-temperate Atlantic coasts of Europe, W. Africa and America (incl. Mediterranean) (van den Hoek 1982, p. 134, map 16).

In southern Australia, from South Perth, W. Aust., to Manly, N.S.W.

Selected specimens: Baird Bay, S. Aust., upper sublittoral (Womersley, 11.ii.1954; ADU, A19443). Venus Bay, S. Aust., upper sublittoral (Womersley, 17.i.1957; ADU, A13750). Sleaford Bay, S. Aust., reef pools (Womersley, 16.ii.1959; ADU, A22489). Ballast Head, Kangaroo I., S. Aust., lower eulittoral (Womersley, 31.x.1947; ADU, A6103).

Fig. 65. A,B. Cladophora valonioides (A, Isotype in TCD; B, ADU, A50892). A. Upper branch system. B. Upper branches to same scale as C-D. C-D. Cladophora lehmanniana (C, ADU, A52670; D, ADU, A52616). C. Upper branch system. D. Upper reproductive cells. E. Cladophora laetevirens (ADU, A22489). Upper branch system. F. Cladophora dalmatica (ADU, A52561). Upper branch system. G. Cladophora vagabunda (C. van den Hoek 81/65). Upper branch system.

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Cl. laetevirens is similar in habit and development to *Cl. lehmanniana* but is more slender. The apical cells are of greater diameter than those of *Cl. vagabunda* and the filaments of the latter increase in diameter more rapidly and to a greater extent than in *Cl. laetevirens*.

11. Cladophora dalmatica Kuetzing 1843: 268. van den Hoek 1963: 186, figs 435, 601-635; 1982: 150, figs 295-312.

FIGS 64D, 65F

Thallus (Fig. 64D) light to medium green, forming dense small tufts 1-2 cm high in areas subject to moderate wave-wash, or loose tufts to 10 cm high in calm-water areas, much branched from a clumped base attached by rhizoids from cells in the basal region, epilithic or epiphytic; filaments tapering distinctly from main axes towards apical cells, branched from almost every cell above, with usually distinctly falcate and unilateral branchlets (Fig. 65F). *Growth* acropetal and mainly apical above, with intercalary divisions in the mid and lower thallus cells thus separating the laterals by 2-5 or more cells but with few intercalated laterals below intercalary cross walls; each parent cell bearing 1-3 (-5) laterals mostly at an angle of 45° or more; basal cross walls of young laterals oblique (sometimes steeply inclined) to parent cell above, becoming almost horizontal later.

Apical cells $15-28 \ \mu\text{m}$ in diameter, L/B 3-9, cylindrical or slightly tapering, occasionally broader near their apex, apically rounded; ultimate branch cells $15-32 \ \mu\text{m}$ in diameter, L/B 4-9; lower thallus cells $65-140 \ \mu\text{m}$ in diameter, L/B 4-10; ratio of lower cell to apical cell diameters 3-6; cell walls thin (0.5-2 \ \mu\text{m}) above, relatively thick (up to $10 \ \mu\text{m}$) below.

Reproduction by apical and subapical cells forming zooidangia; in Europe by biflagellate gametes and quadriflagellate zoospores (van den Hoek 1963, p. 189).

Type from Port of Spalato (Split), Yugoslavia; in L, 937, 281 ... 406.

Distribution: Widely distributed along tropical to warm temperate Atlantic coasts of America, Europe and W. Africa (including Mediterranean) (van den Hoek 1982, p. 153-156, map. 18).

In southern Australia known from Baird Bay, S. Aust., upper sublittoral, mixed with *Cl. laetevirens* (*Womersley*, 11.ii.1954; ADU, A52569). Barker Rocks, Yorke Pen., S. Aust., mid eulittoral depressions (*van den Hoek* 81/63, 20.ix.1981; ADU, A52561—"Marine Algae of southern Australia" No. 224). Barker Rocks, Yorke Pen., S. Aust., low eulittoral, dense cushions composed of basal remnants (*Womersley*, 25.iii.1967; ADU, A31379). American R. Inlet, Kangaroo I., S. Aust., epiphytic on *Heterozostera* (*Womersley*, 26.ix.1946; ADU, A3154).

Cl. dalmatica has the typical glomerate habit and is distinguished from Cl. laetevirens and Cl. vagabunda by its slenderer habit, with apical cells less than 30 μ m in diameter. The filaments increase considerably in diameter, as in Cl. vagabunda, but in contrast to Cl. laetevirens, Cl. lehmanniana and Cl. valonioides where the increase is much more gradual and smaller.

12. Cladophora vagabunda (Linnaeus) van den Hoek 1963: 144, figs 434, 436-439, 470-503, 505-514; 1982; 137, figs 264-294.

Cl. fascicularis (Mertens ex C. Agardh) Kuetzing. Womersley 1956: 358.

Cl. ceratina Kuetzing 1845: 210. Womersley 1956: 360.

Cl. daveyana Reinbold 1899: 40. Lucas 1936: 29.

FIGS 64E, 65G

Thallus (Fig. 64E) light to medium green, forming densely branched tufts 2–6 cm high of fasciculate branch systems or more elongate strands 4–30 cm high, with numerous pseudodichotomous axes attached by rhizoids from the basal region, usually occurring under calm to moderate water movement, epilithic or sometimes epiphytic, also forming diffuse loose masses

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or attached plants in lagoons and saltmarsh ponds; filaments branched from almost every cell above with slightly falcate or straight and usually unilateral fascicles (Fig. 65G), with the filaments increasing markedly in diameter shortly below the apical cells or just below the fascicles; in lagoon plants these fascicles are less distinct. *Growth* acropetal and mainly apical above, with intercalary divisions in the mid and lower thallus cells thus separating the laterals by 2–8 or more cells, with occasional intercalated laterals arising below new cross walls; especially in lagoon plants this intercalary growth may be conspicuous; parent cells bearing 1-3(-6) laterals at acute to (usually) broad angles; basal cross walls of laterals oblique to parent cells, becoming later almost horizontal.

Apical cells (25-)30-50(-70) μ m in diameter, L/B 2-16, cylindrical or often tapering, with rounded apices; ultimate branch cells 25-90 μ m in diameter, L/B 2-17; lower thallus cells 85-215 μ m in maximum diameter (mostly about 150 μ m), L/B 1.5-10; ratio of mid and lower cell to apical cell diameters 2-4(-6); pale plants from lagoons and saltmarsh ponds tend to be slenderer and longer celled; cell walls 1-3 μ m thick above, becoming 10-15 μ m thick and lamellate below.

Reproduction by apical and subapical cells forming zooidangia; in Europe, by biflagellate gametes and quadriflagellate zoospores (van den Hoek 1963, p. 149).

Type from Selsey, England; in OXF (see van den Hoek 1963, pp. 19, 144).

Distribution: Cosmopolitan in tropical and temperate waters, on sublittoral and lower eulittoral rocks, in rock pools, in lagoons and saltmarsh ponds.

From north of Perth (e.g. from N.W. Cape), W. Aust., around southern Australia and Tasmania to Bowen, Qld. Probably a widely distributed species on most coasts of Australia.

Selected specimens: Point Drummond, S. Aust., mid eulittoral sheltered pool (Womersley, 11.i.1951; ADU, A15024). Coffin Bay, S. Aust., upper sublittoral on flats (Womersley, 10.i.1951; ADU, A13632). Barker Rocks, Yorke Pen., S. Aust., 0.5–1 m deep, on *Cladostephus (van den Hoek* 81/65, 20.ix.1981). Coobowie, Yorke Pen., S. Aust., at outflow within lagoon (van den Hoek 81/55, 18.ix.1981; ADU, A52692). American R. inlet, Kangaroo I., S. Aust., on sides of red buoy (Womersley, 25.1.1946; ADU, A3469). North Arm, Port Adelaide, 0.1-0.5 m deep, on pontoons of Commercial Fishing Marina (van den Hoek 81/69, 1.x.1981; ADU, A52643). Coorong, S. Aust., in shallow water 38 km S. of Meningie (Womersley, 31.xii.1981; ADU, A52834). Robe, S. Aust., in drain outlet (Womersley, 31.i.1951; ADU, A52144). Fawthrop Lagoon, Portland, Vic., on stones, shallow, very calm (Womersley, 29.xii.1981; ADU, A52862, A52861). Apollo Bay, Vic., in shallow, brackish lagoon (van den Hoek 81/16, 1.ix.1981; ADU, A52678). Opossum Bay, Port Arthur, Tas., on shell (Cribb 125.4, 5.ii.1951; HO, 44875).

Cl. vagabunda is closely related to *Cl. dalmatica*, differing in its greater diameters and in the marked increase in filament diameter within the upper fascicles though this is less clear in pale plants from lagoons and saltmarsh ponds.

13. Cladophora hutchinsioides van den Hoek & Womersley sp. nov.

FIGS 66A, 67A-D

Thallus (Fig. 66A) medium to dark green, 5–20 cm high, erect, not tufted, loosely to moderately densely branched, more or less flabellate when young, composed of strands of coarse, branched filaments when older, arising from a small basal disc developing radiating rhizoids (Fig. 67C), growing on solid substrates; filaments fairly uniform in diameter to the upper, tapering branchlets, branched largely adaxially (Fig. 67A, B) every few cells above but with long rows of short unbranched cells below (Fig. 67D) and often ending in long unbranched rows of swollen zooidangia. Growth very largely intercalary, with apical and subapical cell divisions above and when young distinctly acropetal; laterals becoming separated by few to many cells when older, composed of coarse pseudodichotomous main filaments bearing unilateral rows of branchlets mainly above, and mostly conspicuously bare below; parent cells

bearing normally only one lateral (occasionally 2) at an angle of about 45°; basal cross walls of laterals oblique, later becoming almost horizontal below.

Apical cells (Fig. 67A,B) usually markedly tapering with obtuse tips, $60-120 \mu m$ in basal diameter and L/B 1.5-3; ultimate branch cells $70-180 \mu m$ in diameter, L/B 1-4; lower thallus cells $200-300 \mu m$ in maximum diameter, L/B 1-5; ratio of lower cell to apical cell diameters 2.5-3.5; cell walls relatively thin above (2-4(-6) μm), thick and lamellate below (up to 20 (-30) μm).

Reproduction by terminal chains of cells becoming slightly swollen zooidangia (Fig. 67D).

Diagnosis: Thallus laete-sive atro-viridis, 5-20 cm altus, moderate non dense ramosus, junior flabelliformis ordinatione distincte acropetali, adultus ex filamentis grossis praecipue irregulariter ramosis seriebus ramellorum longitudine diversa ferentibus compositus. Increscentia praecipue divisionibus intercalaribus. Filamenta terminalia plerumque zooidangiorum seriebus terminata. E cellula axiali unus, raro duo rami oriri possunt ad angulum c.45°. Cellulae apicales conicae apicibus obtusis diametro $60-120 \,\mu\text{m}$, long./diam. 1.5-3. Cellulae versus thalli basin diametro 200-300 μm , long./diam. 1-5.

Type locality: Port Adelaide, S. Aust. 0.3-1 m below water level on old barge at Harbours Board Wharf. (Womersley, 25.xi.1957).

Holotype: ADU, A21325.

Distribution: Apart from the type, known from Topgallant I., off W. coast of Eyre Pen., S. Aust., 20–25 m deep (Shepherd, 8.xi.1980; ADU, A51880). North Arm, Port Adelaide, S. Aust., 0.3–0.5 m deep on Commercial Fishing Marina (Womersley & van den Hoek, 1.x.1981; ADU, A52644 and Womersley, 10.iii.1982; ADU, A52980). Port Phillip, Vic. 0–0.5 m deep at Power Station outfall (Watson, 1.v.1972; ADU, A42340).

This species is similar in morphology and habit to the European *Cl. hutchinsiae* (Dillwyn) Kuetzing (see van den Hoek 1963: 60, figs 131-145) but differs in its smaller dimensions. However, the type of *Cl. daviesii* Harvey (1855b, p. 263) from New Zealand (herb. Harvey, TCD) does belong to the form range of European *Cl. hutchinsiae*, and has similar dimensions.

14. Cladophora montagneana Kuetzing. van den Hoek 1982: 105, figs 145-173.

FIGS 66B, 67E-I

Thallus (Figs 66B, 67F) medium to dark green, forming delicate soft tufts of slender short-celled filaments, one to several cm high, attached by rhizoids in the basal region; or forming 1-4 cm long, loose, dark green, entangled, irregular aggregates in protected bays; composed of distinct main axes which mostly bear several strongly developed main laterals (Fig. 67E,F) with which they form pseudodichotomies; the axis and main laterals may be lined with mostly unilateral rows of tapering branchlets (Fig. 67E1), or be bare over long stretches (Fig. 67E2, G,H). Growth almost exclusively intercalary, with branchlets many cells apart on upper filaments (Fig. 67E1,2); some old plants may be densely branched; parent cells usually with a single lateral, occasionally two, in some densely branched plants up to 4 (Fig. 67F) arising at broad angles (45° or more); basal cross walls of laterals steeply inclined to oblique, in older laterals becoming almost horizontal.

Apical cells (Fig. 671) usually tapering to obtuse apices, $20-30 \ \mu\text{m}$ in diameter and L/B 1.5-4; ultimate branch cells $22-56 \ \mu\text{m}$ in diameter and L/B 1.2-2.5; lower thallus cells 45-70 (-90) μm in diameter, L/B 1-2.5; ratio of basal cell to apical cell diameters 2-4; cell walls $1-3 \ \mu\text{m}$ thick above, up to 10 μm thick and lamellate below.

Reproduction (van den Hoek 1982, p. 107) by long moniliform rows of zooidangia.

Type from Cuba (Montagne); in BM (ex K).

Distribution: Widely distributed along tropical to warm temperate Atlantic coasts of America and Africa (van den Hoek 1982, p. 110, map 13)

In southern Australia, known from Falcon Bay, Peel Inlet, W. Aust., thalli 1-4 cm across and forming loose aggregates ("aegagropilas") massed to 10 cm deep in water 1.5 m deep



Fig. 66. A. Cladophora hutchinsioides (Holotype). B. Cladophora montagneana (ADU, A51018). C. Cladophora albida (ADU, A52682). D. Cladophora crinalis (ADU, A52690).

(Gordon, Dec. 1979; UWA 2806; ADU, A51018). Outer Harbour, S. Aust., low eulittoral on piles (Womersley, 15.vi.1955; ADU, A19900).

Cl. montagneana is a slender species, distinguished by the long, unbranched, short-celled filaments, often with scattered spinous branchlets which extend through most of the thallus. Australian material agrees well with that from the Caribbean, but the Peel inlet plants are considerably more robust than the Outer Harbour specimen.

This species shows a superficial resemblance to the erect filaments of *Cl. subsimplex*, but it lacks this latter species basal tangle of filaments with cells frequently producing a descending rhizoid from their basal poles. *Cl. subsimplex* is also more robust.

15. Cladophora albida (Hudson) Kuetzing. van den Hoek 1963: 94, figs 231-244, 246-316; 1982: 100, figs 133-137, 144.

Cl. gracillima Kuetzing 1849: 400.

Cl. gracillima Harvey 1859b: 340.

Cl. harveyi Womersley 1956: 359.

FIGS 66C, 68A-D

Thallus (Fig. 66C) light to medium green, forming densely branched pompons or dense tufts 0.5-5(-7) cm high, usually in the lower eulittoral on medium to rough-water coasts, with numerous gently tapering axes from a tightly clumped base, irregularly to often unilaterally branched with older and newer laterals inter-mixed (Fig. 68A-C); normally epilithic, attached by rhizoids from basal and often sub-basal cells. Growth weakly (Fig. 68B) or distinctly acropetal (Fig. 68A) (with straight or refract or falcate, mostly unilateral, branchlets) but with frequent intercalary divisions, new cells usually producing a lateral but with occasional rows of several unbranched cells (Fig. 68B); parent cells with 1-2(-3) laterals at acute to broad angles; basal cross walls of laterals steeply inclined to oblique, becoming almost horizontal in older main branches.

Apical cells (Fig. 68D) cylindrical, $16-32 \mu m$ in diameter and L/B 2-6.5; ultimate branch cells $18-32 \mu m$ in diameter and L/B 2-4; lower thallus cells $40-80 \mu m$ in maximum diameter and L/B 2-8; ratio of lower cell to apical cell diameters 2-3; cell walls $0.5-1 \mu m$ thick above, $6-8 \mu m$ thick and lamellate below.

Reproduction by terminal rows of cells forming swollen zooidangia (Fig. 68D); in Europe (van den Hoek 1963, p.100) by biflagellate gametes and quadriflagellate (or biflagellate) zoospores.

Type from Island of Selsey, England (Dillenius); in OXF (see van den Hoek 1963: 94).

Distribution: Widely distributed in temperate waters.

In southern Australia, from North Beach (Perth), W. Aust. to Port Jackson, N.S.W.

Selected specimens: Watermans Bay Perth, W. Aust., reef surface, low eulittoral (*Womersley*, 3.ix.1979; ADU, A50987). Point Sinclair, S. Aust., lower part of mid eulittoral, W. side of granite point (*Womersley*, 7.ii.1954; ADU, A19581). Barker Rocks, Yorke Pen., S. Aust., lower eulittoral depressions (van den Hoek 81/63; ADU, A52567). Pondalowie Bay, Yorke Pen., S. Aust., mid eulittoral wave-washed ledges (van den Hoek 81/58, 19.xi.1981; ADU, A52684). Ardrossan, Yorke Pen., S. Aust., low eulittoral, (van den Hoek 81/67, 20.ix.1981; ADU, A52686). Cape Lannes, S. Aust., mid eulittoral wave-washed rocks (van den Hoek 81/1,

Fig. 67. A-D. Cladophora hutchinsioides (ADU, A21325). A,B. Upper branch systems. C. Basal cell with attachment rhizoids. D. Upper branches with zooidangia. E-I. Cladophora montagneana (E,F ADU, A51018; G-I, ADU, A19900). E1, 2,F. Upper filaments showing branching. G,H. Filaments from upper thallus. I. Apical cells.



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6.ix.1981; ADU, A52369). Portland, Vic., low eulittoral in harbour (van den Hoek 81/5, 3.ix.1981; ADU, A52681). Point Lonsdale, Vic., lower eulittoral (van den Hoek 81/6, 31.viii.1981; ADU, A52682).

Cl. albida is similar in habit, branching and growth to *Cl. sericea* but is distinct in having apical cells with rounded tips and in dimensions of the apical cells and older filaments, in the smaller ratio of lower cell to apical cell diameters and in the often refract to falcate terminal clusters (which often show a distinct acropetal organization). *Cl. albida* may often resemble *Cl. dalmatica* (especially when having acropetal clusters), but differs by its lower shorter cells (produced by frequent intercalary divisions) and its smaller ratio of lower cell to apical cell diameters.

16. Cladophora crinalis Harvey 1855b; 263. Chapman 1956: 449, fig. 102.

FIGS 66D, 68E-G

Thallus (Fig. 66D) medium to dark green, in dense tufts 2–10 cm high and up to 4 cm across, with numerous axes gently tapering towards the apical cells; main filaments basally unbranched or pseudodichotomous, ending in more or less penicillate branch systems (Fig. 68E) and attached by rhizoids from cells in the basal region (Fig. 68G); epilithic. Growth weakly or distinctly acropetal in the terminal fascicles (with straight, mostly unilateral and appressed branchlets), but with frequent intercalary divisions (Fig. 68E), new cells often producing a lateral but also with rows of several unbranched cells; parent cells with 1-2(-3) laterals at acute angles; basal cross walls of laterals oblique, soon becoming horizontal.

Apical cells (Fig. 68E,F) cylindrical with slightly tapering tips, 50-80 μ m in diameter and L/B 3.5-8; ultimate branch cells 55-90 μ m in diameter and L/B 2.5-6; lower thallus cells 80-130 μ m in maximum diameter and L/B 2-8; ratio of lower cell to apical cell diameters 1.5-2.5; cell wall 1.5-2.5 μ m thick in upper cells, up to 16 μ m thick in lower cells.

Reproduction by terminal rows of short, swollen, zooidangia (Fig. 68F), the apical ones with a mamilliform tip; the terminal fascicles may entirely disintegrate by sporulation.

Type from New Zealand (Colenso); in Herb. Harvey, TCD.

Distribution: New Zealand.

In southern Australia, from Venus Bay, S. Aust. to Walkerville Vic. and around Tas. on low eulittoral and upper sublittoral wave-washed rocks.

Selected specimens: Venus Bay, S. Aust., mid eulittoral, shaded (Womersley, 17.i.1951; ADU, A14959). Cape Lannes, S. Aust., mid eulittoral wave-washed rocks (van den Hoek 81/ 1; ADU, A52367). Stinky Bay, Nora Creina, S. Aust., mid eulittoral wave-washed ledges (van den Hoek 81/9a, 5.ix.1981; ADU, A52690). Bridgewater Bay, Vic., mid eulittoral pools (Womersley, 29.xii.1981; ADU, A52851—"Marine Algae of southern Australia" No. 223). Point Lonsdale, Vic., lower eulittoral (van den Hoek 81/6, 31.viii.1981; ADU, A52688). Sandy Cape, Tas., mid eulittoral (Bennett 23, 5.i.1954; ADU, A19724). Blackmans Bay, Tas., lower eulittoral (Curtis, 3.xi.1957; HO, 44868). Retreat, R. Derwent, Tas. (Rodway, Sept.1909; HO, 44877).

Cl. crinalis is similar to Cl. sericea, from which it differs by growing in dense tufts, by having cylindrical apical cells with slightly tapering tips (instead of the whole apical cell tapering), and by the relatively small increase in diameter from apical cells to main axes.



Fig. 68. A-D. Cladophora albida (A,B, ADU, A52369, C,D, ADU, A52567). A-C. Upper branch systems. D. Reproductive filaments. E-G. Cladophora crinalis (ADU, A52367). E. Branch system. F. Upper filaments with zooidangia. G. Base of thallus.

17. Cladophora sericea (Hudson) Kuetzing. van den Hoek 1963: 77, figs 184-240, 245; 1982: 93, figs 138-143.

Cl. gracilis (Griffiths ex Mackay) Kuetzing. Womersley 1956: 359.

Cl. thoreana Kuetzing. Tate 1882: 93. Womersley 1956: 361.

FIGS 69A, 70A,B

Thallus (Fig. 69A) light to medium green, to 25 cm high, forming densely branched erect tufts of one to several pseudodichotomous main axes attached by rhizoids from cells in the basal region (Fig. 70B); these axes bear branch systems composed of filaments which are lined with unilateral rows of appressed branchlets but often with long series of unbranched cells throughout the thallus; main axes distinctly tapering towards the apical cells (Fig. 70A). Growth mainly intercalary, resulting in a feebly acropetal to irregular organisation, the main filaments lined in parts with rows of branches and branchlets (Fig. 70A), the younger ones intercalated between the older (longer) ones; parent cells with 1-2(-3) laterals at an acute angle, basal cross wall of laterals oblique, soon becoming horizontal.

Apical cells (Fig. 70A) more or less tapering, $30-55 \ \mu m$ in diameter and L/B 3-10; ultimate branch cells $30-95 \ \mu m$ in diameter and L/B 2.5-9; lower thallus cells $130-170 \ \mu m$ in maximum diameter and L/B 1.5-6.5; ratio of lower cell to apical cell diameters 2.5-4; cell walls $2-4 \ \mu m$ thick in apical cells, $4-10 \ \mu m$ thick in mid cells and $15-20 \ \mu m$ thick below.

Reproduction (van den Hoek 1963, p. 79) by biflagellate gametes and quadriflagellate (sometimes biflagellate) zoospores formed in chains of short, swollen terminal zooidangia.

Type from England; in OXF (see van den Hoek 1963, p. 77).

Distribution: Widely distributed along cool to warm temperate N. Atlantic, N. Pacific and Southern Hemisphere shores (van den Hoek 1982, p. 96).

In southern Australia from Coffin Bay, S. Aust. to Port Phillip, Vic. and around Tasmania, usually in sheltered bays.

Selected specimens: Entrance to Kellidie Bay, Coffin Bay, S. Aust., very low eulittoral (*Womersley*, 22.viii,1967; ADU, A31817). Kirk Point, Port Phillip, Vic., shallow sublittoral (van den Hoek 81/4, 30.viii.1981; ADU, A52687). Port Effingham, Tamar Est., Tas. (*Perrin & Lucas*, Jan. 1930; HO, 44863-4). Stewarts Bay, Port Arthur, Tas., 3-7 m deep (*Cribb*, 13.vi.1951; ADU, A21041). Southport, Tas., on *Hormosira* (*Cribb* 44.11, 21.iii.1950; HO, 44888).

Cl. sericea is similar to *Cl. crinalis* from which it differs by not forming dense tufts of many axes, by having tapering instead of cylindrical apical cells (with slightly tapering tips), and by the more pronounced increase in diameter from apical cells to main axes. The branched habit with laterals of different ages intermixed is quite characteristic.

 Cladophora vadorum (Areschoug) Kuetzing 1849: 402. van den Hoek 1963: 141, figs 430-432, 441-454, 456-469.

FIGS 69B, 70C

Thallus (Fig. 69B) medium to light green, 5-30 cm high, flexuous, not tufted, attached by rhizoids from cells in the basal region; occasionally as floating masses; a species from sheltered areas. Main axes pseudodichotomous, ending in branch systems with a vaguely acropetal to irregular organisation with patent branches quite widely spaced (Fig. 70C). Growth by divisions of conspicuous apical cells and by intercalary divisions, very feebly acropetal; parent cells usually with only a single lateral, occasionally two, usually at an obtuse angle (more than 45°); basal cross wall of laterals steeply inclined to oblique, becoming almost horizontal below.

Apical cells cylindrical with rounded to tapering tips, $30-50 \ \mu\text{m}$ in diameter and L/B 7-13; ultimate branch cells $40-65 \ \mu\text{m}$ in diameter and L/B 5-10; main lower thallus cells $65-120 \ \mu\text{m}$ in diameter and L/B 3-10; ratio of lower cell to apical cell diameters 2.5-4; cell walls thin $(1-2 \ \mu\text{m})$ in upper cells, becoming $10-20 \ \mu\text{m}$ thick in oldest parts.



Fig. 69. A. Cladophora sericea (ADU, A31817). B. Cladophora vadorum (ADU, A32744). C,D. Wittrockiella salina, C. (ADU, A53315), D. (ADU, A53084).

Cladophora



Fig. 70. A,B. Cladophora sericea (ADU, A52687). A. Upper branch system. B. Base of thallus with rhizoids. C. Cladophora vadorum (ADU, A32744). Upper branch system.

CLADOPHORACEAE

Type from Göteborg, Sweden. Isotype in L, 937, 155 . . . 109.

Distribution: Scattered protected and estuarine localities along tropical to warm temperate Atlantic coasts of Europe, West Africa and America (van den Hoek 1982, p. 160, map 19).

Known in southern Australia from one record: Crawfish Rock, Westernport Bay, Vic., pools, just sublittoral (*Watson*, 15.ix.1968; ADU, A32744). This is a 6 cm high attached plant whose characters are within the range of *Cl. vadorum*.

Cl. vadorum shows some similarity to *Cl. sericea* and calm water forms of *Cl. vagabunda*. It differs from *Cl. sericea* by its longer cylindrical apical cells, and by its much scarcer ramification with spaced patent laterals; it differs from *Cl. vagabunda* by being thicker, by lacking distinct acropetal fascicles, and by its more sparse branching.

Genus WITTROCKIELLA Wille 1909: 16, pls 1-4

Thallus usually as coarse, entangled mats or floating balls of irregularly branched filaments of multinucleate cells, attached by tapering, multicellular rhizoids. Cells short (L/B usually 1-2 in mature cells), of irregular shape and size (usually not cylindrical), the upper cells with occasional, slender, colourless hairs but these not present in some thalli; chloroplasts parietal, reticulate to rounded and numerous, with pyrenoids.

Reproduction by zooids, akinetes and aplanospores (Wille 1909, p. 17).

Type species: W. paradoxa Wille.

A genus of three species, the type from Europe. *W. salina* from Australasia and *W. lyallii* from New Zealand (van den Hock, Ducker & Womersley 1984).

Wittrockiella salina Chapman 1949: 495, fig. 1; 1956: 469, fig. 129. van den Hoek, Ducker & Womersley 1984: 39, figs 1-4.

Cladophorella marina Chapman 1956: 442, fig. 92b,c. Beanland & Woelkerling 1982; 94.

FIGS 69C,D, 71

Thallus (Fig. 69C,D) dark green, coarse, forming *either* prostrate branch systems scarcely visible on the substrate, *or* densely branched mats 1–6 cm across and 3–7 mm thick, *or* subspherical to ovoid, free floating, hollow balls 1–12 cm in diameter (Fig. 69C). *Filaments* (Fig. 71A,C,E,F) rigid, interwoven, usually of similar diameter throughout apart from slenderer, young filaments, producing one (rarely 2) branches from most cells and many lower cells with 1–2 subterminal, multicellular, tapering rhizoids from their lower sides; hairs (seen on Cape Bridgewater collections only) slender, unicellular, colourless (Fig. 71A). *Growth* largely apical, laterals usually subterminal and at a wide angle to parent cells but sometimes becoming sub-parallel, with their basal cross wall vertical to steeply inclined to parent cell; cells usually irregular in shape, with curved and often bulging walls (Fig. 71A); chloroplasts parietal, discoid and numerous or tending to form a reticulum, variable in size (often angular), the larger with a pyrenoid (Fig. 71D); oil droplets present.

Apical cells cylindrical or tapering, with rounded tips, (60-)90-200 μ m in diameter, L/B 1.5-4(-9); lower mature cells 100-300 μ m in diameter, L/B 0.8-3; ratio of basal cells to apical cell diameters 1-3(-6); wall 2-8 μ m thick in apical cells, 10-15 μ m thick below.

Reproduction unknown.

Type from Stanmore Bay (near Auckland), New Zealand; not located in AK.

Distribution: New Zealand (Auckland region north).

In Australia, from Spencer Gulf, S. Aust. (see Beanland & Woelkerling 1982, Table 4) to Lake Bunga, Vic., and from Huon R. mouth, Tas. and Avoca Lagoon, N.S.W.

Selected specimens: Ardrossan, S. Aust., mid eulittoral on jetty piles, shaded (van den Hoek & Womersley, 20.ix.1981; ADU, A53566). Onkaparinga Estuary at Old Noarlunga, on pebbles and fallen tree trunks, emergent at low water (Womersley, 10.iii.1983; ADU, A54012). Nelson lagoon, Vic., lower eulittoral (Beauglehole; 10.v.1959; ADU, A24805 and Womersley, 29.xii.1981 and 14.v. 1982; ADU, A52838 and A53084 resp.). Cape Bridgewater, Vic., very high rock pool (van den Hoek, 3.ix.1981; ADU, A52650). "Moss Ball Pool" (Mullachie Swamp), off Bunga Arm of Lake King, S.W. of Lakes Entrance, Vic., as floating balls (Ducker 1423, 28.v.1964; ADU, A52350 and 11.v.1976; MELU, 22328). Lake Bunga (N.E. of Lakes Entrance), Vic., in a side arm of lake (Womersley, 12.xi.1982; ADU, A53827—"Marine Algae of southern Australia" No. 232).



Fig. 71. Wittrockiella salina. A. Filaments from Cape Bridgewater, with slender hairs (ADU, A52650). B. Base of a hair (ADU, A52650). C. Filaments from jetty piles at Ardrossan (ADU, A52566). D. Chloroplasts with bilenticular pyrenoids (ADU, A52566). E. Filaments from ball form from Gippsland Lakes (MELU, 22328). F. Filaments from Nelson Lagoon (ADU, A24805). All figures from van den Hoek, Ducker & Womersley 1984.

This species is discussed by van den Hoek, Ducker & Womersley (1984). It shows a remarkable range of variation from filaments forming a thin, microscopic layer on wooden jetty piles at Ardrossan, to coarse mats a few centimetres across and with much associated mud sediment in the Onkaparinga Estuary and at Nelson lagoon, to the extensive mats in a side pool of Lake Bunga, and to the remarkable, floating aegagropila type balls in Mullachie Swamp off Lake King. In the Onkaparinga Estuary, the mats are very much reduced during winter freshwater river flow.

FAMILY ANADYOMENACEAE Hauck

Thallus reticulate, essentially monostromatic, stipitate or not, attached by rhizoids from basal segments or the stipe, flabellate or ovate or becoming irregular with an obscure base. Blade formed by anastomoses of un-modified or modified segments (tenacula), with the network remaining open or becoming largely filled in by development of small lateral cells. Cells multinucleate, dividing by ingrowth from the lateral walls. Homoplastic, chloroplast reticulate with numerous pyrenoids.

Life history of isomorphic generations, with biflagellate anisogametes and quadriflagellate zoospores.

The three genera described below were earlier placed in the Siphonocladales, but several species have been shown to have centripetal cross wall formation and not segregative division. Some authors (e.g. Egerod 1952, p. 332) maintain two families on the basis of the presence or not of tenacula connecting lateral branches to other branches and the development of juvenile stages. On this basis, *Microdictyon* and *Anadyomene* belong to the Anadyomenaceae and *Struvea* to the Boodleaceae (with tenacula). Such differences are of generic significance but doubtfully of family significance.

KEY TO THE GENERA OF ANADYOMENACEAE

- 1. Thallus with obscure base, becoming irregular; blade network open, meshes irregular MICRODICTYON
- - 2. Thallus flabellate, blade network largely closed with small cells, stipe cells not markedly larger than cells of the veins, tenaculae absent ANADYOMENE

Genus MICRODICTYON Decaisne 1841: 115

Thallus composed of non-stipitate, reticulate blades with open meshes, holdfast usually obscure; primary and secondary cell filaments forming veins, branching opposite, alternate or flabellate, anastomosing by means of un-modified tertiary cells; cross walls formed by ingrowth from periphery (Enomoto & Hirose 1971).

Reproduction with isomorphic generations, the sporophyte producing quadriflagellate zoospores and the gametophyte biflagellate isogametes (Iyengar & Ramanathan 1941).

Type species: M. agardhianum Decaisne.

A genus of some 20 species (Setchell 1929), largely tropical or subtropical, with one species known from southern Australia.



Fig. 72. Microdictyon umbilication (ADU, A51823). A. Thallus. B. Branching pattern of the net. C. Detail of branching of the net.

Microdictyon umbilicatum (Velley) Zanardini. Setchell 1929: 503, figs 21-27. Womersley 1956: 362.

FIG. 72

Thallus (Fig. 72A) medium to dark grey-green, 10–30 (-45) cm across, firm but delicate, irregularly lobed and lacerate, with an obscure umbilicate base, probably usually epiphytic. Blade essentially monostromatic but with occasional tertiary branches displaced to one side of an earlier branch; branching of filaments alternate, opposite, or with up to six secondary filaments radiating from one point (Fig. 72B). Primary filaments 180–220 μ m in diameter, cells L/B 1.5–3; secondary filaments 80–140 μ m in diameter, L/B 2–4, with a rounded tip when free; attachment of filaments by smooth adherence of un-modified ultimate segments (Fig. 72C); meshes of net irregular; division of segments by ingrowth from the peripheral wall; chloroplast reticulate, composed of numerous, round, pyrenoid-bearing areas with narrow connections.

Reproduction unknown.

Type from New South Wales (Port Jackson?); holotype in LIV.

Distribution: Rottnest I. and Cape Riche, W. Aust and from Coobowie, Yorke Pen. to Victor Harbor, and American River Inlet, Kangaroo I., S. Aust., Port Jackson, N.S.W. and Southport, Qld. Usually in calm bays and inlets. New Zealand? (Chapman 1956, p. 441).

Selected specimens: Cape Vlaming, Rottnest I., W. Aust., lower eulittoral (*Smith*, Nov. 1951; ADU, A50594 and UWA 310). Cape Riche, W. Aust. (*Harvey*, Alg. Aust. Exsicc. 568C, in NSW). Coobowie, S. Aust., uppermost sublittoral (*Brock*, 17.x.1980; ADU, A51823 and *Womersley*, 12.ii.1981; ADU, A51994—"Marine Algae of southern Australia" No. 225). E. side of Ballast Head, Kangaroo I., S. Aust., drift (*Womersley*, 28.xii.1948; ADU, A10461). Balmoral, Port Jackson, N.S.W. (*Lucas*, Dec. 1932; ADU, A62). Nerang R., Southport, Qld (*Cribb* 53.1, 11.v.1950; ADU, A14460).

M. umbilicatum is a distinctive species growing under moderate water movement only. Superficially it can apppear like an *Ulva* until its reticulate thallus is observed.

Genus ANADYOMENE Lamouroux 1812: 187

Thallus foliose, flabellate, monostromatic or becoming corticated, attached by rhizoids from the lower stalk and adjacent cells. *Blade* formed by polychotomous, flabellate, primary cell rows, with the interstices becoming closed by smaller lateral cells; growth marginal, with the primary cells becoming smaller above; cell division by peripheral cross wall formation.

Reproduction by the sporophyte producing quadriflagellate zoospores, and male and female gametophytes producing isogametes or anisogametes (Enomoto & Hirose 1970, for *A. wrightii*).

Type species: A. stellata (Wulfen) C. Agardh.

A genus of some 10 species, largely confined to tropical and subtropical seas. A. brownii (Gray) J. Agardh occurs around northern Australia and as far south as Port Denison, W. Aust., but the tropical---subtropical A. stellata is known from a single locality in southern Australia.

Anadyomene stellata (Wulfen) C. Agardh. Boergesen 1913: 25; 1925: 25, figs 2, 3. Bold & Wynne 1978: 215, fig. 3.151. Mayhoub 1975: 587, figs 1-4. Taylor 1960: 125, pl. 7 fig. 2, pl. 8 fig. 2. Womersley 1981c:303.

FIG. 73A

Thallus (Fig. 73A) dark green, growing in mats or tufts, flabellate, ovate to reniform, 2-10 mm high and across, with 1-4 basal stipe cells attached by a cluster of slender rhizoids

with occasional cross walls. *Blade* monostromatic, with a primary system of elongate-clavate cells bearing at their apices 3-6 similar but progressively smaller cells, with the interstices largely to entirely filled with smaller cells (Fig 73A) cut off laterally from the primary cells and joined to adjacent cells with a smooth attachment. Chloroplast closely reticulate, becoming fragmented, with rounded areas of variable size (the larger containing pyrenoids) joined by narrow connections.

Reproduction with isomorphic generations, the gametophytes dioecious, anisogamous and the sporophyte producing quadriflagellate zoospores (Mayhoub 1975), or reproducing by zoospores only (Jonsson 1962).

Type from the Adriatic sea, Mediterranean.

Distribution: Widely distributed in the Mediterranean and tropical and sub-tropical coasts of the Americas and the Indo-Pacific. Commonly found as a short mat in shaded intertidal areas, with larger plants subtidally.

In southern Australia, A. stellata is known only from Cape Lannes (near Robe) in South Australia where it occurs on near-vertical rock, completely shaded, left emergent at low tide above a pool at the rear of the rock platform (*Skinner & Lyons*, 25.ii.1977; ADU, A47973 and *Womersley*. 13.ii.1978; ADU, A49506). The short mat of *Anadyomene* is a metre or so across and includes sand; on some occasions the mat (and the pool) are completely covered with sand. Wave action on the mat at mid to high tide would be considerable. This habitat is very similar to that reported for the species in the Mediterranean and the American tropics. The Cape Lannes plants are dwarf and not well developed, but have been grown in culture up to 1 cm high, and then compare very well in form with larger specimens from the Mediterranean and tropical America, where the height range is given as 2.5-10 cm.

This isolated, temperate Southern Hemisphere occurrence of *A. stellata* is of interest in that it is on a rough-water coastline not adjacent to a harbour and not where an introduction might be expected.

Genus STRUVEA Sonder 1845: 49

Thallus erect, with a slight to (usually) distinct stipe attached by basal rhizoids, above forming an ovate to elongate reticulate blade. Blade largely complanate, formed of opposite primary branches with interconnecting secondary and tertiary branches, the ends of which attach to adjacent branches by means of short tenacula cells (tertiary branches may remain free in the ultimate spaces of the net). Cells comparatively large (to several mm long in the net), dividing probably by ingrowth of walls; stipe to several cm long, usually with annular constrictions; chloroplast reticulate, with numerous pyrenoids.

Reproduction unknown.

Type species: S. plumosa Sonder.

A genus of about 6 species, distributed mainly in tropical and subtropical seas.

Boergesen (1913, pp.52,56) claimed that cells are formed in *Struvea elegans* and *S. anastomosans* by segregative division, but his illustrations are not convincing and it seems more likely that cross walls develop by peripheral ingrowth as in *Microdictyon, Anadyomene* and Cladophorales generally.

Struvea plumosa Sonder 1845:50; 1846: 151. Harvey 1858: pl. 32. Womersley 1956: 377. S. macrophylla Harvey 1855c:564; 1858: pl. 7.

FIG. 73B,C

Thallus (Fig. 73B) light to medium green, 3-15(-20) cm high, epilithic, with a mass of densely clustered, elongate-clavate stipe cells each 2-8 cm long and (1-)2-4(-5) mm in diameter,



Fig. 73. A, Anadyomene stellata. Frond from culture (ADU, A49506). B,C. Struvea plumosa. B. A well developed plant (ADU, A51959). C. Details of margin of net (ADU, A50877).

often broadest in their mid part, with numerous annular constrictions throughout their length or confined to their upper and lower narrower parts; thallus often remaining as the basal stipes only, especially near the distributional margins, in shallow water and in winter. *Blades* (Fig. 73B) produced from ends of stipes, largely complanate, ovate to elongate, sometimes obovate, reticulate, 1–10(-17) cm long and 0.5–4(-12) cm across. Axial row of blade cells (1-)2–6(-10) mm long and 0.3-1.5 mm in diameter, each producing from its apex opposite primary branches of smaller cells except for the outermost few which curve towards the blade apex (Fig. 73C) and attach to a subapical cell of the next anterior primary row, producing only inner (adaxial) secondary branches; most primary cells producing opposite secondary branches which grow towards the primary rows above and below, attaching to a primary cell or the base of a secondary cell to give a zig-zag appearance (Fig 73B, C); tertiary cells formed similarly but often not attaching to secondary cells; all branches of the net lie in essentially one plane but distortion due to crowding frequently occurs; attachment of younger to older cells by means of small, isodiametric tenacula cells; chloroplast openly reticulate, with numerous pyrenoids.

Reproduction unknown.

Type from W. Aust. (Preiss); in MEL, 502116.

Distribution: From Port Denison, W. Aust. around southern Australia to Encounter Bay (Victor Harbor), S. Aust., from about low tide level to 33 m deep.

Selected specimens: Port Denison, W. Aust., 2m deep on jetty pile (*Ricker & Krafi*, 11.xii.1980; ADU, A51959). Grant Str. reef, Cottesloe, W. Aust., in pothole (*Smith*, 27.xi.1944; ADU, A2043). Ward I., S. Aust., 13–17 m deep (*Shepherd*, 3.iii.1980; ADU, A50877—"Marine Algae of southern Australia" No. 169b). Elliston, S. Aust., low eulittoral just inside bay (*Womersley*, 9.i.1976; ADU, A46771—"Marine Algae of southern Australia" No. 169b). Elliston, S. Aust., low eulittoral just inside bay (*Womersley*, 9.i.1976; ADU, A46771—"Marine Algae of southern Australia" No. 169). Pearson I., S. Aust., 12 m deep (*Turner*, 27.iii.1982; ADU, A53069). 4 km W. of Cape Dutton, Kangaroo I., S. Aust., 9 m deep (*Ottaway*, 18.i.1979; ADU, A50266). Encounter Bay, S. Aust., uppermost sublittoral pools (*Parsons*, 15.i.1968; ADU, A32266).

S. plumosa is one of the most distinctive of the southern Australian marine algae and shows remarkable seasonal development of the complanate nets from the often densely massed stipes. The latter by themselves are scarcely recognizable as Struvea and are remarkably similar to the basal stipes of Apjohnia laetevirens.

ORDER ACROSIPHONIALES Jonsson

Thallus (gametophyte) simple or branched, slender to robust, filaments uniseriate. *Cells* usually multinucleate (uninucleate in *Spongomorpha*) with nuclear division occurring in the plane of cross wall formation prior to ingrowth of the cross wall from the periphery; chloroplast single, parietal, continuous but perforate, containing several to many polypyramidal pyrenoids; cell wall without cellulose I but with mannan, xylan and pectic substances (fibrils similar to cellulose II also suggested). *Sporophyte* (Codiolum stage) minute, unicellular, ovoid with a basal rhizoid.

Life history diplohaplontic and heteromorphic, or haplontic (see Tanner 1981, p. 229).

Reproduction by biflagellate iso- or anisogametes or biflagellate zoospores from the gametophytes, developed in almost any thallus cell, liberated through an operculate pore (at least in *Acrosiphonia*), and by quadriflagellate meiospores from the unicellular sporophyte; or parthenogenetic from either phase.

The order Acrosphoniales is separated from the Cladophorales by most recent authors, but the features considered characteristic of the order have been established in only a few species, and their general application remains to be verified. Several of these features are at a subcellular or ultrastructural level (e.g. wall structure) and not easy to detect, but the chloroplast form and nature of the pyrenoids, the operculate pores to the zooidangia, and the heteromorphic life history are the more readily observable (Jonsson 1962, p. 199; van den

Hoek 1963, pp. 20-22). However, the presence of operculate pores appears not to have been established for *Urospora*, where illustrations show only simple pores.

FAMILY ACROSIPHONIACEAE Jonsson

The only family, with the characters of the order.

The family includes three genera of cold-water algae, superficially similar to genera of the Cladophorales. One genus, *Urospora*, is now recorded from southern Australia. *Urospora* Areschoug is conserved over *Hormiscia* Fries (Farr *et al.* 1979, p. 1830) but Kornmann (1966) redefines both genera, using *Hormiscia* for plants producing anisogametes and restricting *Urospora* to species without gametes but with asexual biflagellate zoospores.

Genus UROSPORA Areschoug 1866: 15, nom. cons.

Thallus (gametophyte) of slender to coarse, unbranched filaments, basally attached to solid substrates by an elongate basal cell and rhizoids descending from the lower few cells. *Cells* multinucleate, L/B from less than 1 to 4(-6); chloroplast single, parietal, continous but perforate, with several polypyramidal pyrenoids; cell wall often mucoid and filaments slippery. *Sporophyte* the unicellular *Codiolum* stage.

Life history diplohaplontic and heteromorphic, with the gametophyte filamentous and the sporophyte as the Codiolum stage.

Reproduction by biflagellate anisogametes (gametophytes unisexual) and by quadriflagellate meiospores from the sporophyte; also parthenogenetic.

Type species: U. mirabilis Areschoug [= U. penicilliformis (Roth) Areschoug].

A genus of about 10 species. A single record of *Urospora* is known from Tasmania, and is provisionally referred to the cold temperate species U. *penicilliformis;* some authors prefer to use the name U. *mirabilis* for what is probably the same taxon.

Urospora peniciliiformis (Roth) Areschoug 1874: 4, figs 1-6. Abbott & Hollenberg 1976: 94, fig. 49. Gain 1912: 32, figs 36-42. Kylin 1949: 46. Papenfuss 1964: 8. Taylor 1957: 77.

U. mirabilis Areschoug 1866: 15. Printz 1932: 273, figs 1-3, 8, 9, 14, 15, 18-20. Rosenvinge 1893: 918. Scagel 1966: 78, pl. 36A-D.

Hormiscia penicilliformis (Roth) Fries. Chapman 1956: 469, fig. 128.

PLATE 12 fig. 3; FIG. 74A-F

Thallus (gametophyte) dark green (Pl. 12, fig. 3), to 3 cm high, of slender, somewhat mucoid filaments forming a dense felt on rock at a lower eulittoral level; filaments unbranched, cylindrical (15-) $20-25 \,\mu\text{m}$ in diameter near the base, attached by the basal cell and external descending rhizoids from the lower several cells (Fig. 74A): mature cells $25-40 \,\mu\text{m}$ in diameter, L/B (0.5-)1-3, not or only slightly incised at cross walls (Fig. 74B,C); chloroplast (Fig. 74D,E) parietal, continous, with perforations and often open on one side, containing several polypyramidal pyrenoids. Sporophyte (the Codiolum stage) unknown in Australia.

Reproduction by anisogametes from upper cells of the filaments (Fig. 74F), liberated through a simple pore; gametes arranged more or less radially, with their pointed posterior ends inward.

Type from Germany (North Sea); probably lost.

Distribution: Cold temperature waters of both hemispheres; Arctic and Antarctic.

Australian record. Tesselated pavement, Eaglehawk Neck, Tasmania, lower eulittoral densely covering a single rock about 50 cm across (*Parsons & Womersley*, 30.x.1982; ADU, A54021).



Fig. 74. A-F. Urospora penicilliformis (ADU, A54021). A. Base of filament with rhizoids. B. Mid filament with clongate cells. C. Upper filament with recently divided cells. D. Mid cells showing chloroplast, pyrenoids and lipid bodies. E. Ditto from upper cells. F. Upper cells with zooids and empty cell with pore. G-J. Dictyosphaeria sericea (ADU, A53381). G. Surface view of thallus, showing recently divided cells and rows of hapteroid lenticular cells. H. Cross section showing old cell walls and lenticular cells prior to sloughing off of older walls. I. Detail of hapteroid lenticular cells. J. Chloroplasts with pyrenoids.

VALONIACEAE

This single collection is placed in *U. penicilliformis* provisionally. It agrees in form and dimensions, but has frequent longer cells than given in most descriptions which record their L/B as about one, or within the range 0.5-2. However, Scagel (1966, p. 79) extends the range to 4, Chapman to 2.5 for New Zealand material, and Gain (1912, p. 34) to 3 for Antarctic specimens. Rosenvinge (1893, p. 918, fig. 35) described a var. *elongata* from Greenland, with cells L/B 2.5-6, and Hagem (1908, p. 295, fig. 5) raised this variety to a species and gave L/B 4-10.

Clearly the Australian taxon needs further study from living material and other collections, but the habitat is very similar to that of the species from the northern hemisphere.

ORDER SIPHONOCLADALES (Blackman & Tansley) Oltmanns

Thallus globular, expanded and membranous, or filamentous or clavate, simple or branched, formed of few to many large multinucleate cells which develop by segregative division, with the new segments expanding endogenously or exogenously. Chloroplasts reticulate, without pyrenoids.

Life history probably diplohaplontic, the sporophyte producing quadriflagellate zoospores and the gametophyte(s) biflagellate gametes where known.

Many authors include the Siphonocladales within the Cladophorales, and in this account the Anadyomenaceae is placed under the latter order rather than under the Siphonocladales, where it is retained by Bold & Wynne (1978, p. 214). The genera of the Anadyomenaceae do not appear to show segregative division but new cells are formed by ingrowth of cross walls from the periphery. The order Siphonocladales is retained here for the single southern Australian genus which does show segregative division, on the basis that this rather distinctive type of cell formation does warrant ordinal recognition.

FAMILY VALONIACEAE Naegeli

Thallus formed by an aggregation of large vesiculate cells, without a central axis, usually with small lenticular cells with hapteroid extensions connecting the large cells or at the base of the thallus.

A single genus occurs in southern Australia.

Genus DICTYOSPHAERIA Decaisne 1842a:328

Thallus a parenchymatous cushion, remaining globose and solid or hollow, or opening out to an irregular membrane of large cells somewhat variable in size, with small hapteroid lenticular cells joining adjacent large cells. Cells formed by segregative division, maturing endogenously.

Life history with isomorphic generations, the sporophyte producing quadriflagellate zoospores, and male and female gametophytes producing biflagellate isogametes which also develop parthenogenetically (Enomoto & Okuda 1981).

Type species: D. cavernosa (Forskål) Boergesen.

Dictyosphaeria is a well defined genus of about 12 species, largely tropical-subtropical in distribution. The type species has been studied in detail by Enomoto & Okuda (1981) and Enomoto, Hori & Okuda (1982). A single species is widespread on southern Australian coasts.

Dictyosphaeria sericea Harvey 1855c: 565; 1859b: 339, pl. 196A. Lucas 1936: 31, fig. 13. Womersley 1956: 376.

PLATE 13 fig. 3; FIG 74G-J

Thallus (Pl. 13, fig. 3) medium green, shallowly cupulate to irregularly lobed, single or grouped, 2-10 cm across and 1 cell thick (Fig. 74H), consisting of a thick, irregular margined

membrane from a central (often broad), sessile attachment by coarse rhizoids, epilithic. Cells isodiametric, round to polygonal in surface view, (100-) 150-250 (-300) μ m across in upper parts and 300-500 (-1000) μ m across near the base of the thallus, 400-600 (-1500) μ m thick, with small hapteroid lenticular cells forming rows joining the surface margins of the cells (Fig. 74G-I); new cells formed by segregative division, endogenous, with successive outer walls remaining for some time (Fig.74H) and later sloughed off; chloroplasts numerous (Fig. 74J), forming a reticulum, the larger ones with a pyrenoid.

Reproduction unknown.

Type from W. Aust. (Clifton); in TCD (see Womersley 1956, p. 376).

Distribution: From Rottnest I., W. Aust. around southern Australia to Walkerville, Vic. and the north coast of Tasmania, from low tide level to 23 m deep on rough-water to moderate coasts.

Selected specimens: Natural jetty reef, Rottnest I., W. Aust., upper sublittoral (*Woelkerling*, 10.xi.1968; ADU, A33333). Off Troubridge I., S. Aust., 23 m deep (*Shepherd*, 4.ii.1969; ADU, A33809). Aldinga, S. Aust., 20 m deep (*Mitchell*, 12.ii.1961; ADU, A24767). Pennington Bay, Kangaroo I., S. Aust., outer pools on reef (*Womersley*, 6.i.1947; ADU, A4406). N. side of the Bluff, Victor Harbor, S. Aust., 1 m deep (*Clarke*, 23.viii.1982; ADU, A53381). Walkerville, Vic., near low tide level on bluff (*Sinkora* A1498, 21.ii.1972; ADU, A42316). Rocky Cape, Tas., upper sublittoral pools (*Wollaston & Mitchell*, 24.ii.1964; ADU, A27648).

This is a common species along southern Australia and when in shallow water is often found in shaded areas. Larger cells often show 2-5 inner cells formed by segregative division and the outer walls remain distinct as 2-4 successive layers until the outermost are sloughed off.

ORDER CODIALES Feldmann

Thallus applanate, globose or erect and usually branched, composed of densely entwined filaments forming a medulla and a cortex of elongate utricles bearing lateral gametangia; cross walls absent, but in many species one medullary filament adjacent to the base of each utricle with a plug largely blocking the filament; cell walls of mannan; homoplastic, with chloroplasts only, containing siphonein and siphonoxanthin.

Life history diplontic with gametic meiosis, anisogamous.

This order (Feldmann 1954) contains only the single genus *Codium* in the family Codiaceae. Some authors (e.g. Bold & Wynne 1978, p. 191) include it as a family of the Caulerpales.

FAMILY CODIACEAE (Trevisan) Zanardini

The family has the characters of the order.

Genus CODIUM Stackhouse 1797: xvi, xxiv

Thallus medium to dark green, epilithic, applanate or pulvinate and often lobed, or subglobose, or erect and simple to repeatedly subdichotomous, from a few cm across when applanate to about 1 m high with branches 3–10 mm in diameter in erect dichotomous species. Thallus diploid, with an internal medulla of slender, branched, interwoven filaments and a peripheral cortex of swollen utricles. Utricles with (1-)2–4 slender, basal medullary filaments, one of which in many species is largely closed by a plug of wall material, situated near to the utricle base; new utricles arising from medullary filaments or in some species from the lower part of primary utricles. Apex of utricle wall characteristically thickened and internally sculptured in some species from the utricles shortly below their apices, caducous but usually leaving a distinct scar. Gametangia borne laterally on the utricles, usually with a very short pedicel, clongate-ovoid, discharging anisogametes apically; plants usually dioecious, fertile usually in winter.

Type species: C. tomentosum (Hudson) Stackhouse [= C. dichotomum (Hudson) Gray].

A genus of some 80 species, present in most seas and well represented with 16 species on southern Australian coasts.

KEY TO SPECIES OF *CODIUM*

1. 1.	Thallus applanate or subglobose 2 Thallus erect, simple or dichotomously branched 8
	2. Thallus applanate or pulvinate, often lobed 3 2. Thallus subglobose 7
3. 3.	Utricles mostly less than 100 μm in diameter 4 Utricles mostly greater than 100 μm in diameter 6
	 4. Utricles devoid of hairs
5.	Utricles 600–1300 μ m long, regularly and conspicuously capitate, apices symmetrical
5.	Utricles 435–800(-1150) µm long, irregularly constricted below the apex, apices asymmetrical 3. C. lucasii
	 6. Utricles in small clusters, apical wall thickened into a galeate cap to 56 μm thick 6. Utricles in large clusters, apical wall thin or moderately thickened (-32 μm) 5. C. spongiosum
7. 7.	Utricles mostly $450-1000 \ \mu m$ in diameter near their apex
	 8. Thallus simple or once-divided, broad and flat, felt-like
9. 9.	Utricles not mucronate
	10. Utricle apices with spinous internal trabeculae 9. C. silvae 10. Utricles without spinous trabeculae 11
[]. [].	Utricles often longer than 1 mm
	12. Utricles with galeate thickening at apex
13.	Medullary filaments usually with plugs close to point of departure from utricle
13.	Medullary filaments with plugs conspicuously distant from point of departure from utricle
	14. Utricles prominently introrsely umbonate 13. C. muelleri 14. Utricles not introrsely umbonate 14. C. australicum
15. 15.	Utricles mostly longer than 1 mm

1. Codium dimorphum Svedelius 1900: 300. Silva & Womersley 1956: 262, fig. 1.

FIGS 75A, 76A

Thallus (Fig. 75A) medium to dark green, smooth and firm, applanate and strongly adherent, rounded with marginal lobes, 2.5-6(-10) mm thick, to 10 cm across. Utricles (Fig. 76A) in small to large clusters, (45-)55-80(-100) μ m in diameter, 0.5-1(-1.5) mm long, usually slightly constricted just below apices then slightly broader below, apices rounded to subtruncate with slightly thickened wall (4-7 μ m thick), often more so peripherally; utricles from thallus margin often broader (to 125 μ m in diameter) below their apices, which are thickened (to 30 μ m); hairs absent. Medullary filaments extending from the evenly tapering lower part of utricles, wall undulate, (15-)20-35 μ m in diameter, without plugs. Gametangia narrowly ellipsoid to cylindrical, 44-75 μ m in diameter, 240-380 μ m long.

Type from Guaitecas I., Chile; in Herb. Svedelius, UPS.

Distribution: Chile, Chatham I., New Zealand (South I., Stewart I.).

In southern Australia, known only from south-east Tasmania. This is probably a subantarctic species which just reaches Tasmania. It occurs in the lowest eulittoral or uppermost sublittoral among the stipes of *Durvillea*, forming thin, rounded, tightly adherent patches on the rock.

Selected specimens: Cape Forestier, Tas., lower eulittoral (Bennett, 21.vi.1954; ADU, A19830). Wineglass Bay, Freycinet Pen., Tas., low eulittoral (Edyvane, 26.iii.1982; ADU, A53000). Bicheno, Tas., upper sublittoral amongst Durvillaea (Womersley, 3.xi.1982; ADU, A54027).

2. Codium capitulatum Silva & Womersley 1956: 263, fig. 2, Pl. 1 fig. 1.

FIGS 75B, 76B

Thallus (Fig. 75B) firm, dark green, applanate and lobed, closely adherent to rock, to 1 cm thick and to 15 cm across. *Utricles* (Fig. 76B) in large clusters; primary utricles 70–140 μ m in diameter at apices, constricted 50–85 μ m below apices, usually expanded below to 230 μ m in diameter, 600–1300 μ m long; secondary utricles 40–85 μ m in diameter at apex, prominently constricted just below apices and capitate, expanding to 115 μ m in diameter below, 600–1000 μ m long, separated from adjacent utricles by a plug; wall of utricles thin, not or only slightly thickened at apices; hairs (or scars) prominent just below constriction on primary and often on secondary utricles. Medullary filaments distinctly slenderer than utricles, 16–45 μ m in diameter, without plugs. *Gametangia* fusiform, 60–110 μ m in diameter, 240–380 μ m long.

Type from Elliston, S. Aust. (Womersley, 14.ii.1954); in ADU, A19384.

Distribution: From Hopetoun, W. Aust., to Walkerville, Vic., in the lower eulittoral and uppermost sublittoral on rock platforms on rough-water coasts, often where shaded and with slight shelter.

Selected specimens: Hopetoun, W. Aust., drift (Gordon, 20.xi.1968; ADU, A34173). Elliston, S. Aust., lower eulittoral in shade (Womersley, 15.i.1951; ADU, A13623 and Woelkerling, 16.v.1968; ADU, A32491—"Marine Algae of southern Australia" No. 18). Entrance to Kellidie Bay, Coffin Bay, S. Aust., lower eulittoral, shaded (Womersley, 22.viii.1967; ADU, A31823). Seal Bay, Kangaroo I., S. Aust., drift (Womersley, 31.x.1966; ADU, A30958). Walkerville, Vic., low eulittoral (Womersley & Sinkora, 11.xi.1982; ADU, A53974).

C. capitulatum is closely related to C. lucasii but is distinguished by its longer, regularly constricted utricles with symmetrical apices.

3. Codium lucasii Setchell in Lucas 1935: 200; 1936: 50, fig. 31. Silva & Womersley 1956: 265, fig. 3.

FIGS 75C, 76C, D

Thallus (Fig. 75C) firm, dark green, applanate, lobed, closely adherent, to 1 cm thick and to 15 cm across. *Utricles* (Fig. 76C,D) in clusters, (45-)50-100(-130) μ m in diameter at apex and slightly to markedly constricted just below apex, 400-800(-1200) μ m long; utricle wall at apex slightly (Fig. 76C) to markedly (up to 65 μ m, see Fig. 76D) thickened, internally often pitted; hairs (or scars) common on older utricles. Medullary filaments 12-35 μ m in diameter, without plugs. *Gametangia* fusiform, 60-125 μ m in diameter, 210-360 μ m long.



Fig. 75. A. Codium dimorphum (ADU, A19830). B. Codium capitulatum (ADU, A19384). C. Codium lucasii (ADU, A45051). D. Codium perriniae (ADU, A37803). E. Codium spongiosum (ADU, A1581).

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Type from Bondi, N.S.W.; in UC, 395199.

Distribution: From Port Denison, W. Aust. around southern and eastern Australia to Redcliffe. Qld, and the north coast of Tasmania, in the lower eulittoral and uppermost sublittoral on rough-water to moderate coasts.

South Africa (subsp. capense Silva 1959: 111, fig. 3).

Selected specimens: Port Denison, W. Aust., outer reef pools (Woelkerling, 8.xi.1968; ADU, A33142). Cottesloe, W. Aust., drift (Royce 1039, 12.vi.1951; PERTH, UC). Sceale Bay, S. Aust., upper sublittoral (Womersley, 11.ii.1954; ADU, A19416). Elliston, S. Aust., lower eulittoral (Womersley, 15.i.1951; ADU, A20401). Port Noarlunga, S. Aust., low eulittoral on reef (Womersley, 15.iv.1945; ADU, A16395). Vivonne Bay, Kangaroo I., S. Aust., 1–5 m deep on jetty pylon (Kraft, 19.i.1974; ADU, A45051). Walkerville, Vic., at low tide level, shaded (Sinkora A1528, 22.ii.1972; ADU, A42317). Currie R., Tas. (Perrin & Lucas, March 1935; Perrin 43b in BM).

C. lucasii is most closely related to C. capitulatum but has shorter utricles with less symmetrical apices.

4. Codium perriniae Lucas 1935: 203. Silva & Womersley 1956: 267, fig. 4.

FIGS 75D, 76E

Thallus (Fig. 75D) firm, medium green, pulvinate to lobed, to 2 cm high and 2-8(-12) cm across. *Utricles* (Fig. 76E) in small clusters, irregularly cylindrical to slightly clavate, $130-240 \,\mu\text{m}$ in diameter near apices, to $375 \,\mu\text{m}$ in diameter somewhat below apices, $900-1700 \,\mu\text{m}$ long; utricle wall at apex thickened to form a moderate to prominent, lamellate, galeate cap (to $60 \,\mu\text{m}$ thick); hairs absent. Medullary filaments 26-60 μm in diameter, without plugs. *Gametangia* fusiform, 65-100 μm in diameter, $370-450 \,\mu\text{m}$ long.

Type from Low Head, Tas.; in Herb. Lucas, NSW (ex CANB).

Distribution: From Cliff Head, W. Aust. to Sorrento, Vic. and the north coast of Tasmania, in the upper sublittoral in pools on rock platforms and to 32 m deep, usually on rough-water coasts.

Selected specimens: Cliff Head, W. Aust., 5-6 m deep (Kirkman & Joll, 18.ix.1979; ADU, A51188). Strickland Bay, Rottnest I., W. Aust, 0-1.5 m deep (Engler & Clarke, 5.ix.1979; ADU, A51104). D'Estrees Bay, Kangaroo I., S. Aust., outer reef pools (Womersley, 11.i.1950; ADU, A12781). Robe, S. Aust., upper sublittoral shaded pools (Womersley, 16.xii.1970; ADU, A37803—"Marine Algae of southern Australia" No. 22). 16 km N.W. of Cape Bridgewater. Vic., 26-32 m deep (Watson, 16.v.1969; ADU, A34760). Currie R., Tas. (Perrin & Lucas, March 1935; ADU, A47088).

5. Codium spongiosum Harvey 1855c:565; 1858: pl. 55. Lucas 1936: 51. Silva & Womersley 1956: 268, fig. 5.

FIGS 75E, 76F

Thallus (Fig. 75E) light to medium green, pulvinate or undulate, with irregular lobes, to 15 cm thick and to 20(-50) cm across, moderately firm when living, soon becoming spongy,

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Fig. 76. Utricle clusters with gametangia. A. Codium dimorphum (ADU, A19830). B. Codium capitulatum (ADU, A13623). C. Codium lucasii (ADU, A20401). D. Codium lucasii (Royce 1039 in PERTH, UC). E. Codium perriniae (ADU, A12781). F. Codium spongiosum (ADU, A19383). (After Silva & Womersley 1956.)



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moderately adherent to substratum. Utricles (Fig. 76F) in large clusters, older utricles $400-520 \,\mu\text{m}$ in diameter at apices, enlarging below to $850 \,\mu\text{m}$, 2-6 mm long; younger utricles $130-400 \,\mu\text{m}$ in diameter, 1-4 mm long; utricle apices rounded, wall very slightly to moderately (to $32 \,\mu\text{m}$) thickened, becoming lamellate; hairs (or scars) abundant. Medullary filaments $30-100 \,\mu\text{m}$ in diameter, without plugs. Gametangia lanceolate-ovoid, $50-175 \,\mu\text{m}$ in diameter, $210-360 \,\mu\text{m}$ long, usually several per utricle.

Lectotype from King Georges Sound, W. Aust.; in Herb. Harvey, TCD (Alg. Aust. Exsicc. 577).

Distribution: From Point Cloates (22°42'S, 113° 40'E), W. Aust. around southern Australia to Apollo Bay, Vic., and in Qld. and Tasmania (?).

South Africa, Mauritius, Lord Howe I., New Caledonia, Hawaiian Is, Brazil (Silva 1960, p. 503).

Selected specimens: South Passage, Shark Bay, W. Aust., 5 m deep (Cambridge, 16.vii.1979; ADU, A 51761). Elliston, S. Aust., upper sublittoral inside bay (Womersley, 14.ii.1954; ADU, A19383). Wallaroo, S. Aust., drift (Harris, 25.vi.1945; ADU, A1581). Pig I., Pelican Lagoon, American R. inlet, Kangaroo I., S. Aust., upper sublittoral (Womersley, 12.iv.1947; ADU A4489). Haylings Reef, Apollo Bay, Vic. (Pope & Bennett, 17.i.1949; ADU, A15276).

C. spongiosum occurs under moderately calm conditions, from just below low water to several metres deep, particularly in warmer areas; its occurrence on the colder south-eastern coasts of Australia is sparse and doubtful in Tasmania though recorded by Guiler (1952, p. 75).

6. Codium mamillosum Harvey 1855c:565; 1858: pl. 41. Lucas 1936: 53. Silva & Womersley 1956: 269, fig. 6.

FIGS 77A, 78A

Thallus (Fig. 77A) medium green, more or less globose, to 8 cm in diameter, attached by a tuft of rhizoids, firm when living but becoming soft. *Utricles* (Fig. 78A) in small clusters, elongate-clavate, $(400-)450-1000 \,\mu\text{m}$ in diameter at the apices and often expanded shortly below (to 1500 μ m) then tapering to the base, $(3-)4-7(-9) \,\text{mm}$ long; utricle apex rounded to subtruncate, wall slightly to moderately thickened (to 40 μ m) and becoming finely lamellate; hairs absent. Medullary filaments $40-100 \,\mu\text{m}$ in diameter, with several from the much broader utricle base, often branched or contricted near their origin. *Gametangia* narrowly ellipsoid to ovoid, often tapering above, $130-250 \,\mu\text{m}$ in diameter, $(350-)500-800 \,\mu\text{m}$ long, 1-3 per utricle. $1-2 \,\text{mm}$ below apices.

Lectotype from "Swan River", W. Aust. (probably near Fremantle); in Herb. Harvey, TCD (Alg. Aust. Exsicc. 578).

Distribution: From Dongara, W. Aust., to Warrnambool, Vic.

Hawaiian Is., Japan.

Selected specimens: Seven mile beach, N. of Dongara, W. Aust., drift (*Womersley*, 14.ix.1979; ADU, A51341). City Beach, Perth, W. Aust. (*Royce* 1200, 7.v.1952; in PERTH, UC). Northern Great Australian Bight, S. Aust., 42 m deep (*Symond*, 5.v.1973; ADU, A43513). Off Outer Harbour, S. Aust., 16 m deep (*Loan*, 9.viii.1963; ADU, A26646). Rocky Point beach, Kangaroo I., S. Aust., drift (*Womersley*, 26.viii.1950; ADU, A13361). Dutton Bay, Portland, Vic., drift (*Womersley*, 13.iv.1959; ADU, A22663).

C. mamillosum occurs at low tide level in shaded situations under moderate wave action, but is essentially a sublittoral species extending down to 42 m. It is a distinctive species in form and in the very large utricles.



Fig. 77. A. Codium mamillosum (ADU, A43513). B. Codium pomoides (ADU, A46816). C. Codium laminarioides (ADU, A50719). D. Codium silvae (ADU, A50695, type). E. Codium galeatum (ADU, A46820). F. Codium duthieae (ADU, A37513).

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7. Codium pomoides J. Agardh 1849a:100. Lucas 1936: 53. Silva & Womersley 1956: 271, fig. 7.

FIGS 77B, 78B

Thallus (Fig. 77B) dark green, very firm, more or less globose, to 12 cm in diameter, becoming hollow by breakdown of central medullary filaments, very firmly attached by a mass of rhizoids. Utricles (Fig. 78B) in large clusters, (70-)90-125(-180) μ m in diameter at apex, then slightly constricted and expanding below to 200 μ m in diameter, then gradually tapering, 1-3 mm long; utricles near base of thallus to 280 μ m in diameter; utricle apices symmetrically rounded, wall very slightly to moderately (-30 μ m) thickened, lamellate with a slight introrse umbo; hairs absent but wall scars common. Medullary filaments tapering evenly from lower part of utricles, becoming 30-40 μ m in diameter. Gametangia elongate-ovoid to cylindrical, 50-95 μ m in diameter, 400-500 μ m long.

Type probably from Port Phillip Heads, Vic. (J.B. Wilson), but not located.

Distribution: From Middle I., Recherche Arch., W. Aust., to Walkerville, Vic. and around Tasmania.

Selected specimens: Belinda Beach. Goose I. bay, Middle I., Recherche Arch., W. Aust., 60 cm deep, shaded (*Trudgen* 1190, 14.xi.1974; ADU, A51672). Avoid Bay, S. Aust., drift (*Womersley*, 30.xi.1975; ADU, A46816). Pennington Bay, Kangaroo I., S. Aust., on reef edge (*Womersley*, 28.i.1944; ADU, A2267). Carpenter Rocks, S. Aust., upper sublittoral in shade (*Womersley*, 5.ii.1970; ADU, A35180—"Marine Algae of southern Australia" No. 23). Walkerville, Vic., just above low tide, shaded (*Sinkora* A1529, 21.ii.1972; ADU, A42309). Currie R. mouth, Tas., drift (*Cribb* 75.16, 17.ix.1950; UC). Woody I., D'Entrecasteaux Channel, Tas., 2-7 m deep (*Shepherd*, 17.ii.1972; ADU, A41714).

C. pomoides occurs from low tide level (where shaded) down to 20 m on rough-water coasts. It is easily recognised by its very firm, globular thallus, very dark colour, and small diameter utricles.

8. Codium laminarioides Harvey 1855c:565. Silva & Womersley 1956: 272, fig. 8.

FIGS 77C, 78C

Thallus (Fig. 77C) medium green, with a short, terete stipe (to 12 mm long) expanding to a flat, felt-like frond 1.5-2 mm thick, to 80 cm broad and 40 cm long, simple or once furcate, irregularly lobed. *Utricles* (Fig. 78C) 65-200(-290) μ m in diameter below apex, 470-800 μ m long; apices rounded, thickened to 30 μ m and lamellate; hairs (or scars) common. Medullary filaments 20-55 μ m in diameter, much slenderer than utricle base, with prominent plugs adjacent to utricle base. *Gametangia* elongate-ovoid to cylindrical, 40-90 μ m in diameter, 170-250 μ m long, 1-4 per utricle, borne on a slight protuberance from utricle.

Lectotype from Rottnest I., W. Aust.; in Herb. Harvey, TCD (Alg. Aust. Exsicc. 574).

Distribution: From Port Denison, W. Aust. to Pearson I., S. Aust.

Selected specimens: Port Denison, W. Aust., drift (Parsons, 8.xi.1968; ADU, A33154). Rottnest I., W. Aust. (Cribb 61.42, 10.viii.1950; UC). Green I., Rottnest I., W. Aust., 1-1.5 m deep (Clarke & Engler, 6.ix.1979; ADU, A50719). Ward I., S. Aust., 25-30 m deep (Shepherd,

Fig. 78. Utricle clusters with gametangia. A. Codium mamillosum (Royce 1200, in PERTH, UC). B. Codium pomoides (Cribb 75.16 in UC). C. Codium laminarioides (Cribb 61.42 in UC). D. Codium silvae (ADU, A50695, type). E. Codium silvae, apex of utricle. F. Codium galeatum (lectotype left and Royce 1196 right). G. Codium duthieae (ADU, A13624). (After Silva & Womersley 1956.)


31.iii.1982; ADU, A53090). Pearson I., S. Aust., 10–15 m deep (*Shepherd*, 28.iii. 1982; ADU, A53024).

This species, remarkable for its flat, essentially unbranched form, is usually a deep water species, collected from shallow areas (often in shade) to 30 m deep.

9. Codium silvae Womersley sp. nov.

FIGS 77D, 78D,E

Thallus (Fig. 77D) medium green, erect, to 30 cm high, irregularly dichotomously and laterally branched at intervals of one to several cm, branches terete, tapering gradually from 6-8 mm in diameter near the base to 3-5 mm in diameter near the branch apices. Utricles (Fig. 78D) arising singly from medullary filaments, elongate clavate to subterete and often of greatest diameter shortly below the apex, 125-250 µm in diameter when mature and $(750-)850-1150 \,\mu\text{m}$ long; utricle wall thin near the base, thickening towards the apex and forming a finely lamellate, often galeate, cap 25-40 µm thick; internal spinous trabeculae (Fig. 78D.E) formed profusely from the galeate cap, occurring with less frequency and smaller size downwards over the upper quarter to one third of the utricle; trabeculae $10-30 \,\mu\text{m}$ long, basally 5-20 μ m thick, tapering to a point, simple or rarely with a branch, often appearing to have an internal cavity which extends into the utricle wall; hairs probably rare, only a few possible hair-scars observed about one quarter of the length of the utricle from the apex. Medullary filaments $25-50 \,\mu\text{m}$ in diameter, with a prominent plug adjacent to the utricle base. Gametangia borne one third to a half the utricle length from the apex, terete to lanceolate, one or two per utricle, 180–300 μm long by 50–70 μm in diameter (only discharged gametangia seen).

Diagnosis: Thallus viridis erectus ad 30 cm altus, irregulariter dichotome et in lateribus. cum spatio unius vel plurium cm inter ramos interposito, ramosus. Rami teretes, 6–8 mm diametro in baso ad 3–5 mm diametro prope apices decrescentes. Utriculi, ex filamentis medullariis singulatim orti, elongati clavati vel subteretes. saepe maximi diametri paulo infra apicem, 125–250 μ m diametro et (750-) 850–1150 μ m longo maturitate; membrana utricularis in baso tenuis, ad apicem incrassata, galericulata, subtiliter lamellosa 25–40 μ m crassitie. Trabeculae internae spinulosae in galero profuse et deorsim minus saepe atque minori amplitudine in superiorem partem quantam vel tertium utriculi. Trabeculae 10–30 μ m longae, in baso 5–20 μ m crassae, ad apicem decrescentes, simplices, rariter ramosae, saepe facie cavernosae ad membrana utricularia 25–50 μ m diametro, obturamento perspicuo prope basam utriculi. Gametangia in parte dimidio vel tertia. longitudinis utriculi infra apicem portata, teretolanceolata 1–2 per utriculum, 180–300 μ m longia et 50–70 μ m diametro. (Gametangia emissa solum visa sunt).

Type : Eucla, W. Aust. (Womersley, 5.x.1979).

Holotype: ADU, A50695. Isotypes distributed to MEL, PERTH and UC,

Distribution: Only known from the type collection of a single plant.

Named after Dr Paul C. Silva, who has contributed most significantly to our knowledge of *Codium*.

C. silvae is similar in dimensions to *C. galeatum* but differs in having irregularly placed, often short, lateral branches. The utricles are also similar in dimensions and have a pronounced galeate cap, but differ strikingly in the internal, spinous trabeculae which occur for some distance down the wall of the utricle. These spines appear to be trabeculae in the sense of Silva (1951, p. 93) and show internal structure corresponding to the "conspicuous axial filament" referred to by Silva. However, this structure in *C. silvae*, which is very similar to that illustrated by Silva (1951, figs 17-19) in *Codium globosum* from Queensland, appears to be a cavity within the trabeculae, and which often extends into the utricle wall. Setchell (1940, p. 447, figs 3-5) considered the trabeculae had a "distinct core (or tube)?" when describing *C. cranwelliae* (from New Zealand), but Silva considered them to be solid structures.

Codium

CODIACEAE

C. silvae appears to be the only erect, dichotomous species of Codium showing trabeculae, the other such species being prostrate or globose taxa. Lucas (1935, p. 206) however mentioned trabeculae in a Lord Howe Island plant he (probably incorrectly) referred to C. cuneatum Setchell & Gardner.

10. Codium galeatum J. Agardh 1887: 42, pl. 1 fig. 1. Lucas 1936: 54, fig. 35a. Silva & Womersley 1956: 273, fig. 9.

FIGS 77E, 78F

Thallus (Fig. 77E) medium green, firm, erect, regularly and frequently dichotomously branched, to 1 m high, with branches uniformly terete, not tapering, 4–7 mm in diameter. *Utricles* (Fig. 78F) stout, irregularly cylindrical to clavate, (130-)200-500(-700) μ m in maximum diameter (below apex), (650-)750-1300(-1500) μ m long; utricle apical wall rounded to truncate, moderately to (usually) markedly thickened forming a laminate galeate cap up to 125 μ m thick; hairs (or scars) occasional, one to few per utricle. Medullary filaments usually 30-80 μ m in diameter, with a prominent plug adjacent to origin from utricle. *Gametangia* elongate-ovoid to cylindrical, 55-185 μ m in diameter, 275-530 μ m long.

Lectotype from Port Phillip, Vic.; in Herb. Agardh, LD, 15588.

Distribution: From Champion Bay, W. Aust. around southern Australia and Tasmania to Ballina, N.S.W.

Selected specimens: Port Denison, W. Aust., drift (Parsons, 8.xi.1968; ADU, A33155). City Beach, Perth, W. Aust. (Royce 1196, 7.v.1952; PERTH, UC). Avoid Bay, S. Aust., drift (Womersley, 30.xi.1975; ADU, A46820). Pennington Bay, Kangaroo I., S. Aust., sublittoral fringe (Womersley, 29.xii.1948; ADU, A10536). Margaret Brock Reef, Cape Jaffa, S. Aust., 10 m deep (Lewis, 15.ii.1974; ADU, A45022). Sorrento, Vic., shaded pool (Womersley, 2.vi.1953; ADU, A18831).

C. galeatum is a common species on rough-water coasts along southern Australia, from low tide level down to 37 m. The robust, regularly dichotomous thallus and large utricles with galeate caps are characteristic.

11. Codium duthieae Silva in Silva & Womersley 1956: 275, fig. 10, pl. 1 fig. 2.

FIGS 77F, 78G

Thallus (Fig. 77F) light to medium green, erect, subdichotomously to laterally branched, to 60 cm high, with branches terete and 3–10 mm in diameter but usually compressed (to 2 cm broad) at and near points of branching, branches moderately soft. Utricles (Fig. 78G) cylindrical to clavate, (130-)175-500(-700) μ m in diameter near apices, (450-)650-1800(-2500) μ m long; apices broadly rounded, wall usually remaining thin, occasionally slightly thickened; hairs (or scars) occasional to numerous. Medullary filaments usually 40–75 μ m in diameter, with plugs usually adjacent to utricle base. Gametangia elongate-ovoid, usually tapering above, 70–160 μ m in diameter, (230-)270–430 μ m long, several per utricle and borne on a short protuberance from utricle.

Type from Strandfontein, South Africa; in UC, 920260.

Distribution: From Champion Bay, W. Aust. to Walkerville, Vic. and the north coast of Tasmania.

South Africa, from Saldanha Bay to Limpopo River mouth, Mozambique.

Selected specimens: Safety Bay, W. Aust., drift (*Womersley*, 29.ix.1979; ADU, A50742). Pearson I., S. Aust., 20-25 m deep (*Shepherd*, 7.i.1969; ADU, A33651). Elliston, S. Aust., C. duthieae is usually found on coasts of slight to moderate water movement but occasionally on rough-water coasts, from low tide level to 25 metres deep. It is characterised by its form, flattening near the points of branching, and by the relatively large, often clavate, utricles usually with thin apical walls.

12. Codium harveyi Silva in Silva & Womersley 1956: 277, fig. 11, pl. 2 fig. 1.

FIGS 79A, 80A

Thallus (Fig. 79A) medium green, erect, repeatedly dichotomous, to 30 cm high, branches terete, 3-5 mm in diameter below, tapering to 1-2 mm in diameter at apices. Utricles (Fig. 80A) short and irregularly swollen, 170-600 μ m in diameter, 340-850 μ m long, apices broadly rounded with wall scarcely to slightly thickened to 24 (-50) μ m; hairs (or scars) frequent. Medullary filaments 30-60 μ m in diameter, with the plug usually closely adjacent to utricle, in some plants more distant on older utricles. Gametangia elongate-ovoid, often tapering above, 70-140 μ m in diameter and 150-240 μ m long, 1-4 per utricle, borne on a short protuberance on lower half of utricle.

Type from Vivonne Bay, Kangaroo L. S. Aust. (Womersley, 2.i.1949); in ADU, A10557.

Distribution: From Shark Bay, W. Aust. around southern Australia and Tasmania to Lake Macquarie, N.S.W.

New Zealand.

Selected specimens: South Passage, Shark Bay, W. Aust., 5 m deep (Cambridge, 16.viii.1979; ADU, A51759). Seal Bay, Kangaroo I., S. Aust., drift (Gordon, 31.x.1966; ADU, A30964). Robe, S. Aust., drift (Womersley, 7.ii.1970; ADU, A35175---"Marine Algae of southern Australia" No. 20). Walkerville, Vic., drift (Sinkora A2288, 6.iii.1976; ADU, A48462). East Cove, Deal I., Bass Str., 15 m deep (Shepherd & Lewis, 5.v.1974; ADU, A45252). Low Head, Tas. (Perrin, Sept. 1950; in UC). Tamar R. mouth, Tas., (Mackay; in K).

C. harveyi occurs in the sublittoral, from low tide level to 30 metres deep, on coasts of moderate water movement. It is distinguished by its short, squat utricles with the medullary filament plug adjacent to the utricle.

13. Codium muelleri Kuetzing 1856: pl. 95 fig. II. Silva & Womersley 1956: 278, fig. 12.

FIGS 79B, 80B

Thallus (Fig. 79B) moderately firm, medium green, erect, repeatedly dichotomous, to 25 cm high, branches terete, 2.5–5 mm in diameter, decreasing slightly to about 1.5 mm in diameter near apices. *Utricles* (Fig. 80B) relatively short and often broadest somewhat below the apex, 130–520 μ m in diameter and 290–960 μ m long, apices broadly rounded to subtruncate, with wall thin or occasionally thickened (to 50 μ m) but always with a distinct introrse umbo to 45 μ m long; hairs (or scars) common. Medullary filaments 30–60 μ m in diameter, with the plug distant (80–350 μ m) from the utricle base. *Gametangia* elongate-ovoid, often tapering above, 70–150 μ m in diameter and 120–290 μ m long, 1–4 per utricle, borne on a slight protuberance on lower half of utricle.

Type from Lefevre Peninsula, S. Aust.; in L, 937, 337 ... 772.

Distribution: From Dongara, W. Aust. to Walkerville, Vic.



Fig. 79. A. Codium harveyi (ADU, A10557, type). B. Codium muelleri (ADU, A35176). C. Codium australicum (ADU, A38221). D. Codium fragile (ADU, A34854). E. Codium spinescens (ADU, A19240, type).

CODIACEAE

Selected specimens: Rottnest I., W. Aust., upper sublittoral (*Wollaston*, 31.i.1957; ADU, A21058). Avoid Bay, S. Aust., drift (*Womersley*, 30.xi.1975; ADU, A46819). Vivonne bay, Kangaroo I., S. Aust., drift (*Womersley*, 17.i.1950; ADU, A12609). Marino, S. Aust., drift (*Womersley*, 21.v.1953; ADU, A18661 and UC). Robe, S. Aust., drift (*Womersley*, 7.ii.1970; ADU, A35176— "Marine Algae of southern Australia" No. 21). Queenscliff, Vic., drift (*Wollaston*, 17.viii.1956; ADU, A20574).

This is a sublittoral species (to 11 m deep) on coasts of moderate wave action, and is distinguished by the introrse umbo on the apical wall of the utricles, as well as by utricle dimensions and position of the plug.

14. Codium australicum Silva in Silva & Womersley 1956: 280, fig. 13, pl. 2 fig.2.

FIGS 79C, 80C

Thallus (Fig. 79C) firm, dark green, erect, repeatedly dichotomous, to 50 cm high, branches terete, 4-8(-10) mm in diameter below, tapering gradually to 2-3 mm in diameter near apices. Utricles (Fig. 80C) cylindrical to slightly clavate, (100-)130-210)(-300) μ m in diameter, 460-800 μ m long; apices rounded to truncate, wall thin or slightly thickened (-15 μ m, rarely to 35 μ m, then lamellate); hairs (or scars) common, borne shortly below apices. Medullary filaments 20-35 μ m in diameter with the plug 65-200 μ m distant from utricle base. Gametangia elongate-ovoid, 80-160 μ m in diameter and 230-390 μ m long, 1-3 per utricle, borne on a protuberance at or below middle of utricle.

Type from Robe, S. Aust. (Wollaston, 17.iii.1956); in ADU, A20409.

Distribution: From Geographe Bay, W. Aust. around southern Australia and Tasmania to Tuggerah Lakes, N.S.W.

New Zealand.

Selected specimens: Emu Beach, King Georges Sound, W. Aust., drift (*Mitchell*, 27.ix.1966; ADU, A30817). Investigator Str., S. Aust., 33 m deep (*Watson* Stn Y18A, 24.i.1971: ADU, A38221). Robe, S. Aust., upper sublittoral pool (*Womersley*, 11.xii.1969; ADU, A34857—"Marine Algae of southern Australia" No. 17). Walkerville, Vic., drift (*Sinkora* A2106, 28.ii.1975; ADU, A48550). Fluted Cape, Bruny I., Tas., 23 m deep (*Shepherd*, 12.ii.1972; ADU, A41907). Port Arthur, Tas. (*Cribb* 150.1, 20.vi.1951; UC 949773).

C. australicum is a sublittoral species known from low water level (usually shaded) to 33 metres deep, on rough-water to moderate coasts. It is most closely related to C. harveyi and C. muelleri but differs in the utricle dimensions and apical characteristics, and also from C. harveyi in the plug position.

15. Codium fragile (Suringar) Hariot. Lucas 1936: 54, fig. 35b, 37. Silva & Womersley 1956: 282, figs 14, 15.

FIGS 79D, 80D,E

Thallus (Fig. 79D) medium to dark green, erect, terete, repeatedly subdichotomously and often laterally branched, 5-30 cm high, attached by a broad, spongy, basal disc, relatively soft, often tomentose with profuse hairs. *Utricles* (Fig. 80D,E) cylindrical to slightly clavate, (70-) 130-330(-400) μ m in diameter, (700-) 1000-1450 (-1750) μ m long, apices pointed and thickened forming a mucro to 75 μ m long; hairs stout, abundant, 50-100 μ m in diameter. Medullary filaments 25-50 μ m in diameter, with a plug adjacent to utricle base. *Gametangia* elongate-ovoid to cylindrical, 90-130 μ m in diameter and 260-450 μ m long, 1-4 per utricle, borne on a slight protuberance.

Type from Japan; in L, 910, 187 . . . 1712.

Distribution: From Victor Harbor, S. Aust. to Ballina, N.S.W. and around Tasmania, in the lowest eulittoral and uppermost sublittoral.

Widespread in cooler temperate waters of both hemispheres.

Selected specimens: Port MacDonnell, S. Aust., lower eulittoral (*Womersley*, 11.xii.1969: ADU, A34854—"Marine Algae of southern Australia" No. 19). Point Lonsdale, Vic., uppermost sublittoral (*Womersley*, 21.i.1967; ADU, A31711). Walkerville, Vic., at low tide level (*Sinkora*



Fig. 80. Utricle clusters with gametangia. A. Codium harveyi (Perrin in UC and Mackay in K (right)). B. Codium muelleri (ADU, A18661). C. Codium australicum (Cribb 150.1 in UC). D. Codium fragile s.sp. tasmanicum (Cribb 126.9 in UC). E. Codium fragile s.sp. novae-zelandiae (ADU, A31711). F. Codium spinescens (Royce 616 in PERTH). (After Silva & Womersley 1956.)

A1526, 21.ii.1972; ADU, A42281). Green Point, west coast Tas., in deep pools (*Wollaston & Mitchell*, 27.ii.1964; ADU, A27549). Woody I., D'Entrecasteaux Channel, Tas., 0-2 m deep (*Shepherd*, 17.ii.1972; ADU, A41642). Port Arthur, Tas. (*Cribb* 126.9, 6.ii.1951; in UC).

Several varieties (or subspecies) of *C. fragile* are recognised, of which subsp. *tasmanicum* (J. Agardh) Silva in Silva & Womersley (1956, p. 283) occurs from Victor Harbor, South Australia, to Walkerville, Victoria and around Tasmania. Subspecies *novae-zelandiae* (J. Agardh) Silva is a New Zealand form which also occurs from Robe, South Australia to Ballina, New South Wales, and around Tasmania. Subspecies *tasmanicum* has acuminate, sharply mucronate utricles (e.g. Cribb 126.9, in UC—Fig. 80D) whereas in subspecies *novae-zelandiae* they are more rounded and bluntly mucronate (e.g. ADU, A31711—Fig. 80E). Intergrades, however, are common.

16. Codium spinescens Silva & Womersley 1956: 285, fig. 16, pl. 3.

FIGS 79E, 80F

Thallus (Fig. 79E) firm, medium to dark green, regularly dichotomous, to 20 cm high, branches terete, slender, tapering slightly from 3 mm in diameter near the base to 1–2 mm near the apices. Utricles (Fig. 80F) slender when young, becoming stout, irregularly cylindrical, $80-270 \ \mu\text{m}$ in diameter, $470-680 \ \mu\text{m}$ long, apices asymmetrical and strongly acuminate (to $80 \ \mu\text{m}$ long) with the wall of the mucro thickened, finely lamellate and often chambered; hairs (or scars) common. Medullary filaments $20-30 \ \mu\text{m}$ in diameter, $175-240 \ \mu\text{m}$ long, $1-3 \ \text{per utricle}$, borne on a short protuberance just below middle of utricle.

Type from 16 km E. of Eucla, W. Aust. (Womersley, 3.ii.1954); in ADU, A19240.

Distribution: Known from the Abrolhos I., W. Aust., to the Head of the Great Australian Bight, S. Aust.

Selected specimens: North Beach, Perth, W. Aust., drift (Norris 1745, 27.iii.1959; ADU, A22260). Cottesloe, W. Aust., shallow sublittoral (Koh, March 1968; UWA). Torpedo Rocks, Yallingup, W. Aust., drift (Royce 616, I.vi.1950; in PERTH). Head of Great Australian Bight, S. Aust., drift (Woelkerling, 4.xi.1968; ADU, A34200).

This appears to be a western species, just extending into South Australia and usually from deeper water. It is most closely related to C. *fragile* but differs in habit and the short, stout, strongly spinous utricles.

ORDER CAULERPALES Feldmann

Thallus coenocytic, formed of much branched filaments either associated in tufts or interwoven, *or* morphologically differentiated into a basal stolon with rhizoids and erect, variously branched fronds; cell walls of microfibrilar xylan; heteroplastic, with chloroplasts and amyloplasts, and the chloroplasts containing siphonein and siphonoxanthin.

Life history diplontic with gametic meiosis, isogamous or (usually) anisogamous.

The Caulerpales were separated from the broader and older "Siphonales" by Feldmann (1946, p. 753; 1955) on the basis of their heteroplasty and wall structure with xylan replacing cellulose. Parker (1970) reviewed the value of wall structure in separating orders of the Chlorophyta. The Caulerpales contain three families, two of which are represented on southern Australian coasts. The Udoteaceae have a thallus of tufted or, more usually, interwoven filaments showing considerable structural similarity to the Codiaceae. The Caulerpaceae are quite different in their structure and morphology, with a distinctive thallus plan and a great variety of frond morphologies which characterise the species.

Some authors (e.g. Bold & Wynne 1978, p. 190) recognise a much broader order Caulerpales, including the families here placed in the Codiales and Derbesiales.

UDOTEACEAE

KEY TO FAMILIES OF CAULERPALES

- 1. Thallus composed of tufted, subdichotomous filaments or of filaments interwoven to form a macroscopic, often flattened, usually branched thallus UDOTEACEAE

FAMILY UDOTEACEAE (Endlicher) J. Agardh

Thallus either of tufted, subdichotomous filaments, or of interwoven filaments forming a compressed to complanate, simple or branched thallus differentiated into a medulla and cortex consisting either of filaments similar to the medulla or forming a surface layer of small, inflated "utricles". Heteroplastic, with chloroplasts and amyloplasts, wall containing xylan.

Life history diplontic with meiosis at gametogenesis as far as known; gametangia borne singly or in clusters on cortical filaments or utricles, anisogamous.

Most genera and species of the Udoteaceae are tropical or subtropical, many being calcified (especially *Halimeda*). Eight genera occur along southern Australia, most with only a single species in this region.

KEY TO GENERA OF UDOTEACEAE

1.	. Thallus filaments free, simple or branched, forming a loose	e tuft .		
1.	. Thallus of slender, interwoven or laterally attached filam	ients f	forming	a macroscopi
	thallus, usually compressed			

- 2. Thallus under 2 cm high, filaments slender (less than 60 μ m in diameter), branched and constricted at their base, simple above PSEUDOCHLORODESMIS
- 2. Thallus usually 5-15 cm high, filaments coarse (over 200 μ m in diameter), subdichotomous above and constricted just above branchings CHLORODESMIS

5. Thallus usually simple, tufted or flabellate to ovate and several filaments thick, spongy

- 6. Thallus to 1.5 cm high and 0.5 cm across, of loose tufts of filaments with occasional tenacula connecting lower filaments
 6. Thallus over 2 cm high when mature, compressed, spongy, several filaments thick,

UDOTEACEAE

Genus PSEUDOCHLORODESMIS Boergesen 1925: 77

Thallus uncalcified, tufted, composed of free, slender filaments basally branched and moniliform, and simple or irregularly branched above, attached by rhizoids. Filaments constricted at each dichotomy at the base but not constricted at upper branchings.

Reproduction unknown.

Type species: P. furcellata (Zanardini) Boergesen.

This is a small genus of three species, differing from *Chlorodesmis* in having very slender filaments and in lacking constrictions at the upper dichotomies.

Pseudochlorodesmis australis (Womersley) Womersley, comb. nov.

Chlorodesmis australis Womersley 1955: 388, fig. 3.

FIGS 81A, 82A,B

Thallus (Fig. 81A) medium to dark green, 0.5-1.5 cm high, forming loose tufts, branching only at the base with 2-4 dichotomies close together, attached by rhizoids. *Filaments* (Fig. 82A) constricted immediately above each dichotomy, above linear, 25-45 (-60) μ m in diameter; cell wall thin, slightly thickened at basal constrictions (Fig. 82B); chloroplasts dense, round to ovoid, $1.5-3.0 \ \mu$ m across; amyloplasts probably present.

Reproduction unknown.

Type from Robe, S. Aust. (Womersley, 28.vii.1949); in ADU, A12250.

Distribution: Known from the type and from Vivonne Bay, Kangaroo I., S. Aust., in shaded pool, S. side of Ellen Point (*Womersley*, 22.xi.1968; ADU, A32887). Pennington Bay, Kangaroo I., S. Aust., in shaded pool (*Womersley*, 4.i.1948, ADU, A53380). Robe, S. Aust., lower eulittoral in sand, slipway reef (*Womersley*, 24.viii.1960; ADU, A24431).

This species needs further investigation but seems best referred to *Pseudochlorodesmis* rather than *Chlorodesmis* which has much broader and frequently branched and constricted filaments. It differs from *P. furcellata* in dimensions and lack of upper branching and from *P. parva* Gilbert (1962, p. 141) and *P. tenuis* Ercegovic (1957, p. 33) in lack of upper branching.

Genus CHLORODESMIS Harvey & Bailey 1851: 373

Thallus uncalcified, tufted, composed of coarse, free filaments, distantly subdichotomous, arising from a dense, entangled, rhizoidal base. *Filaments* constricted above each dichotomy, constrictions symmetrical or asymmetrical.

Reproduction (known in *C. baculifera*) by zooids formed in ovoid zooidangia in dense lateral clusters on upper branches (Ducker 1965).

Type species: C. comosa Harvey & Bailey.

Chlorodesmis is a genus of some 6 species (Ducker 1967) in the Indo-Pacific region. It differs from most other genera (except *Pseudochlorodesmis*) of the Udoteaceae in that the filaments are free, not entangled or united to form a complanate or slightly compressed thallus.

Chlorodesmis baculifera (J. Agardh) Ducker 1966: 245; 1967: 155, pls 10, 11.

Bryopsis baculifera J. Agardh 1887: 21. Womersley 1956: 363.

Chlorodesmis bulbosa (Womersley) Ducker 1965: 149, figs 1-4.

Cladophoropsis bulbosa Womersley 1955: 391, figs 8, 9; 1956: 376.

FIGS 81B, 82C,D

Thallus (Fig. 81B) medium to dark green, erect, densely tufted, 4-10(-16) cm high, attached by colourless rhizoids and when adult arising from a matted bulbous base up to 2 cm high,



Fig. 81. A. Pseudochlorodesmis australis (ADU, A12250, type). B. Chlorodesmis baculifera (ADU, A51906, right hand specimen fertile). C. Halimeda cuneata (ADU, A50610). D. Pseudocodium australasicum (ADU, A13618, type).

formed of entangled rhizoids. Filaments (Fig. 82C) sparsely branched, of uniform width throughout, (250-)300-500(-600) μ m in diameter; wall lamellate, 6-10 μ m thick; lateral branches slightly basally constricted; chloroplasts ovoid to lenticular, 2-4 μ m long; amyloplasts elongate-ovoid, 6-10 μ m long.

Reproduction (Ducker 1965) in much branched fertile tufts borne laterally on the filaments, with each branch of the tuft bearing numerous ovoid laterals (Fig. 82D) which form biflagellate reproductive bodies (probably gametes) which are discharged through the branch apex; fertile in early summer (Nov.-Dec.).

Type from Port Phillip Heads, Vic.; in Herb. Agardh, LD, 14898.

Distribution: From Waterloo Bay (Elliston), S. Aust. to Waratah Bay, Vic. and the north coast of Tasmania. This is an uncommon species, apparently confined to deep water or shaded habitats.

Selected specimens: Waterloo Bay (Elliston), S. Aust., 9 m deep (Shepherd, 8.xi.1980; ADU, A51906.). Pearson I., S. Aust., 30–35 m deep (Shepherd, 7.i.1969; ADU, A34149). Pennington Bay, Kangaroo I., S. Aust., drift (Womersley, 31.xii.1949; ADU, A12825). Robe, S. Aust., upper sublittoral in bay (Dawes, 18.v.1964; ADU, A27842). Point Nepean, Vic., in deep pool (Price, 9.xii.1963; MELU, 1352). Waratah Bay, Vic., drift (Sinkora A2124, 1.iii.1975; ADU, A48299).

Genus HALIMEDA Lamouroux 1812: 186

Thallus erect or flaccid, arising from a rhizoidal holdfast, moderately to much branched, with the branches consisting of a series of calcified internodes or segments connected by small, uncalcified, flexible nodes; segments usually compressed to flat, in some species cylindrical, discoid or cuneate to reniform. *Structure* of slender filaments, with a multiaxial core of medullary filaments surrounded by a cortex of layers of utricles, with the walls of the peripheral utricles usually adherent; the nodal medullary filaments remain separate, anastomose in small groups, or unite into a large plate unit.

Reproduction by biflagellate gametes formed in globular to pyriform, stalked, gametangia arising from the segment margin or surface.

Lectotype species: H. tuna (Ellis & Solander) Lamouroux.

A genus of some 30 species (Hillis-Colinvaux 1980), largely confined to tropical-subtropical seas, with one species extending from the west coast into southern Australia.

Halimeda cuneata Hering. Hillis 1959: 345, pl. 1 fig. 6, pl. 5 figs 1,2, pl. 6 fig 10, pl. 7 fig. 7, pl. 9. Hillis-Colinvaux 1980: 124, figs 36, 61. Womersley 1956: 375.

FIGS 81C, 82E-G

Thallus (Fig. 81C) light green, to 15 cm high, arising from a distinct holdfast 0.5-1 cm long, calcification light, surface smooth; branching dichotomous to occasionally polychotomous, the basal segment subcylindrical, upper segments cuncate to subcuneate or discoid, to 16 mm long and 18 mm broad, 0.5-1(-1.5) mm thick, occasionally with a small cushion segment at the node. Cortex (Fig. 82F) of 2-4 layers of utricles, outermost remaining firmly attached after decalcification, $25-65 \,\mu$ m in surface diameter (Fig. 82E), $55-100(-135) \,\mu$ m long, and usually 4 on each secondary utricle. Nodal medullary filaments (Fig. 82G) united in groups of 2 or 3, the fused units entangled.

Fig. 82. A,B. Pseudochlorodesmis australis (ADU, A12250, type). A. A tuft of filaments. B. Detail of basal dichotomies. C,D. Chlorodesmis baculifera (ADU, A51906). C. Part of filament showing branching. D. Fertile filaments with zooidangia. E-G. Halimeda cuneata (ADU, A50610). E. Surface view of cortical cells.

F. Peripheral, secondary and tertiary utricles. G. Nodal organisation, with filaments united in groups at base of node.

UDOTEACEAE



Reproduction not recorded.

Type from Durban, South Africa (Krauss); in BM (see Hillis 1959, p. 346).

Distribution: Subtropical waters of south-eastern Africa, Lord Howe I.

Western Australian coast from the tropics around to Middle I., Recherche Arch., on the south coast; from low water level to 6 m deep.

Selected specimens: City of York Bay, Rottnest I., W. Aust., 3 m deep (*Clarke & Engler*, 6.ix.1979; ADU, A51138). Hamelin Bay, W. Aust., uppermost sublittoral (*Womersley*, l.ix.1979; ADU, A50610—"Marine Algae of southern Australia" No. 190). Goose I. Bay, Middle I., Recherche Arch., W. Aust., uppermost sublittoral (*Trudgen*, Nov. 1974; ADU, A51665).

Genus PSEUDOCODIUM Weber van Bosse 1896: 209

Thallus erect, uncalcified, subdichotomous, branches compressed, more or less linear. Growth apical, with a medulla of more or less longitudinal, branched filaments producing a cortex of elongate utricles which adher, closely to form a firm surface layer. Cross walls and plugs absent.

Reproduction unknown.

Type species: P. devriesii Weber van Bosse.

A small genus of three species, the type from South Africa and also *P. floridanum* Dawes & Mathieson (1972) from deep water off Florida. *P. devriesii* and *P. australasicum* both appear to be confined to shallow water.

Pseudocodium australasicum Womersley 1955: 390, figs 5,6.

FIGS 81D, 84A

Thallus (Fig. 81D) dark green, erect, subdichotomous to irregularly branched partly in one plane, to 6 cm high, branches 1-2 mm broad, compressed, holdfast small. Medulla (Fig. 84A) of longitudinal, branched filaments $13-28 \,\mu$ m in diameter, forming a surface cortical layer ($12-27 \,\mu$ m wide) of short clavate branches $4-7 \,\mu$ m in diameter (Fig. 84A) adhering together as seen in surface view. Chloroplasts ovoid, $2-3 \,\mu$ m long; amyloplasts sparse. Reproduction unknown.

Type from Point Sinclair, S. Aust., uppermost sublittoral (*Womersley*, 25.i.1951); in ADU, A13618.

Distribution: From Hopetoun, W. Aust. to Point Sinclair, S. Aust.

Selected specimens: Hopetoun, W. Aust., 2-3 m deep (Kraft (6995) & Ricker, 16.viii.1979; ADU, A 50717). 16 km E. of Eucla, S. Aust., drift (Womersley, 3.ii.1954; ADU, A19239).

Genus CALLIPSYGMA J. Agardh 1887: 65

Thallus uncalcified, more or less complanately branched with numerous laterals, with elongate upper branches bearing alternate, distichous, flabellate branch systems. Lower axes denuded but covered with short, branched, chains of moniliform cells which develop into a thick layer near the base of the thallus. *Flabellate systems* formed of di-(tri-) chotomous filaments of large elongate "segments" (probably multinucleate), occasionally laterally attached; cross walls formed by ingrowth from the periphery and with a small gap normally remaining. Chloroplasts numerous, discoid, without pyrenoids; amyloplasts present, and also acicular vacuolar crystals.

Reproduction unknown.

Type species: C. wilsonis J. Agardh.

Callipsygma is known only from the type species.

Callipsygma wilsonis J. Agardh. Cribb 1958: 207-208, figs 1-4. Gepp & Gepp 1911: 63, figs 144-146. Womersley 1956: 372; 1971a: 116, fig. 11.

FIGS 83A, 84B-F

Thallus (Fig. 83A) medium green, usually 10-35 cm high, more or less complanately and alternately branched, holdfast to 3 cm across, with lower axes of thallus irregularly subdichotomous to laterally branched and considerably thickened (0.5-1.5 cm in diameter); young branches probably developed seasonally, elongate, bearing subdistichous, alternate, fastigiate (Fig. 84B) to flabellate and complanate branch systems. *Flabellate systems* (Fig. 84C) 0.5-1.5 cm long, often complanately and di-(tri-) chotomously branched usually 1-2 segments apart, consisting of cylindrical segments with occasional lateral attachment (Fig. 84D) and with perforate end walls (Fig. 84E); upper segments usually (80-)150-200 μ m in diameter and 1-3 (-4) mm long, basal segments to 300 μ m in diameter and 300-500 μ m long. *Axes* denuded below but densely covered with chains of short, subspherical to ovoid segments 100-200 μ m in diameter (Fig. 84F) which are initiated close the apices and develop to form a very thick layer over the axial row of segments in the lower parts of the thallus.

Reproduction unknown.

Type from Sorrento, Port Phillip Heads, Vic.; in Herb. Agardh, LD, 15723.

Distribution: From Vivonne Bay, Kangaroo I., and Port Elliot, S. Aust. to Sorrento, Vic., Deal I. and Cape Barren I., in Bass Strait, and Musselroe Bay, Tasmania. Usually a deepwater species (to 10 m) or in heavily shaded pools.

Selected specimens: Seal Bay, Kangaroo I., S. Aust., drift (Womersley, 22.xi.1968; ADU, A32954). Robe, S. Aust., drift (Bailey, 18.xi.1967; ADU, A32028). Nora Creina, S. Aust., 1 m deep in shaded pool (Womersley, 16.xii.1970; ADU, A37818—"Marine Algae of southern Australia" No. 16). Point Lonsdale, Vic., shaded low pools (Woelkerling, 6.xi.1977; ADU, A48837). East Cove, Deal I., Bass Strait, 10 m deep (Shepherd & Lewis, 7.v.1974; ADU, A45090). Musselroe Bay, Tas. (Perrin, Feb. 1940; HO, 57914).

Callipsygma is a most distinctive alga. While placed in the Udoteaceae, it differs from most other genera (except *Rhipiliopsis robusta*—see below) in that the thallus is partitioned into regular, multinucleate segments by ingrowing cross walls which almost meet at the centre but usually leave a small perforation. Such regular segments and ingrowing cross walls are similar to the Cladophorales, but *Callipsygma* is heteroplastic and preliminary microchemical tests indicate that the wall does not contain cellulose.

Genus RHIPILIA Kuetzing 1858: 12, pl. 28

Thallus uncalcified, usually complanate, relatively thin, stipitate to subsessile, occasionally tufted, sometimes zonate, ecorticate. Structure of irregularly aggregated or laxly interwoven filaments which are repeatedly subdichotomous, basally constricted or not, and connected by short lateral branches terminated by a tenaculum of 2-6 short processes.

Reproduction unknown.

Lectotype species: R. tomentosa Kuetzing.

Rhipilia is a tropical genus of some 8 or 9 species in which R. pusilla is aberrant and may not be best placed in this genus.

Rhipilia pusilla (Womersley) Ducker 1967: 170, pls 9, 19. Chlorodesmis pusilla Womersley 1955: 389, fig. 4.

FIGS 83B, 85A-C

Thallus (Fig. 83B) dark green, 0.5-1.5 cm high, densely and irregularly tufted but not compressed, with basal filaments weakly or not attached by lateral tenacula (Fig. 85B).

Filaments (Fig. 85A) of erect branches sparsely subdichotomously or irregularly branched, 24–50 μ m in diameter, linear but with undulate walls and usually constricted shortly above the branchings; wall thin, very slightly thickened at the constrictions; heteroplastic, chloroplasts dense, round to elongate-ovoid, 1–2.5 μ m long, amyloplasts present (Fig. 85C).

Type from Pennington Bay, Kangaroo I., S. Aust. in a shaded pool (*Womersley*, 4.i.1948); in ADU, A7020.

Distribution: Only known from the type locality and from heavily shaded pools on the south side of Ellen Point, Vivonne Bay, Kangaroo I. (*Womersley*, 29.viii.1950; ADU, A15460, 30.i.1956; ADU, A20290, 29.i.1957; ADU, A20789 [illustrated by Ducker (1967, pl. 43 fig. 1) but incorrectly cited as A20290], and 22.xi.1968; ADU, A32893).

While this taxon is clearly not a *Chlorodesmis*, it also differs from other species placed in *Rhipilia* and until further studies are carried out on possibly more mature plants, its systematic position remains uncertain. It differs from typical *Rhipilia* in that a complanate thallus is not formed and the filaments are loosely aggregated, weakly attached by tenacula only near their base. If a *Rhipilia*, it is probably a simple, perhaps primitive, species.

Genus RHIPILIOPSIS Gepp & Gepp 1911: 45

Thallus uncalcified, complanate, irregularly ovate to elongate, arising from a short stipe, fronds relatively thin and soft. *Structure* of a lax felt of subdichotomous filaments attached by circular areas or by short protrusions from adjacent filaments. *Reproduction* from ovoid to pyriform zooidangia.

Type species: R. peltata (J. Agardh) Gepp & Gepp.

A genus of some 9 species [Farghaly & Denizot (1979, p. 173)].

KEY TO SPECIES OF *RHIPILIOPSIS*

- Thallus to 9 cm high, stipe to 3 cm long, filaments of lamina robust, 150-200 μm in diameter, distinctly moniliform
 R. robusta
- 1. Rhipiliopsis peltata (J. Agardh) Gepp & Gepp 1911: 45, figs 118-122. Womersley 1956: 376; 1971a: 116, fig. 12.

FIGS 83C, 85D,E

Thallus (Fig. 83C) medium to dark green, (1-)2-4(-6) cm high and (0.5-)1-2(-7) cm across, with a short stipe to 1 cm long broadening gradually or very rapidly into an ovate, reniform or irregularly elongate lamina, occasionally slightly lobed or lacerate, usually faintly zonate, thin (0.5-1 mm and several filaments thick), felt-like and spongy. Filaments (Fig. 85D) slender, (12-) 18-25 μ m in diameter, thin walled, repeatedly subdichotomous and laxly interwoven, constricted adjacent to a subdichotomy, with branch ends forming the surface layer: chloroplasts ovoid, amyloplasts present (Fig. 85E).

Reproduction from ovoid to pyriform, stalked zooidangia formed laterally on the medullary filaments (Fig. 85D).

Type from Port Phillip Heads, Vic.; in Herb. Agardh, LD, 15800.

Distribution: From Hopetoun, W. Aust., to Inverloch, Vic., from low tide level (shaded) to 31 m deep on rough-water coasts.



Fig. 83. A. Callipsygma wilsonis (ADU, A37818). B. Rhipilia pusilla (ADU, A32893). C. Rhipiliopsis peltata (ADU, A37817). D. Rhipiliopsis robusta (ADU, A41215). E. Avrainvillea clavatiramea (ADU, A33962).



Selected specimens: Hopetoun, W. Aust., 3-4 m deep near jetty (Kraft (6982) & Ricker, 16.viii.1979; ADU, A50720). Topgallant I., off W. coast of Eyre Pen., S. Aust., 20-25 m deep (Shepherd, 8.xi.1980; ADU, A51874). Tiparra reef, Spencer Gulf, S. Aust., 6 m deep (Shepherd, 5.xi.1971; ADU, A38304). Pennington Bay, Kangaroo I., S. Aust., shaded pool (Womersley, 4.i.1948; ADU, A6467). Nora Creina, S. Aust., in heavily shaded pool (Womersley, 17.i.1971; ADU, A37817—"Marine Algae of southern Australia" No. 24). Inverloch, Vic., rock pool (Ducker, 28.i.1969; MELU, 4267).

R. peltata is often common in shaded, just subtidal areas on rough-water coasts.

2. Rhipiliopsis robusta Womersley 1971a:117, figs 9, 13.

FIGS 83D, 85F-H

Thallus (Fig. 83D) dark green to green-grey, usually 4–9 cm high, uncalcified; holdfast to 1 cm across, stipe 1–4 cm long and 2–3 mm in diameter, simple or occasionally branched above; lamina 2–5 cm high and 2–3.5 cm across, undivided but often lacerate or slightly lobed, faintly zoned, about 1 mm and several filaments thick, spongy but moderately dense and firm; surface of lamina without a distinct cortex but ends of some filaments lying at the surface. Filaments (Fig. 85F) robust, 150–200 μ m in diameter, subdichotomous, distinctly moniliform with ovoid segments L/B 1.5–2(-3), with thickened wall plugs ingrowing from the periphery of the constrictions, laterally attached by circular areas without projections from the filaments (Fig. 85G); chloroplasts round to ovoid, 2–3 μ m long, without pyrenoids; amyloplasts ovoid, 3–5 μ m long (Fig. 85H).

Type from Tiparra Reef, Spencer Gulf, S. Aust., 11 m deep (*Shepherd*, 24.ii.1971); in ADU, A38130.

Distribution: Only known from the type locality and from Pearson I., S. Aust., 30 m deep (*Shepherd*, 10.i.1969; ADU, A34049). Other Tiparra Reef collections, all *Shepherd*, are 11 m deep (20.viii.1971; ADU, A39349), 11 m deep (24.ix.1971; ADU, A39479—"Marine Algae of southern Australia" No. 25b), 13 m deep (13.xii.1971; ADU, A41215—"Marine Algae of southern Australia" No. 25a) and 13 m deep (18.x.1972; ADU, A42788).

R. robusta appears to be a deep water species, known from 11 to 30 m deep. The moniliform, ovoid segments, with perforate end walls and lateral attachment to adjacent segments, are very similar to those in *Callipsygma* and may indicate a closer relationship between these taxa.

Genus AVRAINVILLEA Decaisne 1842b: 108

Thallus uncalcified, usually flabellate and stipitate, arising from an erect rhizoidal holdfast or rhizomatous, with a felt-like lamina. *Filaments* interwoven, subdichotomous, without lateral appendages or attachment; constrictions present in filaments, sometimes strongly marked at dichotomies.

Reproduction involving gametangia which are terminal on filaments exserted from the lamina.

Type species: A. nigricans Decaisne.

Avrainvillea is a tropical-subtropical genus of some 18 species, often common in shallow, sandy mud areas. One species, A. clavatiramea, is known on southern Australian coasts.

Fig. 84. A. Pseudocodium australasicum (ADU, A13618). Longitudinal thallus structure. B-F. Callipsygma wilsonis. B. Loosely branched filaments (ADU, A32028). C. Flabellate tuft largely complanately branched. D. Detail of C showing lateral attachments. E. Apex of cell with two daughter cells and perforations between cells; lateral attachment to cell on left; chloroplasts, amyloplasts and acicular crystals. F. Cross section of older part showing short lateral chains of cells. C-F (ADU, A37818)



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Avrainvillea clavatiramea Gepp & Gepp 1911: 33, figs 92, 93. Womersley 1956: 372; 1971a: 116, fig. 10.

FIGS 83E, 85I-K

Thallus (Fig. 83E) dark green to brown-green, usually 10-25 cm high, with a matted holdfast giving rise to 1 to 8 fronds each with a long stipe expanding above to a cuncate lamina; stipes (4-)8-15 cm long and 0.5-1 cm in diameter; lamina usually 4-8 cm long and 4-8 cm broad, often zoned, (0.2-)0.5-1(-2) mm thick. Filaments (Fig. 85I) of lamina 35-55 μ m in diameter, relatively straight to slightly undulate, often torulose near their subclavate apices (Fig. 85J), constricted at dichotomies (Fig. 85K); chloroplasts and amyloplasts ovoid (Fig. 85K); a yellowish inclusion often present in upper filaments.

Reproduction unknown.

Type from Corio Bay, Port Phillip, Vic. (Wilson); in BM.

Distribution: From Rottnest I., W. Aust., to Port Phillip, Vic.

Selected specimens: Point Clune, Rottnest I., W. Aust., 14 m deep in cave (*Ricker & Kraft*, 5.xii.1980; ADU, A52187, MELU, 2252). Eucla, W. Aust., drift (*Parsons*, 5.xi.1968; ADU, A33962). Waldegrave I., off Eyre Pen., S. Aust., 22 m deep (*Shepherd*, 23.x.1970; ADU, A47193—"Marine Algae of southern Australia" No. 15). Aldinga, S. Aust., 3 m deep (*Clarke*, 14.xii.1981; ADU, A52785). Investigator Strait, S. Aust., 27 m deep (*Watson*, Stn X4, 9.i.1971; ADU, A38605).

A. clavatiramea appears to be essentially a deep water species (14-27 m deep), usually growing in a sandy substrate; off Aldinga, it grows in 2-4 m depth near the base of vertical faces (and so shaded) with considerable sediment around it.

A collection from Hopetoun, Western Australia, 3-4 metres deep near jetty (*Kraft* (6993) & *Ricker*, 16.viii.1979; ADU, A50721) is provisionally referred to *A. clavatiramea* but differs in being only 5-6 cm high and with 1-3 branches from the stipe and irregularly lobed above. However, the filament characteristics are similar to those of *A. clavatiramea* and it is likely that these are only young, perhaps somewhat unusual, plants of this species.

FAMILY CAULERPACEAE Greville ex Kuetzing

Thallus coenocytic but with trabeculae across the lumen, differentiated into a horizontal stolon attached by rhizoids and erect, simple to much branched fronds; wall of xylan; heteroplastic.

Life history diplontic, with meiosis at gametogenesis.

A monotypic family.

Genus CAULERPA Lamouroux 1809: 332

Thallus with a horizontal stolon attached by rhizoidal outgrowths and bearing erect photosynthetic fronds which are branched in various ways; coenocytic throughout but generally with firm walls and slender cylindrical wall ingrowths (trabeculae) crossing the lumen; chloroplasts with or without pyrenoids; amyloplasts present.

Fig. 85. A-C. Rhipilia pusilla (ADU, A32893). A. Filaments of thallus. B. Filaments with lateral tenaculum attachment. C. Filament with tenaculum, and chloroplasts and amyloplasts. D-E. Rhipiliopsis peltata (ADU, A51874). D. Filaments with lateral zooidangia on lower filaments and several lateral attachment areas. E. Details of filaments near surface, with chloroplasts and amyloplasts. F-H. Rhipiliopsis robusta (ADU, A41215). F. Filaments with several lateral connections as seen in lengthwise section of the thallus. G. Segments with perforated end walls and lateral connections. H. Part of segment with chloroplasts and amyloplasts. I-K. Avrainvillea clavatirannea (ADU, A33962). I. Filaments from upper thallus. J. Upper branch. K. Branch of a filament, with chloroplasts and amyloplasts.

CAULERPACEAE

Reproduction (known in a few species only) by clumping of the cytoplasm and chloroplasts, and differentiation of anisogametes which are discharged through papillae on the surface of the ramuli (Price 1972); meiosis occuring at gametogenesis.

Lectotype species: C. prolifera (Forskal) Lamouroux.

A large and common genus of about 70 species, frequent in tropical-subtropical seas but particularly rich and distinctive on southern Australian coasts. Weber van Bosse (1898) monographed the genus and recognised 12 subgenera. These were supported by Calvert, Dawes & Borowitzka (1976) on the basis of chloroplast ultrastructure, and these authors suggested southern Australia may be the geographical origin of *Caulerpa*.

The branching of the erect fronds distinguishes the species. In all southern Australian species they are branched to two or three orders, but in a few species the erect frond is essentially unbranched (e.g. C. filiformis on N.S.W. coasts).

The axes of the erect fronds comprise the first-order branches; they are occasionally branched in some species (e.g. *C. simpliciuscula*) but are of similar diameter throughout. They may bear only ramuli as second-order branches or may have distinct and regular second-order laterals which bear the ramuli as third-order branches. The ramuli may be vesiculate or terete to flattened, and the terete type may be unbranched, furcate or with a few subdichotomous or lateral branches which, when branched, are of similar diameter throughout.

KEY TO THE SPECIES OF CAULERPA

1. Ramuli compressed or terete (simple or branched), not vesiculate 2 1. Ramuli vesiculate, unbranched 14
 2. Erect axes bearing (directly) distichous, simple, terete or compressed ramuli3 2. Erect axes and/or second-order laterals bearing ramuli usually in more than two rows or on all sides; ramuli terete, usually filiform, simple or branched
 Ramuli terete, linear, (1-)1.5-2.5(-3) mm long, and less than 0.5 mm in diameter, alternately arranged
 4. Ramuli scattered, separated by at least their basal width, (2-)4-6(-10) mm long, 0.5-1(-1.5) mm broad 4. Ramuli regular and adjacent, separated by less than or about their basal width5
 5. Axes of erect fronds slightly compressed, 0.5-1 mm broad, ramuli opposite and only slightly compressed, 1-2(-3) mm long
 6. Ramuli convex on lower side, straighter on upper side, usually broadest (1.5-4 mm) at base, 3-10 mm long 6. Ramuli convex on upper side, straighter on lower side, basally constricted, 4-8 mm long, 0.7-1.5 mm broad
 Frect axes without second-order laterals but bearing simple or 1-4 times branched ramuli in rows or on all sides Erect axes bearing numerous distichously or radially arranged second-order laterals, each of which bears numerous simple or furcate ramuli

Caulerpa

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	8. Ramuli unbranched
9. 9.	Ramuli in distinct longitudinal rows, relatively straight 10 Ramuli usually not in distinct longitudinal rows, soft and incurved, 0.5–1.5 cm long 6. C. longifolia f. crispata
	10. Ramuli in 3 rows (2 when juvenile), 3-5(-9) mm long7. C. trifaria10. Ramuli usually in 5(4-6) rows, 0.5-1.5 cm long.6. C. longifolia
11. 11.	Ramuli once, or more usually twice, furcate near their base, rigid, straight to slightly curved, 1.5–4 mm long; stolon bearing simple ramuli 0.5–2.5 mm long8. C. brownii Ramuli 1–5 times laterally branched in their lower half, 1–3 cm long; stolon naked 9. C. cliftonii
	 Second-order laterals irregularly radially arranged around erect axes, 1-3(-4) cm long, bearing usually simple ramuli 2-7(-10) mm long, subdistichously to irregularly arranged; stolon covered with spinous ramuli
13. 13.	Ramuli once furcate usually near their base, 1–3 mm long, with a single or twinned spinous apex
	14. Ramuli distichously arranged on axes1514. Ramuli on all sides of axes17
15. 15.	Ramuli ovoid to elongate-ovoid, 3–7 mm long, usually L/B less than 213. C. geminata Ramuli elongate, clavate, usually over 6 mm long, L/B usually greater than 216
	16. Ramuli (5-)6-9 mm long; 1.5-2.5 mm broad 14. C. annulata 16. Ramuli 1-3 cm long; 3-8(-10) mm broad 15. C. cactoides
17.	Ramuli elongate clavate, (1.5-)2-5(-7) mm long, (0.5-)1-1.5(-2) mm broad near apex
17.	Ramuli sub-spherical to ovoid, elongate-ovoid or pyriform, usually less than 4 mm long, in some species constricted below the spherical-ovoid terminal part
	 Ramuli with a slight to prominent swollen base protruding from the axes, then constricted with a sub-spherical or ovoid terminal part. Ramuli with the constriction adjacent to the axis, ovoid to clavate or ovoid-pyriform.
19. 19.	Ramuli with a prominent papillate base, subspherical above the constriction and 150-550(-600) μ m in diameter, with more than 14 around the axes

- 20. Ramuli densely arranged on the axes, touching, (6-)8-14 around the axes, 0.7-1.5 mm long and 300-700(-850) μm in diameter
 19. C. simpliciuscula [less dense, 6-10 around the axes, in var. laxa].
- Ramuli usually loosely and irregularly arranged, 2-6 around the axes (subdistichous to radial), ovoid, L/B 1.5-2, (1.5-)2-4 (-7) mm long, 1-3 mm broad 13. C. geminata

1. Caulerpa alternans Womersley 1956: 364.

C. alternifolia J. Agardh 1887: 129. Weber van Bosse 1898: 298, pl. 15 fig. 1.

FIGS 86A, 87A

Stolon very slender, (250-)400-600 μ m in diameter, naked, usually epilithic. Erect fronds (Fig. 86A) medium green, simple or irregularly branched 1-4 times, to 10 cm high, with a terete axis 250-500 μ m in diameter bearing alternately and distichously arranged ramuli usually (0.2-)0.5-1 mm apart. Ramuli (Fig. 87A) straight to slightly upwardly curved, terete to slightly tapering, (1-)1.5-2.5(-3) mm long and (150-)200-300 μ m in diameter, with a short, spinous tip.

Lectotype from Port Phillip Heads, Vic. (Wilson); in Herb. Agardh, LD, 16416.

Distribution: Only known from the type locality and from deep water (13-40m) in Gulf St Vincent and Spencer Gulf, S. Aust.

Selected specimens: Off Troubridge Light, Gulf St Vincent, S. Aust., 17 m deep (Shepherd, 4.ii.1969, ADU, A33416—"Marine Algae of southern Australia" No. 5). W. of Tapley Shoal, Gulf St Vincent, S. Aust., 14 m deep (*Wood*, 17.i.1981; ADU, A51964).

This is the slenderest species of *Caulerpa* on southern Australian coasts, and is distinguished by the narrow, terete, distichous ramuli. It appears to be a relatively rare species confined to deep water.

2. Caulerpa remotifolia Sonder. Harvey 1859a: pl. 107. Weber van Bosse 1898: 286. Womersley 1956: 369.

FIGS 86B, 87B

Stolon usually relatively slender, (0.5-) 0.7-1 mm in diameter, naked, usually in a sandy mud substrate (or on jetty piles). *Erect fronds* (Fig. 86B) medium green, simple to several times irregularly branched, usually 15-30 cm high, terete below and above with a flattened axis 1-2(-3.5) mm broad, bearing alternately and distichously arranged ramuli usually separated when mature by at least their basal width but often distantly scattered and occasionally absent on some axes. *Ramuli* (Fig. 87B) compressed, (2-)4-6(-10) mm long and 0.5-1(-1.5) mm broad, linear or basally broadest adjacent to the axis, tapering throughout or more so near their apices, with a short spinous tip.

Lectotype from Lefevre Peninsula, S. Aust. (F. Mueller); in MEL, 503816.

Distribution: In very sheltered bays on the north coast of Kangaroo I. (Bay of Shoals, American River inlet) and Gulf St Vincent, S. Aust., Port Phillip and Western Port, Vic., and Spring Bay on the east coast of Tasmania.

Selected specimens: Outer Harbour, S. Aust., drift (*Womersley*, 16.vii.1950; ADU, A13290). Muston, American R. inlet, Kangaroo I., S. Aust., edge of channel (*Womersley*, 29.ix.1964; ADU, A28219). Kirk Point, Port Phillip, Vic., drift (*Womersley*, 30.viii.1971; ADU, A39516). Crawfish Rock, Westernport Bay, Vic., 4 m deep (*Watson*, 29.v.1974; ADU, A45395). Spring Bay, Tas. (*Perrin* 68, Mar. 1935; ADU, A47096).

C. remotifolia is confined to very sheltered inlets where it occurs from low water level to at least 10 metres deep. The density of the ramuli is very variable and some plants approach *C. scalpelliformis* in appearance (e.g. the Westernport Bay, Victoria, and Spring Bay, Tasmania specimens cited above). Most plants of these two species are, however, distinct in habit and in habitat, the latter occurring in moderate to strong water movement.



Fig. 86. A. Caulerpa alternans (ADU, A33416). B. Caulerpa remotifolia (ADU, A28219). C. Caulerpa distichophylla (ADU, A50590). D. Caulerpa scalpelliformis (ADU, A31660). E. Caulerpa scalpelliformis (ADU, A31825). F. Caulerpa ellistoniae (ADU, A13426).

3. Caulerpa distichophylla Sonder. Harvey 1860: pl. 161. Weber van Bosse 1898: 341, pl. 31 fig. 1. Womersley 1956: 366.

FIGS 86C, 87C

Stolon slender, 0.5-1 mm in diameter, naked, epilithic or in sand. Erect fronds (Fig. 86C) medium to dark green, simple to several times branched, usually 4–15 cm high and 3–4 (-8) mm broad, terete below with the axis becoming compressed above and 0.5-1 mm broad, bearing opposite, distichously arranged (rarely with odd non-distichous ramuli), closely adjacent ramuli. Ramuli (Fig. 87C) slightly compressed, 1–2(-3) mm long, slightly upwardly curved and broadest (0.2–0.5 mm) just above the slightly constricted base, tapering in their upper quarter to one third to a broad point.

Holotype from Western Australia (probably near Fremantle), (Preiss); in MEL, 503814.

Distribution: From Seven mile beach, Dongara, to King Georges Sound, W. Aust.

Selected specimens: Seven mile beach, N. of Dongara, W. Aust., 0.5-2 m deep (Kirkman, 17.ix.1979; ADU, A51296). Whitfords Beach, Perth, W. Aust., 6 m deep (Kirkman, 16.viii.1979; ADU, A50590). Frenchmans Bay, King Georges Sound, W. Aust., lower eulittoral (Womersley, 29.viii.1979; ADU, A51659).

C. distichophylla is relatively common on the west coast of Western Australia in subtidal rock pools and to 6 metres deep, but apparently rare on the south coast. It is distinguishable by its dimensions and the crowded, opposite ramuli. Specimens from Kangaroo Island and Bridgewater Bay, Victoria, previously referred (Womersley 1956, p. 366) to *C. distichophylla*, have alternate ramuli and are now considered to be small plants, with unusually short ramuli, of *C. scalpelliformis*.

 Caulerpa scalpelliformis (R. Brown ex Turner) C. Agardh. Harvey 1858: pl. 17. Lucas 1936: 34, fig. 16. Weber van Bosse 1898: 286, pl. 22 fig. 11, pl. 23 figs 1-4. Womersley 1956: 369.

FIGS 86D,E 87D,E

Stolon slender (0.5–1 mm in diameter) in small forms of young plants, robust [1.5–2.5 (-3) mm in diameter] in large, rough-water plants, cartilaginous, naked, epilithic. Erect fronds (Fig. 86D,E) medium to dark green, simple to occasionally branched, from 4–10 cm high and 3–6 mm broad in slender forms, to 20 cm high and 2(-3) cm broad in robust plants, terete for the basal 1–3 cm, then strongly compressed with an axis 2–3 mm broad in slender plants to 4–8(-10) mm broad in robust plants, bearing alternately distichous, closely adjacent ramuli. Ramuli (Fig. 87D,E) 2–4 mm long and 1–2 mm broad in slender plants (Fig. 87E), to 1–1.5 cm long and 3–5 mm broad in robust plants (Fig. 87D), strongly compressed, scalpelliform, basally broadest but often slightly constricted, usually slightly upwardly curved and with an acute angle between adjacent ramuli, tapering gradually over their lower half to three quarters, then abruptly to a distinct spinous tip.

Type from the southern coast of Australia (R. Brown); in BM.

Fig. 87. A. Caulerpa alternans (ADU, A33416). B. Caulerpa remotifolia, upper (B1) and mid (B2) parts of erect frond (ADU, A2829). C. Caulerpa distichophylla, upper (C1) and mid (C2) parts of erect frond (ADU, A50590). D. Caulerpa scalpelliformis, upper (D1) and mid (D2) parts of erect frond (ADU, A31660). E. Caulerpa scalpelliformis, upper (E1) and mid (E2) parts of erect frond (ADU, A31825). F. Caulerpa ellistoniae, upper (F1) and mid (F2) parts of erect frond (ADU, A13426).

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Distribution: From Whitfords Beach, Perth, W. Aust. around southern Australia (and Tasmania) to Jervis Bay, N.S.W. Common in rock pools and to 36 m deep on rough-water coasts. Var. *denticulata* (Decaisne) Weber van Bosse is known from the Red Sea and other tropical regions.

Selected specimens: Whitfords Beach, Perth, W. Aust., 4 m deep (Kirkman, 16.viii.1979; ADU, A50569). Elliston, S. Aust., in deep pools (Woelkerling, 16.v.1968; ADU, A32490— "Marine Algae of southern Australia" No. 10). Entrance to Kellidie Bay, Coffin Bay, S. Aust., low eulittoral (Womersley, 22.viii.1967; ADU, A31825—"Marine Algae of southern Australia" No. 10a). Mt Dutton Bay, Coffin Bay, S. Aust., 0–1 m deep (Womersley, 1.xii.1975; ADU, A46806—"Marine Algae of southern Australia" No. 10b). Port MacDonnell, S. Aust., upper sublittoral pools (Womersley, 25.i.1967; ADU, A31660). Walkerville, Vic., just below low tide at bluff (Sinkora A1509, 21.ii.1972; ADU, A42275). Bridport, Tas., pools (Wollaston & Mitchell, 4.iii.1964; ADU, A27947).

C. scalpelliformis is very variable in robustness and breadth, depending on degree of water movement and depth, but is generally a distinctive species. Some slender specimens (e.g. from Coffin Bay in relatively calm water) however, do approach robust forms of *C. remotifolia* with dense ramuli. In both these species the ramuli are alternately produced at the apices, in contrast to *C. distichophylla* where they are opposite.

5. Caulerpa ellistoniae Womersley 1955: 387, fig. 2; 1971a: 115.

FIGS 86F, 87F

Stolon robust, 2–4 mm in diameter, cartilaginous, naked, epilithic. Erect fronds (Fig. 86F) medium to dark green, several times branched, often di- to polychotomous, usually 10–25 cm high and 8–12 mm broad; axes terete and naked below, above compressed, 1–2 mm broad, bearing distichous, closely adjacent, alternate ramuli. Ramuli (Fig. 87F) separated by about their basal width, strongly compressed, 4–8 mm long and 0.7–1.5 mm broad, basally constricted with a fairly straight lower edge and convex upper edge, tapering in the upper quarter to one third to an acute tip.

Type from Elliston, S. Aust., drift (Womersley, 13.i.1951); in ADU, A13426.

Distribution: From Rottnest I. and Cape Hamelin, W. Aust., Pearson I., Elliston, and Vivonne Bay, Kangaroo I., in S. Aust. Usually confined to deep water [(7-)25-68 m].

Selected specimens: 10 km S.W. of Rottnest I., W. Aust., 64 m deep (*Wilson*, Feb. 1960: ADU, A24584 and UWA, A330). Pearson I., S. Aust., 36 m deep (*Shepherd*, 10.i.1969; ADU, A35153). Elliston, S. Aust., drift (*Woelkerling*, 28.xii.1976; ADU, A47859). 13 km S. of Vivonne Bay, Kangaroo L, S. Aust., 50-68 m deep from cray pots (*Latz*, 24.xi.1968; ADU, A32992).

C. ellistoniae is most closely related to C. scalpelliformis, differing in the form of the ramuli and branching of the erect axes.

6. Caulerpa longifolia C. Agardh. Lucas 1936: fig. 18. Womersley 1956: 367.

FIGS 88A, 89A

Stolon coarse, (1-)2-4 mm in diameter, cartilaginous, naked, epilithic. Erect fronds (Fig. 88A) medium to dark green, with simple or rarely branched axes, usually 15-50 (-65) cm high and 1-2(-3) cm across; axes terete, naked below and 1-3 mm in diameter above, bearing normally 5 regular rows (occasionally 4 or 6 rows) of slender, terete, ramuli. Ramuli (Fig. 89A) separated by about their basal width, 0.5-1.5 cm long and 300-450 (-600) μ m in diameter, linear, directed and curved upwards, tapering near their apices to a short, blunt or spinous tip.



Fig. 88. A. Caulerpa longifolia (ADU, A39569). B. Caulerpa longifolia f. crispata (ADU, A34035). C. Caulerpa trifaria (ADU, A33516). D. Caulerpa brownii (ADU, A26535). E. Caulerpa brownii (ADU, A46864). F. Caulerpa cliftonii (ADU, A34037). G. Caulerpa obscura (ADU, A38574). H. Caulerpa hedleyi (ADU, A38175).

Type from southern Australia; in PC.

Distribution: From Eucla, W. Aust. to Wilsons Promontory, Vic., and around Tasmania, on rough-water coasts from rock pools down to 40 m.

Selected specimens: D'Entrecasteaux Reef, E. of Head of Great Australian Bight, S. Aust., 15-20 m deep (Shepherd, 27.iii.1980; ADU, A52146). Point Avoid, Eyre Pen., S. Aust., drift (Womersley, 2.xii.1975; ADU, A46863). Nora Creina, S. Aust., 3-8 m deep (Owen, 3.ix.1971; ADU, A39569). Seal Bay, Kangaroo I., S. Aust., drift (Womersley, 31.x.1966; ADU, A30952). Walkerville, Vic., drift (Sinkora A2060, 26.ii.1975; ADU, A48346). Musselroe Bay, Tas. (Perrin 86, Jan. 1939; ADU, A47101).

forma crispata (Harvey) Womersley 1950: 147; 1956: 368.

FIGS 88B, 89B

Stolon relatively slender to coarse, (0.5-)1-2(-3.5) mm in diameter, naked, epilithic. Erect fronds (Fig. 88B) medium green, simple or with a few, often clustered (sometimes from several cm up the erect axis), branches 5-30 cm high and 0.5-1(-2) cm across; axes terete, naked near their base, bearing irregularly placed (occasionally partly in rows), slender, upwardly incurved, terete, ramuli (Fig. 89B) 0.5-1(-3) cm long and 200-300 μ m in diameter, tapering near their apices to a blunt or shortly spinous tip.

Type from Port Phillip Heads, Vic. (Harvey); in TCD.

Distribution: From Whitfords Beach, Perth, W. Aust. to Waratah Bay, Vic. and around Tasmania. In rock pools on rough-water coasts and also in sheltered bays (e.g. Port Phillip). Recorded to 40 m deep.

Selected specimens: 3 km W. of Whitfords Beach, Perth, W. Aust., 6 m deep (Kirkman, 11.xii.1979; ADU, A50856—"Marine Algae of southern Australia" No. 226). Garden I., W. Aust., in pools on west reefs (Smith, Nov. 1946: UWA 116, ADU, A4556). Hamelin Bay, W. Aust., uppermost sublittoral (Womersley, 1.ix.1979; ADU, A50609). Pearson I., S. Aust., 20-25 m deep and 35 m deep (Shepherd, 7.i.1969; ADU, A33649 and A34035 resp.). Off Troubridge Light (Edithburgh), S. Aust., 18 m deep (Shepherd, 4.ii.1969; ADU, A3558). Slipway Reef, Robe, S. Aust., rock pools (Tugwell, 25.v.1963; ADU, A26436). Pennington Bay, Kangaroo I., S. Aust., in pools (Womersley, 26.xii.1948; ADU, A10506). Kirk Point, Port Phillip, Vic., drift, (Womersley, 11.viii.1970; ADU, A36022). Great Taylor Bay, Bruny I., Tas., 9 m deep (Shepherd, 14.ii.1972; ADU, A42101).

This form is often slenderer than that typical of the species, and differs in having the ramuli irregularly arranged, not in rows; they are also more incurved. As Harvey (1959a, pl. 95) noted, f. crispata often appears specifically distinct from C. longifolia but intergrades (even on one plant) do occur. It may be in part an ecological variant but probably with some genotypic differences. The Western Australian plants (as cited above) and some South Australian (e.g A33558) also differ in that each erect axis produces a cluster of branches several cm (2-12) above the base, while most specimens from eastern southern Australia have the erect axes simple or only occasionally branched. In other aspects these western plants appear to be very similar to f. crispata.

Fig. 89. A. Caulerpa longifolia, ramuli (ADU, A39569). B. Caulerpa longifolia f. crispata, ramuli (ADU, A34035). C. Caulerpa trifaria, ramuli (ADU, A33516). D. Caulerpa brownii, ramuli (ADU, A26535). E. Caulerpa cliftonii, branched ramulus (ADU, A34037). F. Caulerpa obscura, secondary lateral with ramuli (F1) and apex of ramulus (F2) (ADU, A38574). G. Caulerpa flexilis, ramuli (ADU, A46868). H. Caulerpa hedleyi, ramuli on axis (H1) and single ramulus (H2) (ADU, A38175).



7. Caulerpa trifaria Harvey 1863: pl. 261. Lucas 1936: 39, fig. 20. Weber van Bosse 1898: 229. Womersley 1956: 371.

FIGS 88C, 89C

Stolon usually moderately slender, 0.7–1.5 mm in diameter, bearing scattered, short spines about 0.5 mm long, epilithic, on jetty piles or in sandy mud substrate. *Erect fronds* (Fig. 88C) medium green, with simple or occasionally branched axes, usually 5–25 cm high and 4–12 mm across; axes terete, 400–600(-700) μ m in diameter, with short spinous ramuli near their base, above bearing 3 (2 when juvenile or rarely on mature fronds) regular rows of slender, terete ramuli. *Ramuli* (Fig. 89C) separted by less than their basal width, 3–5(-9) mm long and 200–300 μ m in diameter, terete, with a slight to moderate upward curve, tapering close to their apices to a short spinous tip.

Type from Port Phillip Heads (Harvey); in TCD.

Distribution: From Cottesloe, W. Aust. to Western Port, Vic. and around Tasmania; usually confined to moderately sheltered to calm water, 2–31 m deep.

Selected specimens: Cottesloe, W. Aust., on reef (*Smith*, 12.viii.1944; ADU, A2089). Inside Tapley Shoal, Gulf St Vincent, S. Aust., 18 m deep (*Shepherd*, 2.ii.1969; ADU, A33516—"Marine Algae of southern Australia" No. 12). Port Noarlunga, S. Aust., 3-4 m deep (*Hergstrom & Owen*, 7.i.1971; ADU, A37792). Lonsdale Bight, Port Phillip, Vic. (*Macpherson* 331, 21.v.1961; ADU, A28158). Marion Bay, Tas., 6 m deep (*Shepherd*, 13.ii.1970; ADU A35624). Great Taylor Bay, Bruny L, Tas., 2–5 and 19 m deep (*Shepherd*, 14.ii.1972; ADU, A42114 and A42151 resp.).

C. trifaria is a distinctive species with normally three rows of slender ramuli. Juvenile plants (less than 3 cm high) often have only two rows of ramuli, but develop three rows as they mature. Some specimens from Great Taylor Bay, Bruny Island, Tasmania (A42114 and A42151, cited above) have distichous ramuli on the lower 6–10 cm, becoming tristichous above.

8. Caulerpa brownii (C. Agardh) Endlicher. Lucas 1936: 42, figs 23, 24. Weber van Bosse 1898: 306, pl. 25, fig. 3. Womersley 1956: 365.

FIGS 88D,E, 89D

Stolon usually robust, (1-) 1.5-3 mm in diameter, moderately densely covered with simple ramuli (0.5-)1-2.5 mm long and (150-)300-400(-500) μ m in diameter, tapering abruptly to a spinous tip, epilithic or on jetty piles. *Erect fronds* (Fig. 88D,E) medium to dark green, with simple or several times irregularly branched axes, usually 3-40 cm high and 3-6(-8) mm across; axes terete, 0.5-1.5 mm in diameter, densely covered throughout with irregularly placed ramuli. *Ramuli* (Fig. 89D) simple on basal part of axes and 1.5-3(-4) mm long, becoming basally furcate and often bifurcate over most of the axes, 3-4 mm long and (100-)250-350 μ m in diameter, terete, upwardly curved, tapering close to their apices to a spinous tip.

Type from Kent I., Bass Strait (R. Brown); in Herb. Agardh, LD, 16647.

Distribution: From Whitfords Beach, Perth, W. Aust. around southern Australia to Walkerville, Vic. and around Tasmania. New Zealand, Chatham I., Snares I., Lord Howe I. Common on rocks at and just below low tide level, often forming a monospecific community, and recorded to 42 m deep.

Selected specimens: Cowaramup Bay, W. Aust., 2-3 m deep (Clarke & Engler, 1.ix.1979; ADU, A50653). Point Avoid, Eyre Pen., S. Aust., drift (Womersley, 2.xii.1975; ADU, A46864). Pondalowie Bay, Yorke Pen., S. Aust., reef pool (Womersley, 14.iv.1963; ADU, A26535). Emu Bay, Kangaroo I., S. Aust., upper sublittoral on jetty piles (Womersley, 10.i.1956; ADU, A20146). Penguin I., Beachport, S. Aust., 1-3 m deep (Lewis, 11.vi.1973; ADU, A43585).

Walkerville Vic., in reef pools (*Sinkora* A1514, 21.ii.1972; ADU, A42265). Fluted Cape, Bruny I., Tas., 16 m deep (*Shepherd*, 10.ii.1972; ADU, A41475).

C. brownii is variable in robustness but readily recognised by its form and the basally furcate or bifurcate ramuli; specimens are more robust under the strongest water movement.

9. Caulerpa cliftonii Harvey. Lucas 1936: 41, fig. 22. Weber van Bosse 1898: 303. Womersley 1956: 366.

FIGS 88F, 89E

Stolon robust, 3-4 mm in diameter, cartilaginous, naked, epilithic. Erect fronds (Fig. 88F) dark green, with simple to several times irregularly branched axes, usually 6-22 cm high and 2-4(-6) cm across; axes terete, 1-1.5 mm in diameter, densely covered with irregularly placed ramuli from near their base. Ramuli (Fig. 89E) (1-)2-3(-4) cm long, alternately branched (1-)3-5 times in their lower third to half, with the branches upwardly curved, terete, 300-500 μ m in diameter, with a tapering, spinous to rounded apex.

Type from W. Aust. (probably near Fremantle) (Clifton); in TCD.

Distribution: From Port Denison and the Abrolhos Is, W. Aust. to Port Phillip Heads, Vic., mainly in shaded rock pools on rough-water coasts, recorded to 50 m deep.

Selected specimens: Port Denison, W. Aust., outer reef pools (*Woelkerling*, 8.xi.1968; ADU, A33141). Pearson I., S. Aust. 35 m deep (*Shepherd*, 7.i.1969, ADU, A34037). Encounter Bay, S. Aust. (*Cleland*, ADU, A3501). Cape du Couedic, Kangaroo I., S. Aust., shaded pools (*Womersley*, 16.i.1965; ADU, A28958). Point Lonsdale, Vic., upper sublittoral pools (*Womersley*, 21.i.1967; ADU, A31708).

C. cliftonii is superficially similar to C. obscura but differs in that the usually 3-5 times branched ramuli are borne directly on the frond axes and the stolon is naked.

10. Caulerpa obscura Sonder. Lucas 1936: 38, fig. 19. Weber van Bosse 1898: 301. Womersley 1956: 308.

FIGS 88G, 89F

Stolon robust, (1-)2-3(-4) mm in diameter, cartilaginous, bearing a sparse to moderate covering of simple or basally furcate, terete to tapering, spinous or rounded-tipped ramuli 1-2(-4) mm long, and 200-300 μ m in diameter, directed forward towards the stolon apex, epilithic. *Erect primary fronds* (Fig. 88G) dark green, with usually simple, occasionally branched axes, usually 10-25(-30) cm high and 2-5(-6) cm across; axes terete, 0.7-2 mm in diameter, bearing on all sides dense second-order laterals 1-3(-4) cm long which bear numerous ramuli irregularly arranged or sometimes tending to lie more or less in two rows; second-order laterals 350-450 μ m in diameter. *Ramuli* (Fig. 89F1) 2-7(-10) mm long and 250-350 μ m in diameter, terete, simple or furcate just below their apices, tapering abruptly to the tip which bears 1-3 single or divided spines (Fig. 89F2).

Type from W. Aust. (Preiss); not located in MEL.

Distribution: From Yanchep Beach, W. Aust. to Walkerville, Vic. and around Tasmania. Common in pools on rock platforms and in the upper sublittoral, under rough to moderate wave action, and recorded to 35 m deep.

Selected specimens: Whitfords Beach, Perth, W. Aust., 6 m deep (*Cook*, 20.viii.1979; ADU, A50576). Ward I., S. Aust., 18–23 m deep (*Shepherd*, 3.iii.1980; ADU, A50889). Tiparra reef, Spencer Gulf, S. Aust., 5 m deep (*Shepherd*, 19.v.1971; ADU, A38574). Emu Bay, Kangaroo I., S. Aust., upper sublittoral on jetty (*Womersley*, 10.ii.1956; ADU, A20149). Penguin I., Beachport, S. Aust., 1–3 m deep (*Lewis*, 11.vi.1973; ADU, A43588). Walkerville, Vic., at low

tide level on bluff (Sinkora A1515, 21.ii.1972; ADU, A42280). Guyton Point, Robbins I., Tas., upper sublittoral (Wollaston & Mitchell, 23.ii.1964; ADU, A27598).

C. obscura is distinguished by the second-order laterals bearing numerous ramuli, and by the spinous ramuli on the stolon. The superficially similar C. cliftonii has a naked stolon and branched ramuli borne directly on the axes, and C. flexilis has distichous second-order laterals and the stolon is covered with minute, much branched ramuli.

Caulerpa flexilis Lamouroux 1813: 283, pl. 13 fig. 3. Womersley 1956: 366.
 C. hypnoides C. Agardh. Harvey 1859a: pl. 84. Lucas 1936: 44, fig. 27. Weber van

Bosse 1898: 342, pl. 29.

FIGS 89G, 90A

Stolon robust, (2-)3-4(-6) mm in diameter, densely covered with small, 2-4 times furcate, ramuli each 150-500 μ m long and 80-120 μ m thick near their base, tapering to spinous (often bifid) apices, epilithic. Erect primary fronds (Fig. 90A) dark green, with simple or occasionally branched axes, usually 5-40 cm high and 2-6 cm across, largely to strictly alternately distichously branched with prominent, lax, second-order laterals usually 1-6 cm long and 2-4 mm across, bearing crowded ramuli on all sides. Ramuli (Fig. 89G) covering all parts of the primary fronds and the second-order laterals on all sides, bifurcate near their bases, 1-3 mm long and (150-)200-300(-350) μ m in diameter, terete, apically directed and slightly upwardly curved, tapering near their apices to 1-3 small, single or bifid, apical spines.

Type from Esperance, W. Aust. (Labillardiere); in CN.

Distribution: From Geraldton, W. Aust., to Collaroy, N.S.W. and around Tasmania. New Zealand (North Island). Common in rock pools and the upper sublittoral on rough-water and moderately sheltered coasts; recorded to 40 m deep.

Selected specimens: Green I., Rottnest I., W. Aust., 1–1.5 m deep (*Clarke & Engler*, 6.ix.1979; ADU, A51062). Point Avoid, Eyre Pen., S. Aust., drift (*Womersley*, 2.xii.1975; ADU, A46868). Pearson I., S. Aust., 30–32 m deep (*Shepherd*, 7.i.1969; ADU, A33676). American R. inlet, Kangaroo I., S. Aust., 2–4 m deep (*Womersley*, 22.viii. 1963; ADU, A26843—"Marine Algae of southern Australia" No. 7). Robe, S. Aust., rock pools (*Tugwell*, 25.v.1963; ADU, A26439). Gabo I., Vic., 28 m deep (*Shepherd*, 19.ii.1973; ADU, A43529). Fluted Cape, Bruny I., Tas., 23 m deep (*Shepherd*, 12.ii.1972; ADU, A41908).

var. muelleri (Sonder) Womersley 1956: 367.

C. muelleri Sonder. Harvey 1858, pl. 2. Lucas 1936: 46, fig. 28.

FIG. 90B

Differing from the species in its more robust and strictly distichous second-order laterals (Fig. 90B), with the ramuli more densely arranged on the laterals (so as to overlap without visible spaces between them) and also more robust than in the type variety (about 300 μ m in diameter compared to about 200 μ m).

Type from Rivoli Bay, S. Aust. (F. Mueller); holotype in MEL, 503815.

Distribution: From Geraldton, W. Aust. to Waratah Bay, Vic., and the north coast of Tasmania.

Selected specimens: 3 km W. of Whitfords Beach, Perth, W. Aust., 6 m deep (Kirkman, 11.xii.1979; ADU, A50855). Elliston, S. Aust., 7 m deep (Shepherd, 21.xi.1970; ADU, A37536). Robe, S. Aust., drift. (Womersley, 10.xii.1973; ADU, A44576—"Marine Algae of southern Australia" No. 143). Port Fairy, Vic., drift (Womersley, 24.i.1967; ADU, A31495). Rocky Cape, Tas., upper sublittoral pools (Wollaston & Mitchell, 24.ii.1964; ADU, A27649).

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C. flexilis is a distinctive species with its normally strictly distichously branched secondorder laterals, the whole thallus (including the stolon) being densely covered with ramuli. In the type variety occasional non-distichous second-order laterals may occur, and the branching is looser and laxer than in var. *muelleri*, which is always strictly distichous. Very few plants are intermediate between the above varieties, and no other varieties are worth recognising.



Fig. 90. A. Caulerpa flexilis (ADU, A46868). B. Caulerpa flexilis var. muelleri (ADU, A44576). C. Caulerpa geminata (ADU, A34106). D. Caulerpa annulata (ADU, A12226).

12. Caulerpa hedleyi Weber van Bosse 1910: 1, pl. 1 figs 1-4. Lucas 1936: 43, fig. 25. Womersley 1956: 367; 1971: 116.

FIGS 88H, 89H

Stolon robust, 1.5-2.5 mm in diameter, covered by a dense, compact layer (200-300 μ m thick) of branched, tapering, spinous-tipped ramuli, probably epilithic. *Erect fronds* (Fig. 88H) medium grey-green, with simple or occasionally branched axes 3-8 cm high and 1-3 cm across, axes (0.5-)1-2 mm thick, bearing alternately distichous and closely arranged second-order laterals above the basal 0.5-3 cm; second-order laterals 0.7-1.3 mm thick with axes about 0.3 mm thick. *Ramuli* (Fig. 89H1) densely covering all parts of the axes and second-order laterals, 0.2-0.5 mm long, several times branched, 50-75 μ m in diameter near their base and tapering evenly to spinous tips (Fig. 89H2).

Type from "off Kangaroo I.," S. Aust. (Hedley); in NSW.

Distribution: Known from Rottnest I., W. Aust., and the Isles of St Francis, Pearson I. and Investigator Strait, S. Aust.

Selected specimens: The Basin, Rottnest I., W. Aust., shallow sublittoral reef (Smith, Jan. 1966; UWA 2584b and ADU, A50545). Egg I., Isles of St Francis, S. Aust., 32–38 m deep (Shepherd, 11.i.1971; ADU, A38084). Pearson I., S. Aust., 22 m deep (Shepherd, 9.i.1969; ADU, A34054). Investigator Strait, S. Aust., 31 m deep (Watson Stn Z13, 25.i.1971; ADU, A38175).

This is usually a deep water species and the Rottnest I. specimens were probably heavily shaded. The distichous second-order laterals and minute, branched spinous ramuli are distinguishing features.

13. Caulerpa geminata Harvey 1855c:564. Womersley 1966: 137.

C. sedoides (R. Brown ex Turner) C. Agardh. Harvey 1859a: pl. 72. Lucas 1936: 47. Weber van Bosse 1898: 387, pl. 34 figs 10, 11. Womersley 1956: 369.

FIGS 90C, 92A

Stolon slender to moderately robust, 0.7-2 mm in diameter, naked, usually epilithic. Erect fronds (Fig. 90C) light to medium green, with simple to several times branched axes, usually 2-8(-15) cm high and 4-10 mm across, axes 0.7-1.5 mm in diameter, basally usually bare and above loosely covered with vesiculate ramuli on all sides or sometimes distichous or almost so, not or slightly constricted between ramuli. Ramuli (Fig. 92A) sub-spherical or ovoid to elongate-ovoid to clavate, rounded apically and basally constricted to a short pedicel on a not or slightly raised area of the axis, (1.5-)2-4(-7) mm long and (1-)1.5-2(-3) mm in diameter, thin walled.

Type from Kent I., Bass Strait (R. Brown); in BM.

Distribution: From Port Denison, W. Aust. around southern Australia and Tasmania to Bowen, Qld. (?). New Zealand. Common in rock pools near low tide level on rough-water platforms and in the upper sublittoral in calmer areas, recorded to 25 m deep.

Selected specimens: Port Denison, W. Aust., outer reef pools (Woelkerling, 8.xi.1968; ADU, A33140). Pearson I., S. Aust., 36 m deep (Shepherd, 10.i.1969; ADU, A34106). Rosetta Bay, Victor Harbor, S. Aust., 2 m deep (Engler, 17.iii.1980; ADU, A50951). Penguin I., Beachport, S. Aust., 1-3 m deep (Lewis, 11.vi.1973; ADU, A43589). Portarlington, Port Phillip, Vic., drift (Womersley, 9.viii.1959; ADU, A23106). Crawfish Rock, Westernport Bay, Vic., 6-9 m deep (Watson, 15.ix.1968; ADU, A32795). Walkerville, Vic., at low tide level (Sinkora A1508, 22.ii.1972; ADU, A42273). Great Taylor Bay, Bruny I., Tas., 9 m deep (Shepherd, 14.ii.1972; ADU, A42102).

Caulerpa

CAULERPACEAE

C. geminata is typically a small species with entangled stolons, short erect fronds and loosely arranged ramuli. In some forms the ramuli are distichous or almost so and become more elongate; such forms give the name to the species. However, intergrades occur from ovoid ramuli on all sides of the axes to distichous, elongate ramuli. In some calm water situations where there is often current flow, the ramuli of distichous forms become unusually elongate (to 5–7 mm long). Such forms occur in Port Phillip Bay and Westernport Bay, Vic. and occasionally on rough-water coasts (e.g. Pearson I. and Beachport in S. Aust.), and need further study.

14. Caulerpa annulata Lucas 1931: 410, pl. 27 fig. 1. Womersley 1956: 365.

FIGS 90D, 92B

Stolon coarse, 2–3.5 mm in diameter, naked, cartilaginous, epilithic. *Erect fronds* (Fig. 90D) medium to dark green, with simple or occasionally branched axes, 3-7(-25) cm high and 1.5–2 cm across, with the axis 1.5–3 mm in diameter and constricted just above the position of the opposite pairs of ramuli, moniliform from the base up with the upper segments L/B 1–1.5. *Ramuli* (Fig. 92B) oppositely and distichously arranged, elongate-ovoid to clavate, 4–10 mm long and 2–3.5 mm in diameter, thick walled (often shiny when dried).

Type from Port Arthur, Tas. (Lucas); in NSW.

Distribution: From Nora Creina, S. Aust. to Walkerville, Vic., and Port Arthur and Actaeon I., Tasmania. Probably mainly a deep water species, known from only a few collections. The Ardrossan, S. Aust. specimen (MEL 584834) (Womersley 1956, p. 365) is now referred to *C. geminata* Harvey.

Selected specimens: Nora Creina, S. Aust., drift (Womersley, 8.viii.1961; ADU, A25466). Cape Banks, S. Aust., sublittoral (*Ottaway*, 31.i.1981; ADU, A52142). Walkerville, Vic., drift (*Sinkora* A2371, 19.iii.1977; ADU, A48232). Port Arthur, Tas. (*Mawle*, Sept.1931; ADU, A12226 ex Lucas Herb.).

C. annulata appears to be a deeper growing species on rough-water coasts, distinguished by its dimensions and the constricted, moniliform axes to the erect fronds. These characteristics separate most specimens satisfactorily from the distichous, clavate ramuli, form of *C. geminata*.

15. Caulerpa cactoides (Turner) C. Agardh. Harvey 1858: pl. 26. Lucas 1936: 48. Weber van Bosse 1898: 390. Womersley 1956: 365.

FIGS 91A, 92C

Stolon very coarse, (2-)3-5 mm in diameter, naked, epilithic or in a sandy mud substrate. Erect fronds (Fig.91A) medium to dark green, with simple or occasionally branched axes, usually 10-25(-40) cm high and 1-3(-5) cm across, with the axis 2-5(-7) mm in diameter bearing opposite (occasionally alternate) distichously arranged vesiculate ramuli; lower part of axes usually bare and constricted in rough-water plants but not in calm-water plants, upper axis usually constricted above the pairs of ramuli. *Ramuli* (Fig. 92C) usually clavate, sometimes sub-pyriform, (0.7-)1-2(-3) cm long and 3-8(-10) mm in diameter, thick walled (especially in rough-water plants).

Type from "southern coast of Australia" (R. Brown); in BM.

Distribution: From Champion Bay, W. Aust. around southern Australia and Tasmania to the Richmond R. mouth, N.S.W. Common in rock pools on rough-water coasts and in the upper sublittoral on both rough-water and sheltered coasts where it may cover extensive areas in a sandy mud substrate (e.g. parts of Coffin Bay, S. Aust. and Westernport Bay, Vic.). Recorded to 38 m deep.
Selected specimens: Champion Bay, W. Aust. (Kraft 1904, 8.vii.1966; MELU). Seven mile beach, N. of Dongara, W. Aust., 0.5-2 m deep (Kirkman, 17.ix.1979; ADU, A51297). Hopetoun, W. Aust., upper sublittoral (Wollaston, 20.ii.1957; ADU, A22155). Kellidie Bay, Coffin Bay, S. Aust., 3-4 m deep (Taylor, 5.xii.1975; ADU, A46706). Penguin I., Beachport, S. Aust., 1-3 m deep (Lewis, 11.vi.1973; ADU, A43586). Carpenter Rocks, S. Aust., upper sublittoral pools (Womersley, 5.ii.1970; ADU, A35181—"Marine Algae of southern Australia" No. 6). Walkerville, Vic., at low tide, edge of bluff (Sinkora A1510, 21.ii.1972; ADU, A42292). East Beach, Low Head, Tas. (Perrin & Lucas, Jan. 1930; ADU, A9056).

C. cactoides is a distinctive species, though the shape and size of the ramuli vary considerably in different ecological situations.

 Caulerpa racemosa (Forskal) J. Agardh var. laetevirens (Montagne) Weber van Bosse. f. cylindracea (Sonder) Weber van Bosse 1898: 366, pl. 33 figs 17-20. Womersley 1956: 368.

Caulerpa cylindracea Sonder. Harvey 1858: pl. 30.

FIGS 91B, 92D

Stolon slender to moderate, 0.7-1.5(-2) mm in diameter, naked, in firm sandy mud substrate or epilithic. Erect fronds (Fig. 91B) medium green, with simple or occasionally branched axes, (1-)4-7(-10) cm high and 3-8 mm across with the axis 0.5-1 mm thick, bearing vesiculate ramuli loosely to moderately densely on all sides. Ramuli (Fig. 92D) upwardly directed, clavate, (1.5-)2-5(-7) mm long and (0.5-)1-1.5(-2) mm in greatest diameter shortly below the rounded apices, tapering gradually to a relatively broad and unconstricted attachment to the axes.

Type (of form) from W. Aust. (Preiss); in MEL, 516014.

Distribution: From tropical W. Aust. around the south-west coast to King Georges Sound, usually in the uppermost sublittoral.

Selected specimens: Whitfords Beach, Perth, W. Aust., 4 m deep (*Cook*, 20.viii.1979; ADU, A50562). Point Peron, W. Aust., upper sublittoral pools (*Womersley*, 29.ix.1979; ADU, A50713— "Marine Algae of southern Australia" No. 189). Hopetoun, W. Aust., upper sublittoral on reef (*Wollaston*, 20.ii.1957; ADU, A22149).

This tropical species just extends into southern Australia. It is readily distinguished by the clavate ramuli with broad attachment to the axes. The ramuli vary considerably in density, being sparser nearer the eastern end of its range.

17. Caulerpa papillosa J. Agardh. Lucas 1936: 48. Weber van Bosse 1898: 383, pl. 34 fig. 8. Womersley 1956: 368.

FIGS 91C, 92E

Stolon slender to moderate, 0.7-2 mm in diameter, naked, epilithic. *Erect fronds* (Fig. 91C) medium to dark green, with simple or branched axes, usually 4–16 cm high and 2–4(-5) mm across, with axes 1–1.5 mm in diameter densely covered to their bases by vesiculate ramuli. *Ramuli* (Fig. 92E) 0.7–1.5 mm long, with a lower, sub-terete pedicel 300–800 μ m long and 200–300 μ m in diameter, then constricted and bearing a subspherical to ovoid-pyriform upper part (250-)350–500(-700) μ m in diameter.

Lectotype from Queenscliff, Vic. (F. Mueller); in Herb. Agardh, LD, 16849.

Distribution: From Middle I., Recherche Archipelago, W. Aust., to Walkerville, Vic. and northern Tasmania, in shaded rock pools and the uppermost sublittoral on rough-water coasts, recorded to 12 m deep.

Selected specimens: Goose I. bay, Middle I., Recherche Arch., W. Aust., low eulittoral (*Trudgen*, Nov. 1974; ADU, A51668). St Francis I., Isles of St Francis, S. Aust., 2 m deep (*Shepherd*, 9.i.1971; ADU, A38119). Elliston, S. Aust., in deep pools (*Woelkerling*, 16.v.1968; ADU, A32489—"Marine Algae of southern Australia" No. 9). Robe, S. Aust., 6 m deep (*Mitchell*, 25.v.1963; ADU, A26451). Walkerville, Vic., at low tide level on bluff (*Sinkora* A1513, 21.ii.1972; ADU, A42282). Currie R. mouth, Tas., low eulittoral (*Womersley*, 28.i.1949; ADU, A10332).

The small, densely packed ramuli, each constricted half way or more along its length, distinguish this species.



Fig. 91. A. Caulerpa cactoides (ADU, A43586). B. Caulerpa racemosa var. laetevirens f. cylindracea (ADU, A50562). C. Caulerpa papillosa (ADU, A26451). D. Caulerpa vesiculifera (ADU, A32487). E. Caulerpa simpliciuscula (ADU, A32488).

18. Caulerpa vesiculifera Harvey. Lucas 1936: 47. Womersley 1956: 371.

C. simpliciuscula var. vesiculifera Harvey 1859a: pl. 65 figs 3.4.

C. ethelae Weber van Bosse 1898: 384, pl. 34 figs 5,6.

FIGS 91D, 92F

Stolon moderately robust, (1-)2-3 mm in diameter, naked, epilithic. Erect fronds (Fig. 91D) medium to dark green with simple or often with several times branched axes, usually 8-25(-35) cm high and 3-5 mm across, with axes 1-2 mm in diameter densely covered to their bases with vesiculate ramuli, 7-9 around the axes. Ramuli (Fig. 92F) with a slight to conspicuous, broadly conical, pedicel from the axis, ovoid above the constriction, (1-)1.5-2.5 mm long and 0.7-1.5 mm in diameter.

Type from Western Port, Vic. (Harvey); in TCD.

Distribution: From Shark Bay, W. Aust. to Phillip I., Vic. and the north coast of Tas. in rock pools and the upper sublittoral on rough-water coasts; recorded to 25 m deep.

Selected specimens: South Passage, Shark Bay, W. Aust., 5 m deep (*Cambridge*, 24.viii.1979; ADU, A51762). Point Peron, W. Aust., reef pools (*Mitchell*, 22.ix.1966; ADU, A30734). Elliston, S. Aust., in deep pools (*Woelkerling*, 16.v.1968; ADU, A32487—"Marine Algae of southern Australia" No. 13b). Cape du Couedic, Kangaroo I., S. Aust., shaded pools (*Womersley*, 16.i.1965; ADU, A28960). Flinders, Vic., upper sublittoral pools (*Womersley*, 18.i.1967; ADU, A31800—"Marine Algae of southern Australia" No. 13a). Rocky Cape, Tas., drift (*Gordon*, 18.i.1966; ADU, A29939).

C. vesiculifera is readily distinguished by the size of the vesicles and the protuberance from the axes before the constriction; in some specimens, however, this basal protuberance is relatively slight.

 Caulerpa simpliciuscula (Turner) C. Agardh. Harvey 1859a: pl. 65 figs 1.2 (not figs 3.4). Lucas 1936: 47. Weber van Bosse 1898: 377. pl. 34 figs 3.4. Womersley 1956: 370.

FIGS 91E, 92G

Stolon slender to moderate, 1-2 mm in diameter, naked, epilithic. Erect fronds (Fig. 91E) medium to dark green, with simple or often branched axes, usually 4-30 cm high and (2.5-) 3-5 mm across, axes 1-2 mm in diameter, densely covered from their bases by vesiculate ramuli with 8-14 around the axis. Ramuli (Fig. 92G) ovoid-pyriform to clavate, 0.7-1.5 mm long and 300-700(-950) μ m in diameter where broadest below apices, constricted immediately adjacent to the axis or with only a very slight protuberance.

Type from Kent I., Bass Strait (R. Brown); in BM.

Distribution: From Port Denison, W. Aust. to Walkerville, Vic. and around Tasmania. Common in rock pools and the upper sublittoral on rough-water coasts, extending into bays with moderate water movement: recorded to 38 m deep.

Fig. 92. A. Caulerpa geminata, ramuli on axis (ADU, A50951). B. Caulerpa annulata, ramuli on axis (ADU, A48232). C. Caulerpa cactoides, lower axis with ramuli, on stolon (ADU, A43586). D. Caulerpa racemosa var. laetevirens f. cylindracea, ramuli (ADU, A50562). E. Caulerpa papillosa, cross section of axis with ramuli (ADU, A26451). F. Caulerpa vesiculifera, cross section of axis with ramuli (ADU, A32487). G. Caulerpa simpliciuscula cross section of axis with ramuli (ADU, A32488).



Selected specimens: Seven mile beach, Dongara, W. Aust., 0.5-2 m deep (Kirkman, 17.ix.1979; ADU, A51301). Elliston, S. Aust., in deep pools (Woelkerling, 16.v.1968; ADU, A32488— "Marine Algae of southern Australia" No. 11). Nora Creina, S. Aust., upper sublittoral pool (Womersley, 14.xi.1955; ADU, A20019). Walkerville, Vic., in pool (Sinkora A2132, 2.iii.1975; ADU, A48283). Great Taylor Bay, Bruny I., Tas., 2-5 m deep (Shepherd, 14.ii.1972; ADU, A42116).

C. simpliciuscula has smaller, usually more densely packed, ramuli than in C. vesiculifera, and the constriction is adjacent to the axis or with only a slight protuberance.

Variety laxa Womersley (1956, p. 370) has less dense ramuli (6–10 around the axis) but is otherwise similar. It is found in calmer-water areas such as American River inlet on Kangaroo Island, Port Phillip and Western Port in Victoria, and the north coast of Tasmania. Intergrades exist between the typical rough-water and the calm-water forms, and it is likely that var. *laxa* is largely an ecological variant.

Selected specimens: (of var. laxa). Rabbit I., Pelican Lagoon, American R. inlet, Kangaroo I., S. Aust., upper sublittoral (*Womersley*, 31.v.1947; ADU, A5804). Williamstown, Port Phillip, Vic., drift (*Maclennan*, 22.vi.1949; ADU, A14126). Crawfish Rock, Westernport Bay, Vic., 0-3 m deep (*Watson*, 15.ix.1968; ADU, A32749). Bombay Rock, Tamar Estuary, Tas., upper sublittorial (*Womersley*, 27.i.1949; ADU, A10371).

ORDER DERBESIALES Feldmann

Thallus heteromorphic, completely or largely coenocytic; sporophyte of free filaments, usually much branched; gametophyte either filamentous and relatively small, or ovoid and vesiculate; wall of sporophyte of mannan, but xylan in gametophyte; homoplastic, chloroplasts with or without pyrenoids and containing siphonein and siphonoxanthin.

Life history diplohaplontic with heteromorphic generations.

Reproduction by multiflagellate (stephanokontic) zoospores from the sporophyte and biflagellate anisogametes from the gametophyte; or direct from the sporophyte. Reproductive organs become separated by plugs (Menzel 1980).

This is a small order of only a few genera, which are satisfactorily separated from the Caulerpales and Codiales by their heteromorphic life history, stephanokontic zoospores, and presence of mannan in the sporophyte wall but xylan in the gametophyte wall. Some authors (e.g. Bold & Wynne 1978, pp. 201, 206) retain the two families within the Caulerpales.

KEY TO FAMILIES OF DERBESIALES

FAMILY BRYOPSIDACEAE Bory

Thallus (gametophyte) erect, usually several cm high, with one to several distinct axes pinnately or radially branched and sub-branched, branches and ramuli basally constricted, cylindrical to slightly tapering; sporophytic thallus filamentous, creeping, slightly branched.

Reproduction. Gametophyte monoecious or dioecious, producing anisogametes within ramuli cut off by a basal septum, liberated through papillae or from lateral gametangia. Sporophytes producing stephanokontic zoospores within the filaments.

Genus BRYOPSIS Lamouroux 1809: 133

Thallus diplohaplontic, heteromorphic, with a much branched gametophyte and small, slightly branched sporophyte. Gametophyte erect, with one or more percurrent axes arising from branched rhizoids; axes radially, bilaterally or pinnately branched, with the laterals in most species becoming similarly branched, with the ultimate branchlets (the ramuli) elongate and cylindrical or terete, often lost from lower parts of the axes and laterals, leaving scars which may disappear below; chloroplasts numerous, discoid to lenticular, with a usually conspicuous pyrenoid. Sporophyte minute, slightly and irregularly branched.

Reproduction. Gametophytes monoecious or dioecious, anisogamous; ramuli cut off by a basal septum to form unisexual or bisexual gametangia. Sporophyte producing stephanokontic zoospores within the filaments.

Lectotype species: B. pennata Lamouroux.

Numerous species of *Bryopsis* have been described, especially from the Mediterranean, but their variability and specific limits are often uncertain. Culture and life-history studies such as those of Rietema (1975) are essential to understanding the species, and these have only been attempted for Australian species by MacRaild (1974, unpublished). Considerable variation occurs in the branching patterns of some species, due in part to ecological factors and also to their growth habit, and in some areas it seems likely that intergrades between species also occur with gene exchange. Thus some species (e.g. *B. foliosa*) are typically radially branched throughout but lower parts of axes may show bilateral arrangement of ramuli or laterals. Other species (e.g. *B. australis*) may have largely unilateral ramuli when growing in dense tufts rather than the typical bilateral arrangement of two irregular rows on each side. This type of variation, from radial in some (usually upper) parts to bilateral with either two alternating rows on each side or an irregular grouping on the opposite sides is often puzzling and needs to be studied from ecological and developmental viewpoints and in culture.

In Europe, *B. plumosa* has been shown to be dioecious, while *B. hypnoides* is monoecious with both male and female gametes in the one gametangium, and *B. monoica* is also monoecious but the male and female gametes are produced in separate gametangia. MacRaild (1974) has shown that in southern Australia, *B. plumosa, B. vestita* and *B. gemellipara* are all dioecious and the diploid microthalli produce stephanokontic zoospores.

Naming and characterisation of the southern Australian species must remain tentative until both further knowledge is available on European species and life-history and ecological studies on Australian species have been carried out. The following key and descriptions are based essentially on morphological features.

KEY TO SPECIES OF BRYOPSIS

1. 1.	Thallus essentially radially branched
	 Ramuli slender, (12-)20-55 μm in diameter, irregularly and sparsely to profusely radially branched. Ramuli stouter, mostly over 70 μm in diameter, laterals usually densely branched 3
3.	Thallus delicate, with slender, usually simple, axes (2-)3-6(-8) cm high, bearing ramuli (which become laterals) separated by two to several times their basal width
	2. B. macraildii
3.	Thallus robust, densely branched, axes often over 8 cm high, strongly developed or with
	irregular long laterals, with ramuli on upper parts usually separated by less than twice

- 5. Thallus mostly bilaterally branched (or radially near apices), with ramuli or laterals on each side mainly in two slightly displaced rows, occasionally mostly unilateral6
 - 6. Thallus 2-4(-5) cm high, usually in tufts of 8-30 axes, axes usually less than 0.5 mm in diameter, ramuli mainly bilaterally arranged (or unilaterally in dense tufts)
 6. B. australis

1. Bryopsis minor Womersley 1955: 387, fig. 1; 1956: 363.

FIGS 93A,B, 94A,B

Thallus (Fig. 93A,B) to 15 cm high, spreading to tufted, much branched irregularly radially, arising from branched rhizoids. *Axes* and main branches (Fig. 94A) 150–350 μ m in diameter, denuded below, scars conspicuous on older axes; laterals 40–80 μ m in diameter; ramuli 1–3 mm long and (12-)20–55 μ m in diameter; chloroplasts ovoid to lenticular, 4–10 μ m long, with starch plates surrounding an indistinct pyrenoid (Fig. 94B).

Reproduction by ovoid gametes (6-)8-10 μ m long and 4-6 μ m broad, each with 3-4 chloroplasts.

Holotype from American River inlet, Kangaroo I., S. Aust., on black buoy (Womersley, 6.ix.1946; ADU, A4124).

Distribution: Known from the type locality and from Port MacDonnell, S. Aust., drift in harbour (*Womersley*, 15.v.1982; ADU, A53161 and 17.v.1983; ADU, A54041).

The large, bushy specimens from Port MacDonnell are placed with the small (to 2 cm high) type specimen from American R. inlet on the basis of habit, branching, dimensions of the slender ramuli and chloroplast structure, but the species clearly needs further investigation from living material in culture.

2. Bryposis macraildii sp. nov.

FIGS 93C-E, 94C,D

Thallus (Fig. 93C-E) delicate, usually much branched, (2-)3-6(-8) cm high, axes and laterals naked or not below, simple or branched, arising from a branched rhizoidal system, epilithic or on shells; mature plants with 3-4 orders or branching, branches lanceolate in outline. Axes and laterals radially branched (Fig. 94C,D) ramuli simple or with 1-2 laterals, regularly and fairly densely arranged but separated by two to several times their basal width, denuded below with scars slightly to moderately conspicuous above, becoming inconspicuous. Axes 0.5-1 mm in diameter, laterals 130-200 μ m in diameter, ramuli 0.5-1 mm long and 70-110 μ m in diameter below, scarcely or distinctly tapering (to 40 μ m near tips) and with rounded ends.

i





Fig. 93. A. Bryopsis minor (ADU, A4124, type). B. Bryopsis minor (ADU, A54041). C. Bryopsis macraildii (ADU, A50706, type). D. Bryopsis macraildii (ADU, A18368, Harvey 572A). E. Bryopsis macraildii (ADU, A5782).

Reproduction unknown.

Diagnosis: Thallus tenuis, saepe ramosus, (2-)3-6(-8) cm altus, axibus et ramis lateralibus infra nonnumquam nudis, simplex vel ramosus ex rhizoideo ramoso exortus, in saxis conchisque affixus; plantae adultae in 3-4 ordinibus lanceolate forma ramificantes. Axes et rami laterales radialiter ramosi, ramuli regulariter denseque dispositi cum spatio inter se duplo vel aliquoties quam latitudinem basalem, infra denudati et super conspicue infraque vix cicatricati. Axes 0.5-1 mm diametro, laterales 130-200 μ m diametro, ramuli 0.5-1 mm longi et 70-110 μ m diametro, vix (vel interdum conspicue) decrescentes, apicibus rotundatis. Reproductio ignota.

Type locality: King Head, Rottnest I., W. Aust., low culittoral on platforms (*Womersley*, 6.ix.1979).

Holotype: ADU, A50706. Isotypes distributed as "Marine Algae of southern Australia" No. 233.

Distribution: Known by the specimens from Rottnest I., W. Aust. (*Harvey*, Alg. Aust. Exsicc. 572A). Point Peron, W. Aust., rear reef pools (*Womersley*, 23.viii.1947; ADU, A5921). Near entrance to Kellidie Bay, Coffin Bay, S. Aust., uppermost sublittoral (*Womersley*, 24.ii.1959; 22.viii.1967, 13.v.1968; ADU, A22560, A31816, A32482 resp.). American River inlet, Kangaroo I., S. Aust., from buoys and tidal flats, just subtidal (*Womersley*, 25.i.1946; 6.ix.1946; 24.vii.1947; ADU, A3467, A4121, A5782 resp.). St Leonards, Port Phillip, Vic., 1–3 m deep (*Womersley*, 9.viii.1959; ADU, A52189). Swan Bay, Port Phillip, Vic., 0.5 m deep (*Watson*, 30.ix.1973; ADU, A44123).

Harvey's 572A, as *B. australis* Sonder, is entirely radially branched and is placed under *B. macraildii* in contrast to true *B. australis* which is bilateral.

B. macraildii is related to B. hypnoides in the radial arrangement of the ramuli, which are distinctly shorter and of smaller diameter than in the latter species. In B. macraildii they are fairly regularly arranged for some distance from the ends of axes and laterals and of fairly uniform length. B. macraildii is slenderer and has more widely spaced ramuli than B. foliosa or B. vestita.

Unfortunately the reproduction of *B. macraildii* is unknown and it is distinguished on morphological features only. While it seems to be a distinct species in southern Australia, comparisons with little known species from the Mediterranean and elsewhere may bring to light an earlier name for this taxon.

3. Bryopsis foliosa Sonder 1845: 49; 1846: 152. Womersley 1956: 363. B. gracilis Sonder 1845: 49; 1846: 152.

FIGS 94E, 95A,B

Thallus (Fig.95A,B) 4–10(-15) cm high, bushy and very densely branched with 3(-4) orders of branching, with few to numerous axes arising from a much branched, extensive, rhizoidal basal system, epilithic or epiphytic on *Posidonia*. Axes irregularly and densely branched above with some laterals strongly developed and basally denuded (Fig.94E); young axes and laterals narrowly lanceolate in outline; branching of axes and laterals essentially radial but on plants epiphytic on *Posidonia* and *Heterozostera* branching on some older axes tending to be limited to opposite sides of the axes (Fig. 95B) but irregularly placed. *Axes* (300-)400-1000 μ m in diameter; main laterals 300-500 μ m in diameter, lesser laterals 1–4 mm long, 100–200 μ m in diameter; ramuli (0.2-)0.5–1 mm long, (50-)75–100(-125) μ m in diameter, upwardly curved and slightly tapering; scars on laterals prominent (Fig. 94E).

Fig. 94. A,B. Bryopsis minor (ADU, A54041). A. Branching system. B. Chloroplasts with starch plates surrounding indistinct pyrenoids (upper from ramuli, lower from axes). C,D. Bryopsis macraildii. C. Branching (ADU, A50706). D. Upper branch (ADU, A5782). E. Bryopsis foliosa. Axes with laterals and ramuli (ADU, A50704).



Reproduction unknown.

Type from Western Australia (Preiss, probably near Fremantle); holotype in MEL, 26486.

Distribution: Apparently limited to the coast from Whitfords Beach to Hamelin Bay, and on Rottnest I., W. Aust., on rock platforms at low tide level and on *Posidonia, Amphibolis* and *Heterozostera* in shallow water.

Selected specimens: Point Peron, W. Aust., low eulittoral on platforms (*Womersley*, 29.ix.1979; ADU, A50704—"Marine Algae of southern Australia" No. 228). Point Peron, W. Aust., uppermost sublittoral on *Amphibolis (Womersley*, 29.ix.1979; ADU, A50703—"Marine Algae of southern Australia" No. 228a). Whitfords Beach, Perth, W. Aust., 5 m deep on *Heterozostera (Kirkman*, 16.viii.1979; ADU, A50570). Hamelin Bay, W. Aust., drift (*Womersley*, 1.ix.1979; ADU, A50602).

Bryopis gracilis Sonder (holotype in MEL, 26487) appears to be only a small, relatively slender, form of *B. foliosa* and shows similar branching and dimensions. Since Sonder (1846) gave the same number for both names, they were presumably from the same collection and habitat.

B. foliosa appears to be a distinctive species with dense, radial branching, especially of the upper parts. Branching of plants on rough-water rock platforms (the type form) is entirely radial, but some specimens on *Posidonia* in more sheltered habitats (e.g. at Point Peron) have the laterals on lower parts of the axes more or less on two sides but still irregularly arranged. These are provisionally placed under *B. foliosa*.

In having largely radial branching, *B. foliosa* shows relationship to *B. vestita*, but the former is more densely branched and often with numerous strongly developed laterals, whereas *B. vestita* has numerous long axes from a common base.

The occasional restriction of laterals to opposite sides of the axes (in the epiphytic form on seagrasses) shows relationship to *B. australis*, with which there may well be gene interchange, and also to *B. gemellipara* from eastern southern Australia (see under the latter species). *B. foliosa* and *B. australis* occur in similar habitats in Western Australia.

Although only known on the west coast of Western Australia, as far south as Hamelin Bay, *B. foliosa* is included here for comparison with other species both in Western Australia and on southern coasts. This and the other Western Australian species need detailed morphological, reproductive and life history studies to clarify their relationships.

4. Bryopsis vestita J. Agardh 1887: 30. Chapman 1956: 475. MacRaild 1974: 156.

FIGS 95C, 96A,B

Thallus (Fig. 95C) epilithic or epiphytic, 5-15(-25) cm high, becoming densely tufted with numerous prominent axes arising from an extensively branched rhizoidal system, epilithic. Axes bearing laterals irregularly radially (Fig. 96A,B) with similarly arranged ramuli clustered near ends of laterals which become denuded below (Fig. 96A); laterals are of limited growth, giving a branch outline 0.5-1(-1.5) cm broad, with axes usually denuded below; lower laterals often with descending rhizoidal outgrowths on parent axes. Axes 0.5-1 mm in diameter, laterals 0.5-1 cm long, and $120-170 \,\mu$ m in diameter; straight to curved, and ramuli 0.5-2(-3) mm long and $70-130(-180) \,\mu$ m in diameter; scars usually inconspicuous, sometimes prominent on laterals; chloroplasts discoid, $4-8 \,\mu$ m long.

Reproduction (MacRaild 1974): thalli dioecious, anisogamous; sporophyte protonemal and uninucleate, producing stephanokontic zoospores.

Lectotype from Warrington, Otago, New Zealand; in Herb. Agardh, LD, 15373.



Fig. 95. A. Bryopsis foliosa (ADU, A50704). B. Bryopsis foliosa (ADU, A50703). C. Bryopsis vestita (ADU, A37734).

Distribution: New Zealand, Chatham Is.

In southern Australia, from Cape Northumberland, S.Aust. to Wilsons Promontory, Vic. and around Tasmania. Epilithic under moderate to rough wave action.

Selected specimens: Cape Northumberland, S. Aust., low eulittoral (Womersley, 2.ix.1971; ADU, A39538). Warrnambool, Vic., edge of low pools (Pope & Bennett, 16.viii.1949; ADU, A12120). Point Lonsdale, Vic., low eulittoral (Ducker & MacRaild, 16.x.1960; ADU, A37738, MELU 20601). Maatsuyker I., Tas., lower eulittoral (Bennett, 26.vi.1954; ADU, A19799). Sandy Cape, Tas., lower eulittoral (Bennett 18, 15.i.1954; ADU, A19725).

B. vestita in New Zealand, and plants within the above range in southern Australia, are entirely radially branched (and in this way distinct from B. gemellipara). B. vestita is the common species of Brvopsis on open coasts of Tasmania. Plants from Western Australia included by MacRaild (1974) under B. vestita are bilaterally branched and better placed as a form of B. foliosa (see above).

Ducker (1979, p. 33; 1980, p. 144) has suggested that B. rosae C. Agardh (1823, p. 450) from the Falkland Islands, is an earlier name for B. vestita, but detailed comparisons of liquidpreserved material are needed to establish this.

5. Bryopsis plumosa (Hudson) C. Agardh. Harvey 1846: pl. 3. Kylin 1949: 66, fig. 64. MacRaild 1974: 158. Richardson 1982: 177. Rietema 1975: 8. Womersley 1956: 364. B. pennata Lamouroux, sensu Womersley 1956: 364.

FIGS 96C, 97A

Thallus (Fig. 97A) broadly spreading, 2-15(-25) cm high, with several to numerous axes arising from a branched, rhizoidal, basal system, usually epilithic. Axes essentially distichously branched (Fig. 96C), less so below, with lower laterals elongating progressively towards the base and often themselves becoming pinnate, usually naked below (scars inconspicuous or slight). Axes 300-1000 μ m in diameter below, laterals 200-400 μ m in diameter, and ramuli (1-)2-5 mm long and (70-)90-130 μ m in diameter, tapering only slightly.

Reproduction: Thalli dioecious, anisogamous; sporophytes only known in culture, protonemal and uninucleate, producing stephanokontic zoospores which produce the normal gametophyte plant.

Type from Exmouth, England; apparently lost.

Distribution: Widespread in temperate waters throughout the world.

Common in sheltered to moderate water movement localities all along southern Australia.

Selected specimens: Rottnest I., W. Aust. (Philson, Oct. 1934; ADU, A50051--- "South Pacific Plants" No. 35). Redbanks, Kangaroo I., S. Aust., eulittoral pool (Womersley, 28.xii.1949; ADU, A12871). 6 km N. of St Kilda, S. Aust., 1 m deep (Steffensen, 11.ix.1975; ADU, A46524). Nora Creina, S. Aust., uppermost sublittoral in bay (Womersley, 25.viii.1973; ADU, A43931). Kirk Point, Port Phillip, Vic., drift (Womersley, 11.viii.1970; ADU, A36029). Low Head, Tas. (Perrin, Aug. 1948; ADU, A47086).

The variation in southern Australian B. plumosa has been discussed by MacRaild (1974). Specimens vary considerably in robustness in different habitats and the branching is often variable; at least near the apices it is clearly distichous, and in most plants this is apparent, though less so, in the lower branching. Many collections agree well with European material.

Fig. 96. A.B. Bryopsis vestita (ADU, A39538). A. Axis with laterals and ramuli. B. Lateral with irregularly arranged ramuli. C. Bryopsis plumosa, part of axis with distichous ramuli (ADU, A43931). D.E. Bryopsis australis. D. Axis with bilateral ramuli in displaced rows (ADU, A34391). E. Axis with unilateral ramuli (ADU, A50705).



B. pennata Lamouroux was recorded from Coffin Bay, South Australia by Womersley (1956, p. 364). This collection is similar to plants of this species from the West Indies and slenderer than most *B. plumosa*, but for the present it is referred to the latter species. Several variable forms of *Bryopsis* occur in Coffin Bay.

6. Bryopsis australis Sonder 1846: 152. Kuetzing 1856: 28, pl. 81 fig. 1. Womersley 1956: 362.

B. indica Gepp & Gepp, sensu Womersley 1956: 363.

FIGS 96D,E, 97B

Thallus (Fig. 97B) 1-4(-5) cm high, often densely tufted, with few to numerous axes arising from a branched, rhizoidal system, epilithic. Axes simple or occasionally branched, lanceolate in outline, denuded below, bearing ramuli bilaterally (Fig. 96D), or unilaterally (Fig. 96E) when densely clumped, with the ramuli on each side arranged more or less in two rows but with occasional ramuli between the rows. Axes (250-)300-500(-600) μ m in diameter below, 150-250 μ m in diameter above, bearing ramuli 0.5-1.5 mm long and 50-120(-200) μ m in diameter with lower ramuli sometimes extending to several mm long; scars on axes conspicuous or not; chloroplasts round to lenticular, 2-6 μ m long.

Reproduction unknown.

Type from Western Australia, probably near Fremantle (Preiss); lectotype in MEL, 26484.

Distribution: Rottnest I. and adjacent mainland coasts (limits uncertain), W. Aust., and from Kingscote and Ballast Head on Kangaroo L, S. Aust.

Selected specimens: Radar Reef, Rottnest I., W. Aust., upper sublittoral (*Woelkerling*, 11.xi.1968; ADU, A34391). King Head, Rottnest I., W. Aust., lowest eulittoral with strong surge (*Womersley*, 6.ix.1979; ADU, A50705—"Marine Algae of southern Australia" No. 227). Kingscote, Kangaroo I., S. Aust., low eulittoral (*Womersley*, 2.i.1950; ADU, A12914). Ballast Head, Kangaroo I., S. Aust., upper sublittoral (*Womersley*, 3.ii.1956; ADU, A20302).

From the type material, *B. australis* is a small, slender species with relatively long, simple axes bearing ramuli only near their apices, denuded below. The ramuli, and scars on mid and sometimes lower axes, are usually bilaterally arranged with two alternating rows on each side of the axes, but in densely clumped plants only one unilateral but double series of ramuli is usually present. *B. australis* was discussed by Gepp & Gepp (1908, p. 170) in describing *B. indica,* which is scarcely different morphologically from the former species. Kangaroo Island specimens, previously placed in *B. indica,* are now referred to *B. australis. B. foliosa* Sonder is typically radially branched, but some plants have older axes with the ramuli on opposite sides but irregularly placed. The eastern *B. gemellipara* also has opposite ramuli in alternating rows on each side, but is a larger and more robust species.

As with other Australian species, life history and variation studies of *B. australis* are needed.

7. Bryopsis gemellipara J. Agardh 1887: 25. MacRaild 1974: 157. Womersley 1956: 363.

FIGS 97C, 98A,B

Thallus (Fig. 97C) robust, 5-15(-20) cm high, with one to a few prominent, simple or branched, axes arising from a rhizoidal system, usually epiphytic, occasionally on rock; older plants with 3-4 orders of branching. Axes and their branches, and sometimes the laterals, bilaterally branched (Fig. 98A) with two rows of laterals or ramuli on each side, laterals with radially (usually) arranged ramuli densely clustered near their apices (Fig. 98B) or in some plants ramuli bilaterally (rarely unilaterally) arranged; axes and laterals denuded below, with prominent scars (Fig. 98B) especially on laterals; lower laterals often with descending rhizoidal

outgrowths on parent axes. Axes (0.5-)1-1.5 mm in diameter, laterals 100-250(-300) μ m in diameter and ramuli 0.3-1.5(-2) mm long and 80-120 μ m in diameter, often slightly curved. Chloroplasts subspherical to discoid, sometimes lenticular, 8-9 μ m across, with a prominent pyrenoid.



Fig. 97. A. Bryopsis plumosa (ADU, A53203), same scale as C. B. Bryopsis australis (ADU, A50705). C. Bryopsis gemellipara (ADU, A53202).

DERBESIACEAE

Reproduction (MacRaild 1974): thalli dioecious, anisogamous; sporophytes only known in culture, protonemal and uninucleate, producing stephanokontic zoospores.

Type from Queenscliff, Vic.; lectotype in Herb. Agardh, LD, 15150. Isotype MEL, 26489.

Distribution: From Streaky Bay, S. Aust. to Wilsons Promontory, Vic. and around Tasmania. Usually epiphytic, occasionally on rock, on rough-water coasts from low-tide level to 2 m deep.

Selected specimens: Streaky Bay, S. Aust., reef pools on back beach (Parsons, 25.viii.1967; ADU, A31932). Waldegrave I., Eyre Peninsula, S. Aust., 8 m deep (Shepherd, 25.x.1973; ADU, A44257). Cape Lannes, S. Aust., low eulittoral (Womersley, 17.xi.1970; ADU, A37795— "Marine Algae of southern Australia" No. 142, previously as B. vestita). Nora Creina, S. Aust., upper sublittoral pools (Womersley, 6.vi.1982; ADU, A53202). Point Lonsdale, Vic., in rock pools (King, 1.viii.1969; ADU, A37739; MELU 4582).

B. gemellipara is usually a distinctive species. Typical epiphytic plants (as in the type) are bilateral in their main branching and have the ramuli radially arranged on the laterals, but some epilithic plants (e.g. from Cape Lannes, S. Aust.) have the ramuli mostly bilaterally arranged but are otherwise very similar to the epiphytic plants. However, such "epilithic" plants may at least commence their development on small algae on the rock.

B. gemellipara is closely related to the partly bilateral form of *B. foliosa* Sonder from the southern west coast of Western Australia, and studies are needed to establish their distinctness. *B. foliosa* occurs on rock platforms and larger plants epiphytic on sea-grasses are morphologically very similar. The branching is largely bilateral on the axes and larger laterals, and often radial on the smaller laterals, but less distinctly so than in *B. gemellipara;* the dimensions in both species are similar, but *B. foliosa* is generally a more densely branched species. For the present, *B. foliosa* is considered restricted to the west coast of Western Australia, while *B. gemellipara* is confined to south-eastern Australia.

B. gemellipara and *B. vestita* are plants of similar robustness and dimensions, and are best differentiated on their branching patterns. New Zealand *B. vestita* and Australian specimens placed in this species are entirely radially branched, whereas the axes and often the laterals of *B. gemellipara* are not.

FAMILY DERBESIACEAE Hauck

Thallus diplohaplontic, heteromorphic, with filamentous sporophyte and ovoid, vesiculate gametophyte, or diplontic with a filamentous sporophyte only. Sporophyte of coenocytic, branched filaments, usually with a double septum at the base of occasional branches; gametophyte ("Halicystis" stage) coenocytic, ovoid, usually 5-10 mm high, attached within the surface of crustose coralline algae by basal rhizoids; chloroplasts lenticular, with or without a pyrenoid.

Reproduction of the sporophyte by ovoid to globular sporangia cut off by a wall plug and borne laterally on the filaments, producing multi-flagellate (stephanokontic) zoospores; the gametophyte by biflagellate anisogametes formed in areas of protoplasm separated by a membrane.

KEY TO GENERA OF DERBESIACEAE

- Thallus sporophytic only, with erect, unbranched, clavate filaments (1-3 mm in diameter) arising from finer filaments and a prostrate base with calcified cell walls PEDOBESIA

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Fig. 98. A,B. Bryopsis gemellipara (ADU, A53202). A. Apex of a young axis with bilateral, slightly displaced ramuli. B. Part of an older axis with bilateral, displaced, laterals and radially arranged ramuli. C-G. Derbesia marina (C-E, ADU, A54010; F,G. ADU, A9477). C. Habit. D. Branch with basal double septum. E. Branch with chloroplasts. F,G. Sporangia.

DERBESIACEAE

Genus DERBESIA Solier 1846: 452

Heteromorphic. Sporophytic thallus tufted, filamentous, subdichotomous to irregularly laterally branched, coenocytic apart from double septa at the base of some older laterals; chloroplasts numerous, usually crowded, lenticular, with or without a pyrenoid. Sporangia lateral, ovoid to pyriform, cut off by a basal wall plug, containing 20–30 stephanokontic zoospores (normally meiospores, occasionally mitospores). Gametophytic thallus ("Halicystis") globular to ovoid, coenocytic, with peripheral cytoplasm containing numerous lenticular chloroplasts with or without pyrenoids, producing biflagellate anisogametes from peripheral areas of cytoplasm.

Type species: D. marina (Lyngbye) Solier.

A genus of several species showing marked heteromorphy between the filamentous, branched sporophyte and the ovoid gametophyte, which was earlier placed in a separate genus *Halicystis* Areschoug. Detailed morphological and life history studies are needed of the two taxa recognized for southern Australia, especially as to the size of chloroplasts and presence or absence of pyrenoids. Dried or liquid preserved material is of limited value for observations of the chloroplasts.

KEY TO SPECIES OF DERBESIA

- Filaments 30-40 μm in diameter, with double septa at bases of some older branches; chloroplasts 4-6 μm long, without a pyrenoid; sporangia 80-105(-135) μm long, usually ovoid
 D. marina
- Derbesia marina (Lyngbye) Solier. Kjellman 1897: 1, figs 1-15. Kobara & Chihara 1980: 214, figs 1-13. Kornmann & Sahling 1977: 53, fig. 21. MacRaild 1974: 99, figs V.1-6. Scagel 1966: 113, pl. 1. Sears & Wilce 1970: 381, figs 1-15, 17-28. Womersley 1956: 371.

FIGS 98C-G, 99A

Sporophytic thallus (Fig. 99A) epiphytic or epilithic, 1-3(-4) cm high, arising from irregularly branched, colourless, rhizoidal attachment filaments, with a fairly densely, but not closely, irregularly branched erect tuft of filaments (Fig. 98C). *Filaments* (25-)30-40 μ m in diameter, cylindrical and fairly straight, slightly contracted at the base of laterals, with a double septum at the base of occasional laterals (Fig. 98D); wall 1-2 μ m thick; chloroplasts (Fig. 98E) numerous, usually densely aggregated, lenticular but usually rounded when preserved or stained, 4-6 μ m long, without pyrenoids but often with 2-5 small starch plates within the chloroplast.

Reproduction. Sporangia (Fig. 98F,G) ovoid, $80-110(-140) \mu m$ long and $50-65 \mu m$ broad, occasionally tapering to their base, cut off by a wall plug soon after initiation.

Gametophytic thallus (Halicystis ovalis) dioecious, ovoid, (3-)5-10 mm long, occurring on crustose coralline algae in low-light habitats; chloroplasts round to lenticular, without a pyrenoid.

Reproduction (Kobara & Chihara 1980) by biflagellate anisogametes.

Type from Quivig, Faroe Is; in C.

Distribution: Widely distributed in cold temperate waters, though not frequently collected.

In southern Australia, from Scott Bay, S. Aust. to Sorrento, Vic. and Bruny L. Tas., usually in shaded pools with moderate water movement. The occurrence of the gametophyte (*Halicystis*) stage in southern Australia still has to be established, since most collections



Fig. 99. A. Derbesia marina (ADU, A53085). B. Derbesia tenuissima (ADU, A20276). C-E. Pedobesia characformis, C. Living thallus with sporangia (ADU, A37816 collection). D,E. Prostrate disc, showing concentric growth sectors, and meristematic periphery. E. Surface detail of prostrate disc (culture material, from MacRaild & Womersley 1954, Figs 7.9).

available have pyrenoids and are therefore referable to H. parvula (= D. tenuissima). Collections which have been referred to H. ovalis are listed below.

Selected specimens: Scott Bay (6 km W. of Fowler Bay), S. Aust., reef pools (Womersley, 27.i.1951; ADU, A14987). Vivonne Bay, Kangaroo I., S. Aust., in shaded pool, S. side of Ellen Point (Womersley, 14.i.1948, 21.viii.1963, 18.xi.1967; ADU, A9477, A27020, A32094 resp.). Nora Creina, S. Aust., in heavily shaded pool (Womersley, 16.v.1982; ADU, A53085 and 28.ii,1983; ADU, A54010). Quiet Corner, Adventure Bay, Bruny I., Tas., 10 m deep (Shepherd, 16.ii.1972; ADU, A41587).

Halicystis stage (all subject to checking of living material from these localities). Nora Creina, S. Aust., on crustose coralline in heavily shaded pool (MacRaild & Womersley, 17.i.1971; ADU, A37810). Point Lonsdale, Vic., low eulittoral pool (Ducker, 21.ii.1975; MELU, 21916). Sorrento, Vic. (Ducker, 17.iv.1975; MELU, 22069).

The southern Australian specimens agree well with descriptions of *D. marina* from the Northern Hemisphere, though the life history of Australian plants has not been reported. Plants of *D. marina* and of *D. tenuissima* can occur in the same rock pool, as at Scott Bay, Vivonne Bay and Nora Creina, and can be separated on dimensions, the chloroplast size and whether a pyrenoid is present or not.

 Derbesia tenuissima (de Notaris) Crouan & Crouan. Boergesen 1925: 107, fig. 45. Feldmann 1937: 235, fig. 32A. Hamel 1930: 73, fig. 23, II, III. Kobara & Chihara 1980: 216, figs 14-23. MacRaild 1974: 99. Newton 1931: 100, fig. 66. Rietema 1975: 70, pls 17, 18. Sears & Wilce 1970: 383, figs 29, 30. Ziegler & Kingsbury 1964: 105, figs 1, 2.

FIGS 99B, 100A-F

Sporophytic thallus (Fig. 99B) epiphytic or epilithic, 1-4(-6) cm high, arising from a branched rhizoidal base, with a tuft of erect, often distantly branched, filaments (Fig. 100A). Filaments (45-)50-80(-90) μ m in diameter, cylindrical and fairly straight, slightly contracted at the base of laterals but usually without a cross septum (Fig. 100B); wall 2-4 μ m thick: chloroplasts numerous and usually densely aggregated, lenticular, mostly 6-10 μ m long and each with a pyrenoid (Fig. 100B).

Reproduction. Sporangia (Fig. 100B,C) usually pyriform, tapering to their base, (160-) 200-300(-400) μ m long and (100-)140-200 (-220) μ m broad, cut off by a double septum at maturity.

Gametophytic thallus (Halicystis parvula) dioecious, ovoid, 3-10 mm long (Fig. 100D), occurring on crustose coralline algae; chloroplasts ovate to lenticular, each with a pyrenoid (Fig. 100E,F).

Reproduction by biflagellate anisogametes (Kobara & Chihara 1980).

Type from Caprara, Italy, in RO(?)

Distribution: Mediterranean and temperate eastern Atlantic.

In southern Australia, known from Scott Bay (6 km W. of Fowler Bay), S. Aust., in reef pools (*Womersley*, 27.i.1951; ADU, A14988) and Vivonne bay, Kangaroo I., S. Aust., in heavily shaded pool, S. side of Ellen Point (*Womersley*, 30.i.1956 and 29.i.1957; A20276 and A20787 resp.). Probably also from Port Adelaide, S. Aust., 10-20 cm deep on Commercial Fishing Marina (*Womersley*, 10.iii.1982; ADU, A52985, sterile).

Halicystis stage. Nora Creina, S. Aust., on crustose coralline in heavily shaded pool (*Womersley*, 28.ii.1983; ADU, A54009). Ninepin Point, Tas., 5 m deep on crustose coralline (A. Brown, 1.xi.1982; ADU, A53825).

The above sporophytic specimens of *D. tenuissima* are often more robust in diameter than the Northern Hemisphere plant. However, the lack of vegetative cross septa, the size of

the pyrenoid-bearing chloroplasts, and the size and form of the sporangia are features of *D. tenuissima*. The Vivonne Bay specimens, in particular, agree well with this species.

Genus PEDOBESIA MacRaild & Womersley 1974: 91

Adult thallus coenocytic, of numerous elongate-clavate branches arising from a branched, filamentous system, derived in turn from a prostrate attachment pad with calcified cell walls; chloroplasts lenticular, without a pyrenoid.



Fig. 100. A-C. Derbesia tenuissima (ADU, A20276). A. Habit, with sporangia. B. Filament (with chloroplasts) with young lateral sporangium. C. Mature sporangium. D-F. Halicystis parvula stage. D. Two thalli on crustose coralline algae (ADU, A53825). E. Chloroplasts (ADU, A54009).

Reproduction. Sporangia subterminal, lateral, cut off by a single wall, producing numerous stephanokontic zoospores. Life history direct, sporophytic.

Type species: P. clavaeformis (J. Agardh) MacRaild & Womersley.

A genus of three species, the type and *P. lamourouxii* (J. Agardh) Rietema (1975, p. 108) from the Mediterranean and Japan, and *P. feldmannii* Abelard (1982, p. 187) from the Galapagos 1s.

Pedobesia differs from *Derbesia* in its direct, diplontic life history and the presence of the calcified, prostrate stage following germination of the zoospore.

Pedobesia clavaeformis (J. Agardh) MacRaild & Womersley 1974; 92. figs 1-15.

Bryopsis clavaeformis J. Agardh 1887: 20.

Derbesia clavaeformis (J. Agardh) De Toní 1889: 425. Womersley 1956: 371.

FIGS 99C-E

Thallus (Fig. 99C) dark green, epilithic, 3-5(-6) cm high, of numerous simple, erect, clavate branches (1-)2-3 mm in diameter, arising from slender, much-branched and lobed filaments; chloroplasts numerous, lenticular, $2-5 \ \mu m$ long, without a pyrenoid but with 1-2 (-3) starch plates within the chloroplast. *Prostrate discs* (winter state) 2-6 mm in diameter (Fig. 99D), often overgrown by secondary discs, with marginal growth and concentric rings of growth or calcification (Fig. 99D,E) divided into radial sectors (Fig. 99E); discs coenocytic but with internal calcified pillars and calcification (aragonite) within the walls which have numerous pores.

Reproduction by sporangia $350-450(-1000) \mu m$ in diameter, borne subapically on the clavate branches, producing stephanokontic zoospores $30-40 \mu m$ in diameter, which produce the disc stage.

Type from Western Port, Vic.; holotype in Herb, Agardh, LD, 14897.

Distribution: From Point Clune, Rottnest L, W. Aust., and from West Bay, Kangaroo L, S. Aust. to Cape Patterson, Vic. and Hogan L, Bass Strait, and Gordon, Tasmania. Northern New Zealand.

Selected specimens: Point Clune, Rottnest L. W. Aust., 11-13 m deep (*Gabrielson*, 2.xii.1980; ADU, A51956). On Clan Ranald Wreck, off Troubridge Hill, S. Aust., 20 m deep (*Shepherd*, 27.xii.1963; ADU, A27315). West Bay, Kangaroo L. S. Aust., drift (*Womersley*, 6.i.1946; ADU, A3200). Nora Creina, S. Aust., in shaded pool (*MacRaild & Womersley*, 17.i.1971; ADU, A37816—"Marine Algae of southern Australia" No. 14). Point Lonsdale, Vic., low eulittoral (*Ducker*, 21.ii.1975; MELU, 21915). Gordon, Tas. (*Harada*, March 1980; HO, 43040).

This distinctive and unusual species has been described in detail by MacRaild & Womersley (1974). It occurs in shaded pools and to 20 m deep, and is probably generally distributed along southern Australia.

ORDER DASYCLADALES Pascher

Thallus diplontic, coenocytic (often with constricted segments but end walls always perforate apart from plug formation), radially symmetrical with an erect axis bearing whorls of lateral branches which are simple or (usually) di- to polychotomously branched, free or with the ultimate segments united laterally to form an outer cortex; vegetative thallus usually at first with a single, giant nucleus in the rhizoidal base, becoming multinucleate later before cyst formation; cell wall of mannar; chloroplasts usually small, without a pyrenoid.

Reproduction by iso- or anisogmates formed in cysts (with a cellulose wall) or freely in gametangia borne on the lateral branches or as gametangial rays, becoming separated by a plug (Menzel 1980); position of meiosis not fully established, probably before or during fragmentation of the giant primary nucleus.

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DASYCLADACEAE

This is a distinctive order with its radial symmetry, coenocytic structure, and presence in most genera of a single giant nucleus before reproductive cysts are formed. The best known genus, *Acetabularia*, has been used extensively in developmental biology (e.g. Woodcock 1977; Bonotto, Kefeli and Puiseux-Dao 1979). Some 9 living genera and over 50 fossil genera are recognised, the latter largely due to their superficial deposition of calcium carbonate on the distinctive whorled thallus.

Most authors have recognised a single family for the living genera, but Valet (1969, p. 577) recognises two families.

KEY TO FAMILIES OF DASYCLADALES

FAMILY DASYCLADACEAE Kuetzing

Thallus consisting of an axis bearing numerous whorls of laterals of one type, each branched to 2 or 3 (or more) orders, either free or in some genera with the terminal cells united laterally to form a cortex.

Reproduction by iso- or anisogametes formed in cysts or freely in gametangia borne terminally or laterally on the inner segments of the laterals.

A family of six living genera, largely tropical-subtropical in distribution, with one genus on southern Australian coasts.

Genus DASYCLADUS C. Agardh 1828: 15

Thallus of an axis bearing numerous, closely arranged but free whorls of laterals each with segments of 3(-4) orders, not terminating in hairs.

Reproduction by gametes formed freely in the gametangia borne on the ends of the primary segments of the whorls.

Type species: D. vermicularis (Scopoli) Krasser.

A genus of three species (Valet 1969, p. 579), with one in southern Australia. Reproduction is only known in the type species.

Dasycladus densus Womersley 1955: 392, figs 10, 11; 1956: 378. Gilbert 1978: 310, fig. 16. Valet 1969: 581, pl. 150 fig. 2.

FIGS 101A, 102A

Thallus (Fig. 101A) medium to dark green, with 1–16 axes arising from a rhizoidal holdfast. Axes 2–6 cm high, 2–4 mm thick, with a central siphon 0.5–1 mm broad with a thick lamellate wall, bearing close whorls of 10–12 branched laterals. Laterals (Fig. 102A) with segments of 3 orders, di- to penta-chotomous, cross walls with open septa; primary segments clavate to pyriform, 400–700 μ m long and 200–400 μ m in diameter; secondary segments terete to slightly swollen, 450–700 μ m long and 120–200 μ m in diameter; tertiary segments clavate, 130–400 μ m long and 100–130 μ m in diameter; secondary and tertiary segments often lost; chloroplasts small, round.

Reproduction unknown.

Type from Point Fowler, Great Australian Bight, S. Aust., uppermost sublittoral in sandy



Fig. 101. A. Dasycladus densus (ADU, A19437 type). B. Acetabularia calyculus, living (ADU, A33400 collection). C-E. Polyphysa peniculus. C. Habit (ADU, A46701). D. Cap of young gametangial rays. E. Mature gametangial rays with cysts (D,E from culture).

hollow (*Womersley*, 6.ii.1954; ADU, A19437, holotype and isotypes---"Marine Algae of southern Australia" No. 26).

Distribution: Only known from the type and from Hopetoun, W. Aust., 3-4 m deep on sand-covered rock near jetty (Kraft (6981) & Ricker, 16.viii.1979; ADU, A50718).

This is a distinctive species for southern Australia, rare (but occurring in patches of many plants) and possibly dependent on slightly warmer temperatures of the Great Australian Bight region. Gilbert (1978) has discussed the differences between *Dasycladus* and the related genus *Chlorocladus* Sonder.

FAMILY POLYPHYSACEAE Kuetzing

Thallus with whorls of laterals of two types, with either numerous whorls of colourless branched hairs and a terminal cupulate or clustered whorl of green, clavate, gametangial rays which may be lost after reproductive maturity and later replaced, or alternating whorls of colourless hairs and green gametangial rays. Superior corona present on the upper, basal side of the gametangial rays, bearing hairs or their scars; inferior corona present or absent, not forming hairs.

Reproduction by gametes formed in cysts produced in the gametangial rays.

A family of three living genera, largely tropical but with one species in each of two genera on southern Australian coasts.

The family Polyphysaceae was established by Kuetzing (1843, pp. 302, 311) to include *Polyphysa* and *Acetabularia*, and predates the family name Acetabulariaceae Naegeli (1847, pp. 158, 252).

KEY TO GENERA OF POLYPHYSACEAE

- 1. Gametangial rays united laterally to form a disc or cup; inferior corona
- present ACETABULARIA 1. Gametangial rays free or at most loosely united; inferior corona absent POLYPHYSA
 - anciangiar rays nee of at most loosery united, methor corona absent ... i of i i i i i

Genus ACETABULARIA Lamouroux 1812: 185, nom. cons.

Thallus single or clumped, stalk often calcified, bearing whorls of colourless hairs and a summit whorl of gametangial rays which are laterally and firmly united to form a shallow disc or cup. Superior and inferior coronas both present, the superior corona producing hairs. Reproduction by cysts formed in the gametangial rays, liberating iso- or anisogametes.

Type species: A. acetabulum (Linnaeus) Silva.

A genus of some 9 species (Valet 1969, p. 605), distributed almost entirely in tropicalsubtropical seas. One species only occurs in restricted habitats on southern Australian coasts.

Acetabularia calyculus Quoy & Gaimard. Valet 1969: 617, pl. 44 figs 7-9. Womersley 1971a: 119, fig. 15.

FIGS 101B, 102B-D

Thallus (Fig.101B) single or in small clusters, 3-5(-7) cm high, axes whitish from calcification, bearing several whorls of branched, colourless hairs (pale green when young) on their upper half, di- to penta-chotomous with 5-7 orders of branching, and one (rarely two) summit whorls of 22-34 gametangial rays united laterally to form a concave disc or cup (Fig. 101B). *Disc* 3-6(-7) mm across, rays 1.5-2.5 mm long and (400-)450-600 μ m broad at their outer end, terminally truncate to slightly bilobed (Fig. 101B); chloroplasts rounded, 2-3 μ m in diameter. *Superior corona* (Fig. 102B,C) lobed and bearing 2-3 branched hairs or scars; *inferior corona* with a single lobe (Fig. 102B,D). Reproduction. Cysts numerous, subspherical, $80-120 \mu m$ in diameter, liberating gametes.

Type from Shark Bay, W. Aust. (Quoy & Gaimard); not located in PC.

Distribution: Widely distributed in tropical and subtropical seas and extending into warm temperate regions. Tropical Australia, extending south to Fremantle, W. Aust., and to Newcastle, N.S.W.

In southern Australia, known from Kellidie Bay, Coffin Bay, S. Aust., 3–4 m deep (*Taylor*, 5.xii.1975; ADU, A46702). Tapley Shoal, off Edithburgh, S. Aust., 13–15 m deep (*Shepherd*, 5.ii.1969; ADU, A33400—"Marine Algae of southern Australia" No. 27). Glenelg, S. Aust., 20m deep, 5 km offshore (*Shepherd*, 15.ii.1969; ADU, A33450). West Beach, S. Aust., 10 m deep (*Shepherd*, 30.xii.1980; ADU, A52040).

This species appears to occur mostly in deep water, on dead cockle shells in sand areas, in isolated localities of the Gulf region of South Australia.

Genus POLYPHYSA Lamarck 1816: 151

Thallus single or usually clumped, stalk usually calcified, bearing successive whorls of colourless hairs and a summit whorl of gametangial rays, free or loosely and partially adherent into a disc or cup. Superior corona present, inferior corona absent.

Reproduction by gametes from cysts formed in the gametangial rays.

Type species: P. australis Lamarck [= *P. peniculus* (Brown ex Turner) C. Agardh].

A genus of some 8 species (Valet 1969, p. 606), with the type species on southern Australian coasts.

Polyphysa has usually been regarded as a subgenus of *Acetabularia* but is considered by Bailey. Rezak & Cox (1976) to be worthy of generic recognition due to the absence of an inferior corona. The latter, however, is represented by a slight bulge in *P. peniculus* and it may be debated whether this distinction is satisfactory at a generic level. Some species of *Polyphysa* also show partial to moderate lateral adherence of the gametangial rays to form a cup. However, *P. peniculus* is superficially the most distinct species of *Polyphysa*, as well as being the type species, and is here kept generically distinct.

Polyphysa peniculus (R. Brown ex Turner) C. Agardh 1823: 473. Bailey, Rezak & Cox 1976: 17, figs 18-21. Harvey 1858: pl. 11.

Fucus peniculus R. Brown ex Turner 1819: 78, pl. 228 (probably published before 1816, see below).

Polyphysa australis Lamarck 1816: 152.

Polyphysa aspergillosa Lamouroux 1816: 252, pl. 8 fig. 2.

Polyphysa cliftonii Harvey 1858: pl. 11; 1863: pl. 255.

Acetabularia peniculus (R. Brown ex Turner) Solms-Laubach 1895: 27, pl. 2 figs 2, 6, 7. Valet 1968b: 56, pl. 24 figs 1, 3-5; 1969: 619, pl. 142 figs 1-3. Womersley 1956: 378.

FIGS 101C-E, 102E-G

Thallus (Fig. 101C,D) of numerous clumped axes attached by rhizoids, pale green or whitish from calcification, 2-6(-10) cm high, with few to numerous whorls of colourless (pale green when young) di- to quadri-chotomous hairs with 5-7 orders of branching, with perforations in the end walls, and a summit whorl of 11-18 green gametangial rays, free from each other and appearing clustered due to crowding. *Gametangial rays* (Fig. 101C-E) clavate, 2-5 mm long and 0.5-1.0(-1.3) mm broad; *superior corona* (Fig. 102E,F) of a single lobe bearing 1-3 hairs or scars (usually only one mature hair), *inferior corona* only a slight bulge (Fig. 102E,G); chloroplasts rounded, ovoid or lenticular, variable in size, 2-6 μ m long, without pyrenoids.

Reproduction with spherical cysts, (150-)200-350 μ m in diameter (Fig. 101E), producing gametes. Cyst-like structures occasionally present within the stalk.

Type from "Nouvelle-Hollande, sur une vénus" (Peron & Lesueur); in PC (?).

Distribution: From Shark Bay, W. Aust. around southern Australia (and Blackmans Bay, Tasmania) to Newcastle, N.S.W., in sheltered bays and inlets, uppermost sublittoral, on dead shells or limestone.

New Caledonia (Valet 1968a, p. 54); Lord Howe I. (Kraft & Allender).

Selected specimens: Princess Royal Harbour, King Georges Sound, W. Aust., lower eulittoral (*Womersley*, 21.viii.1979; ADU, A51384). Venus Bay, S. Aust., low eulittoral (*Womersley*, 17.i.1951; ADU, A13656). Kellidie Bay, Coffin Bay, S. Aust., 3–4 m deep (*Taylor*, 5.xii.1975; ADU, A46701). Salt Creek inlet, Coobowie, S. Aust., 0.5 m deep (*Womersley*, 9.ii.1969; ADU, A33399—"Marine Algae of southern Australia" No. 28). Head of American R. inlet, Kangaroo I., S. Aust., lower eulittoral (*Womersley*, 24.i.1948; ADU, A6767). Coorong, S. Aust. about low water level (*Womersley*, 15.ix.1970, then maintained in culture, ADU, A54173). Swan Bay, Port Phillip, Vic. (*Macpherson*, 5.iv.1963; ADU, A28197). Boomer, Blackmans Bay, Tas. (*Curtis*, 30.xi.1965; HO, 58154).

P. peniculus has been studied extensively in developmental biology (e.g. see Woodcock 1977), usually under its synonym *P. cliftonii*. The latter is only an ecological form with more elongate, clavate gametangial rays; this form usually develops in still-water culture.

Uncertainty surrounds the correct name of this alga. Lamarck described it as *Polyphysa* australis in March 1816, and Lamouroux as *Polyphysa aspergillosa* in October 1816. Fucus peniculus R. Brown ex Turner was described in Volume 4 of Turner's "Fuci", which is dated 1819 but is known to have been issued in fascicles, following Vol. 3 in 1811. Significantly, Lamouroux (Oct. 1816) quotes the page and figure reference of *F. peniculus* in Turner, so the latter must have been issued distinctly earlier than October 1816. Also, Turner in his "Advertisement" prefacing Vol. 4 apologises for the "frequent irregularities in the appearance of later numbers", and *F. peniculus* comes almost exactly half way through Vol. 4, the fascicles of which presumably commenced soon after Vol. 3 was completed in 1811. It therefore seems likely that the fascicle containing *F. peniculus* was issued before 1816, and that this is an earlier name than *P. australis* of Lamarck (March 1816).

8. CHAROPHYTA

Phylum CHAROPHYTA Migula

Thallus macroscopic, from a few centimetres to a metre high, light to dark green with similar photosynthetic pigments to the Chlorophyta and starch as the storage product. Habit characteristically of axes, each developed from an apical cell, anchored by rhizoids in muddy substrate, and bearing whorls of laterals of limited growth at nodes separated by comparatively long internodal cells. Nodes of relatively small uninucleate cells with two central cells and a ring of peripheral cells from which the whorled laterals and appendages develop. Internodes of a single, large, multinucleate cell, corticated or not by filaments originating from nodal cells. Stipulodes (one celled processes) commonly produced from the peripheral nodal cells, and similar bract-cells arise from branchlet nodes. Nuclear division phragmoplastic, cell wall of cellulose microfibrils.

Life history haplontic with zygotic meiosis.

Reproduction oogamous with complex antheridia and oogonia borne laterally on the branchlets and usually subtended by bracts. Antheridia globular, becoming orange-red, consisting of a central stalk cell which bears 8 primary capitula cells with elongate manubrium cells connected to 8 (rarely 4) outer shield cells which are united to form a sphere. The primary capitula cut off near their bases small secondary capitula cells, each of which produces several long, many-celled antheridial filaments with each cell producing a single biflagellate sperm. Oogonia at first naked but becoming surrounded by 5 spiral corticating filaments, closely adjacent soon after fertilisation, and which form 5 (or subdivided to give 10) coronal cells at the apex of the oogonium. Zygote usually becoming black with a thickened, resistant wall, especially between the spiral corticating cells.

The Charophyta are sometimes regarded as a class of the Chlorophyta, but are highly distinctive in thallus construction and in their reproductive organs.

It is generally accepted that the Charophyta contain only a single class, order and family.

Members of the Charophyta are common in freshwater to brackish ponds and lakes with a muddy or silty bottom, and frequently appear in winter pools which dry in summer when the resistant zygotes perpetuate the species. Charophyta in general do not occur in marine situations, but in several parts of southern Australia *Lamprothamnium papulosum* is found in brackish to saline, largely to partly enclosed lakes adjacent to the sea; in some of these areas the salinity at times may be above that of normal sea water, though the *Lamprothamnium* may grow best under slightly lower salinities.

Genus LAMPROTHAMNIUM J. Groves 1916: 336

Thallus ecorticate, with whorled lateral branches; stipulodes in a single tier, each directly below ("opposite") a branch of a whorl; bract-cells 3-5, verticillate on lateral branches. Reproductive organs commonly borne in condensed branch systems forming a spike, with the oogonium usually below the antheridium.

Fig. 102. A. Dasycladus densus (ADU, A19437), cross section of thallus; all walls between segments are perforate. B-D. Acetabularia calyculus (ADU, A33400). B. Sectional view of gametangial ray with superior corona (bearing 2 hairs) and inferior corona. (After Womersley 1971, Fig. 15.) C. Superior corona with hairs. from above. D. Inferior corona, from below. E-G. Polyphysa peniculus (ADU, A54173). E. Sectional view of base of gametangial ray with superior corona (bearing 2 hairs) and slight bulge of inferior corona. F. Superior corona with two hairs, from above. G. Base of gametangial ray, from below. H-K. Lamprothannium papulosum (ADU, A54177, from culture). H. Habit of thallus. I. Nodal branching with opposite stipulodes and bracts on two lateral branches. J. Starch bulbils on rhizoids, from muddy substrate. K. Part of fertile spike with antheridia on first node of branchlets and oogonia (two only shown) at base of whorl.



Type species: L. papulosum (Wallroth) J. Groves 1916: 337.

A genus of 3 or 4 species, characterised (Wood 1965, p. 327) by the "opposite" stipulodes, by features of the coronal cells and oogonia (Daily 1967, p. 204) and by subdivision of the two central nodal cells (Frame & Sawa 1975, p. 202).

Lamprothamnium papulosum (Wallroth) J. Groves. Wood 1965: 330; 1972: 37. Wood & Imahori 1964: figs 162, 165. Delroy 1974: 157. Ducker, Brown & Calder 1977: 59.

FIG. 102H-K

Thallus (Fig. 102H) monoecious, usually 5–30 cm high, not or slightly encrusted, ecorticate. Axes 200–800 μ m in diameter, internodes usually 1-4 cm long. *Branchlets* 6–8 in a whorl, 0.5–2 cm long, of 3–5 segments. *Stipulodes* (Fig. 102 I) in one tier, opposite, decumbent, 1–3 mm long. *Bract-cells* (Fig. 102 I) 3–5, few at distal nodes, verticillate, 500–1000 (-2000) μ m long. *Gametangia* (Fig. 102K) adjacent at 1(-2) lowest branchlet nodes; oogonia 600–1500 μ m long, with 10–15 convolutions, coronal cells 90–135 μ m high; antheridia 300–500 μ m in diameter. *Bulbils* (Fig. 102 J) occasional on lowest axial nodes or rhizoids, 500–1500 μ m in diameter.

Type from Germany (see Wood 1965, p. 336).

Distribution: Widespread, especially in coastal regions, of Europe, Africa, China, Australasia.

In southern Australia, known from "marine" habitats in West Lakes and the Coorong, S. Aust., and the Gippsland Lakes, Vic.

Selected specimens:

West Lakes, S. Aust., on W. side, 2–2.5 m deep (*Thomas*, 22.xii.1975; ADU, A46755). Coorong, S. Aust., in shallow water about 40 km S. of Meningie (*Womerslev*. 15.ix.1970; maintained in culture, ADU, A54177). Coorong, S. Aust., about 25 cm deep, 13 miles (about 21 km) S.E. of Salt Creek (*Wood* 60-9-22-1 & von der Borch, 22.ix.1960; ADU, A38939).

Lamprothamnium papulosum is reported by Delroy (1974) to be a food of waterfowl in the Coorong, where in hypersaline conditions it produces starch bulbils (on which the birds feed). It was found to be widespread in the summers of 1956-66 and 1971-72 in the southern Coorong, but poorly developed in 1970-71 when salinity was high. It does not grow satisfactorily at salinity of over $60^{0}/_{00}$.

Ducker, Brown & Calder (1977, pp. 36, 60) report *L. papulosum* from Lake Reeve, Victoria, where salinity ranges between 10 and $104^{0}/_{00}$ are reported, and from Bunga Arm of Lake King and Lake Tyers with salinities between 6 and $16^{0}/_{00}$. It seems clear that in such areas as the Coorong and the above Gippsland Lakes in southern Australia that *L. papulosum* can exist and grow reasonably well in the salinities of sea water and possibly above. Cultures have been maintained for several years in the Department of Botany, University of Adelaide in salinity of about $28^{0}/_{00}$, with *Polyphysa peniculus* growing well in the same cultures.

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abaxial: on the side of a branch or leaf facing away from the axis.

abscission: the normal shedding from a plant of an aged organ.

achene: a dry indehiscent one-seeded fruit.

acicular: needle shaped and stiff.

acropetal: growth originating at or near the apex of a branch, with lateral branches becoming progressively older away from the apex.

actinomorphic: symmetrical about more than one vertical plane.

acuminate: tapering gradually to a sharp point.

adaxial: on the side of a branch or leaf facing the axis.

adventitious: an organ arising in an abnormal position.

aegagropila: a ball-like mass of filaments.

air canal: an elongate intercellular space.

akinete: a single-celled, thick walled, non-motile spore derived from a vegetative cell. **albumen:** nutritive material stored in the seed.

algae: a general term applied to any group of pigmented (photosynthetic), usually aquatic, non-vascular plants reproducing without cellular-jacketed antheridia and archegonia.

algology: an older term for the study of algae, now usually replaced by "phycology". alternation of generations: the sequence in a life history or life cycle in which a haploid gamete-producing phase alternates with a diploid meiospore-producing phase.

amplexicaul: stem-clasping.

amoeboid: applied to certain gametes of algae which lack a rigid wall and can change in shape as does an amoeba.

amyloplast: a colourless starch-forming or storing plastid.

anastomosis: joining of branches to form a meshwork.

anatropous: an inverted ovule with the micropyle facing the placenta.

anemophilous: pollinated through the agency of wind.

anisogametes: motile gametes which are morphologically dissimilar and referred to as male (the smaller) and female (the larger).

annual: a plant completing its life cycle in one year.

annular: ring like (e.g. ridges, constrictions or scars).

anther: the pollen bearing part of the stamen.

antheridia: a male reproductive organ containing sperms.

anthesis: the time of opening of a flower or release of pollen.

apical growth: growth occurring at the summit of an axis or branch.

aplanospore: a non-motile spore, otherwise comparable to a zoospore.

apocarpous: a gynoecium consisting of one carpel, or several carpels all free and distinct.

apogamy: development of an organism without the normal fusion of gametes.

applanate: flattened and closely appressed to the substratum, and often lobed.

appressed: lying closely on the sustratum for the whole of its length or surface.

aragonite: the orthorhombic crystalline form of calcium carbonate.

articulate: a branch or axis separated into joints or segments by nodes and internodes (as in *Halimeda* and the articulate coralline algae).

asexual: reproduction without the fusion of gametes or the occurrence of meiosis.

asymmetric: a branching pattern or shape which lacks a line of symmetry.

attenuate: tapering gradually.

auricle: an ear-shaped lobe at the base of a leaf.

axis: the main stem or a major branch of a plant.

basipetal: growth originating at or near the base or lower parts of the thallus; the opposite of acropetal.

benthic: applied to an organism attached to or resting on the substrate of an ocean or lake. biconvex: convex on both sides.

bifid: divided, for about half the length, into two.

biflagellate: with two flagella.

bifurcate: twice equally divided into two.

bilateral: with branches on two opposing sides of an axis but not strictly distichous.

bilenticular (pyrenoid): pyrenoids surrounded by starch deposited as two lenticular masses.

biogeography: the study of the geographical distribution of organisms.

biomass: the total amount of living organisms preseent at one time.

biotic: concerned with organisms.

biseriate: arranged in two series or rows.

- **bisexual:** with both sexes produced by the one individual or within the one flower. **blade:** the broad, flattened part of a thallus, usually surmounting the stipe; the expanded part of a leaf.
- **bract:** a leaf-like structure different in form from the normal foliage leaf; a terete, unicellular appendage on lateral branches in Charophyta.

bract-cell: a 1-celled appendage at the branchlet nodes of Charophyta.

branchlet: a smaller lateral branch of a thallus.

bulbils: starch containing structures formed on the rhizoids of certain Charophyta.

bulbous: shaped like a bulb, with a swollen, rounded base narrowing to a smaller apex.

caducous: falling readily; non-persistent.

calcified: involving deposition of calcium carbonate in or on cell walls of the thallus.

calcite: the hexagonal crystalline form of calcium carbonate.

calyx: the outer whorl of the perianth, consisting of the sepals.

campylotropous: an ovule orientated with its axis at right angles to its stalk.

capitate: with an enlargement or rounded head at the upper end.

capitula cells: cells within the antheridium of Charophyta which support the manubrium cells or the antheridial filaments.

capsule: a dry fruit formed by union of 2 or more carpels, dehiscing at maturity.

carotene: orange-yellow isoprenoid polyene pigments containing carbon and hydrogen, present in chloroplasts.

carpel: an organ within a flower, composed of an ovary, style and stigma.

carpophore: the carpel stalk.

cartilaginous: firm and tough but somewhat flexible.

cauline: inserted on the stem.

cellulose: the common carbohydrate of plant cell walls, composed of β -1,4 glucosides, commonly in the form of microfibrils.

chambered: internally subdivided or partitioned.

chlamydomonine: with the basic structure of a Chlamydomonas cell but without flagella.

chlorophyll: the fat soluble, photosynthetic green pigments of plants, consisting of closed tetrapyrrols with magnesium.

chloroplast: a double membrane bounded organelle with membranous sacs (thylakoids) containing chlorophyll *a* and other pigments.

class: a major taxonomic rank, between phylum (division) and order.

clathrate: forming a net or reticulum.

clavate: shaped like a club, broader towards the apex.

coenocytes: a large (usually elongate) multinucleate cell, without or with few cross walls.

comb: a specialised structure (in *Amphibolis*) formed from the endo-skeleton of a pericarpic lobe after the disintegration of the external fleshy tissue. The collection of combs together forms the *grappling apparatus* which anchors the young seedling.

community: a distinctive assemblage of organisms usually in a restricted environment and with one to a few dominant species.

complanate: flattened or branched in one plane.

compressed: flattened but not strongly so, with an ovate to elongate cross section.

concavo-convex: concave on one side and convex on the other.

confervoid: composed of threads.

connate: fused to another organ.

connective: the tissue connecting the microsporangia in an anther.

coralline algae: red algae of the family Corallinaceae, which deposit calcium carbonate in the cell walls.

coralloid: resembling a branched coral in form.

corolla: the inner perianth whorl of a flower, consisting of the petals.

corona: the whorl of appendages above and below the whorl of gametangial rays in Acetabularia and related genera; the five (or ten) cells at the upper end of the oogonium of Charophyta.

cortex: the outer layer of cells or tissue in a thallus, stem or root.

corticated: with an outer layer or tissue of cells formed secondarily.

cosmopolitan: widely distributed in all or most oceans.

cotyledon: the first leaf of a seed plant, present in the embryo.

crisped: curled up with a much and irregularly divided margin.

crustose: forming a firm to hard crust on the substrate.

cuneate: wedge shaped.

cupulate: cup shaped.

cupule: a small cup-like structure.

cymose: with the form of a cyme, i.e. a branched inflorescence in which the terminal bud is a flower bud and subsequent growth is by a lateral axis.

cyst: a resistant, usually thick-walled, cell which later produces reproductive cells; a sac or cavity.

dehiscent: opening when mature to release the contents.

dendroid: tree-like and much branched above.

dentate: with marginal teeth.

denticulate: with small marginal teeth.

diaphragm: a cross partition of cells, e.g. separating air canals in seagrasses.

dichotomous: branching into two equal parts, resulting from equal division of the growing point.

diffuse growth: growth in almost any part of the thallus, not localised in certain regions.

dioecious: having the male and female gametes or flowers produced on separate plants.

diplohaplontic: with separate multicellular diploid (sporophyte) and haploid (gametophyte) phases.

diploid: with two sets of chromosomes (2N) in each nucleus.

diplontic: when the diploid phase is the prominent one and the haploid phase consists only of the gametes; not to be confused with diplobiontic which applies to organisms with two separate phases in their life history.

discoid: forming a disc, or a flattened, rounded shape.

discrete: separate, not joined or coalescent.

distichous: in two opposite ranks along an axis and thus lying in one plane.

distromatic: with two layers of cells, giving a cross-section two cells thick.

division: a major group of plants, equivalent to "phylum".

dominant: an ecological term for a species which is usually most frequent, often largest, and usually influences the composition of the community.

drupe: a fruit with a fleshy outer covering and a hard seed.

ebracteate: without a bract.

ecology: the study of organisms in relation to their environment.

ecorticate: without a cortex.

ecosystems: the organisms in a community together with the abiotic factors which influence them.

eligulate: without a ligule.

ellipsoid: a solid of elliptic shape.

elliptic: shaped like an ellipse; oval with regularly rounded ends (in 2 dimensions).

endemism: restriction of the distribution of a taxon to a particular geographical region.

endocarp: the inner layer of the pericarp (fruit wall).

endogenous: development of a branch from within the tissue of the parent axis.

endophyte: living within the tissues of the host plant.

endosperm: the nutritive tissue of a seed, derived from the triploid fusion nucleus in angiosperms.

entire: with a smooth margin, without teeth or lobes. environment: the situation in which an organism lives.

ephemeral: a plant which completes its life cycle in a short time.

epidermis: the outermost cell layer of plants.

epilithic: living attached to rock or stones.

epiphyte: living attached to a plant, but not parasitic.

eulittoral: the main intertidal zone between the sublittoral (usually dominated by large brown algae) and the littoral fringe (usually dominated by littorinid snails).

euryhaline: tolerant to a wide range of salinity.

exine: the outer layer of the wall of a pollen grain.

exocarp: the outer layer of the pericarp (fruit wall).

exogenous: development of a branch from the outermost cells of the parent axis.

extrorsely: opening away from the centre.

eyespot: orange to red pigmented, light receptive spots in the motile cells of certain algae; the "stigma".

falcate: sickle-shaped; curved, with a broader base and tapering above.

family: a taxonomic group between order and genus, with the name ending in aceae.

fascicle: a cluster or bundle.

fastigiate: with branchlets clustered, erect and subparallel.

filament: a long, thread-like row of cells, one or more thick, of fairly uniform diameter; the stalk of an anther.

filiform: thread-like or filamentous, usually several cells thick.

fimbriate: with the margin bordered by long, slender processes.

flabellate: fan-like and complanate, spreading upwards from a narrow base.

flaccid: limp, flabby.

flagella: long, cylindrical, cytoplasmic extensions of cells conferring motility on the cell; structurally with 9 peripheral doublets and two central microtubular strands.

flexuous: an axis or branch with a zig-zag development, usually with alternate branches to each side.

flounced: with the margin wrinkled or gathered and undulate.

foliose: broadly flattened or leaf-like.

free-floating: not attached but floating at or under the surface of water.

frond: the main part of an algal thallus, above the holdfast and stipe.

fucalean: pertaining to the Fucales (Phaeophyta).

funicle: the stalk of an ovule.

furcate: divided into two, usually fairly equally.

fusiform: spindle shaped, thicker centrally and tapering to both ends.

galeate: with a helmet-like cap to the structure.

gametangia: the sex organs which contain the gametes.

gamete: a haploid reproductive cell capable of uniting with another such cell to form a diploid zygote.

gametic meiosis: meiosis resulting in direct formation of gametes in a diplontic life history. gametogenesis: the process by which gametes are formed.

gametophyte: the multicellular sexual (N), gamete-producing phase in the life-history of a plant.

genotype: the total complement of hereditary factors possessed by an organism and transmissible to its progeny.

genus: a taxonomic group of one to several related species, separable from other such groups. glabrous: without hairs.

globose: nearly spherical.

grappling apparatus: see comb.

gynoecium: the female part of the flower consisting of one or more carpels.

habit: the morphological form of a plant.

habitat: the environment in which an organism lives.

- hairs: elongate, unicellular or multicellular appendages, simple or branched, usually colourless and often readily lost.
- haploid: the phase of the life history of a plant with the nuclei containing a single set (N) of chromosomes.
- **haplontic:** when the haploid phase is the prominent one and the diploid phase consists only of the zygote cell; not to be confused with haplobiontic which applies to organisms with one phase (either gametophyte or sporophyte) in their life history.
- hapteroid: a small lobed or branched extension of a cell which can act as an attachment structure.
- heteromorphic: with morphologically different gametophyte and sporophyte phases in a diplohaplontic life history.
- heteroplastic: with two types of plastids in the cells, chloroplasts and amyloplasts.
- heterotrichous: a filamentous habit involving both prostrate and erect systems.
- hilum: the scar left on the ovule or seed after separation from the funicle.
- holdfast: a basal, attaching cell or organ.
- **holotype:** the single specimen on which an author bases his description of a new taxon; see also isotype and lectotype.
- **homoplastic:** with only one type of plastid in the cells, functioning both as chloroplast and for starch synthesis.
- host: an organism on which another organism grows.
- hyaline: thin and transparent.
- hydrophilous: pollinated through the agency of water.
- hygroscopic: readily absorbing or losing water and thence changing form.
- hypanthium: a cup or tube bearing the floral parts above the base and often above the top of the ovary.
- hypersaline: with a salinity above that of normal sea water.

imbricate: overlapping.

- incised: cut deeply and sharply, often irregularly.
- inferior: below some other organ, e.g. an inferior ovary situated below the attachment of the other floral parts.
- isomorphic: organisms with the gametophyte and sporophyte of similar morphology.
- isotype: a duplicate specimen to the holotype.
- intercalation: arising or interposed somewhere between the base or apex or between branches. intergrade: an intermediate form between two species or varieties.
- internode: the part of an axis or branch between two nodes.
- interstices: the spaces between parts of a thallus.
- intertidal: the region of the shore between extreme low and high tides.
- intravaginales squamulae: see squamules.
- introrsely: inwardly (e.g. on the inside of the apical wall of Codium utricles).
- invagination: an infolded hollow or cavity.
- isodiametric: with approximately equal diameters or dimensions.
- isogametes: gametes morphologically identical.
- isokont gametes: with flagella of equal length.
- **isomorphic:** organisms with the gametophyte and sporophyte of similar morphology. **isotype:** a duplicate specimen to the holotype.
- keel: a prominent ridge.
- kelp: a member of the Laminariales (Phaeophyta); also used in "bull kelp" as applying to *Durvillaea* in the Durvillaeales.
- lacerate: torn or irregularly cleft.
- laciniate: slashed, torn or divided into narrow, usually tapering lobes. lamellate: composed of thin layers or plates of tissue.

lamina: the flattened blade or upper part of larger algae.

laminate: flattened to form a lamina.

lanceolate: lance shaped; long and narrow, tappering to each end.

lateral: a side branch or structure on an axis or larger branch.

- leaf: strictly, the foliar organ of vascular plants; occasionally used in algae for flattened structures similar to leaves in morphology (e.g. in *Sargassum*).
- lectotype: a specimen of the type collection selected as the basis of the taxon in the absence of a holotype.
- lenticular: shaped as in a doubly convex lens.
- life cycle: the cyclic course of development from any given stage to the same again, usually obligatory.

life history: the sum of an organism's morphological, cytological and reproductive phases.

lignicolous: applied to plants which occur on timber.

lignin: a complex carbohydrate deposited in the cell walls of woody tissue.

ligule: a membrane at the junction of the leaf sheath and blade.

linear: narrow with parallel sides and several times longer than wide.

littoral fringe: the zone above the eulittoral, usually dominated by littorinid snails; the lower part of the supralittoral.

littoral zone: loosely used for the main part of the intertidal zone, now largely replaced by "eulittoral".

locule: a chamber of an ovary or anther.

loose lying: not attached to but lying on the substrate or in shallow water. lunate: half-moon shaped.

macro-algae: larger algae readily observed without a microscope.

macroscopic: structures seen clearly with the unaided eye.

mamilliform: with papillate or mamillate protuberances.

mangroves: arborescent angiosperms characteristic of essentially marine, intertidal, usually mud-flat situations in tropical to warm temperate seas, usually with modification of the roots such as pneumatophores.

mannan: a polysaccharide wall component (e.g. of Codiales) which yields mannose on hydrolysis. manubrium cells: cells within the male organ of Charophyta, which support the shield cells. mean sea level: the mean of all the hourly heights of the sea level over a month or year. medulla: the central region of a thallus, within the cortex.

meiosis: nuclear division in which the chromosome number is reduced from 2N to N and genetic segregation occurs.

meiospore: a spore formed directly as a result of meiosis.

membranous: thin, often semi-transparent.

microfibrils: minute, (sub) microscopic, fibrillar components of cell walls.

micropyle: a minute opening between the ovule integuments, through which the pollen tube enters to effect fertilisation.

microscopic: small structures only seen clearly with a microscope.

microsporangium: the part within the anther which produces the microspores (pollen grains). microthallus: the small, filamentous, inconspicuous phase of an organism, alternating with a

larger phase (macrothallus).

mitospore: a spore formed as a direct result of mitosis (normal nuclear division).

moniliform: arranged like a string of rounded beads.

monocarpous: a gynoecium consisting of a single carpel.

monoecious: producing male and female gametes in separate structures but on the same individual.

monopodial: growth by means of a continuous apical growing point.

monostromatic: single layered, normally only one cell thick.

mucilage: a jelly-like or slimy carbohydrate material.

mucro: a short, sharp-pointed structure.

multicellular: composed of numerous cells.

multinucleate: with few to many nuclei in the cell or coenocytic thallus.

neotype: a specimen selected to serve in place of a holotype or lectotype when these do not exist.

node: the region on an axis or branch from which appendages arise.

nom. cons.: nomen conservandum or name formally accepted as the correct one though contrary to the usual principles of nomenclature.

obovate: reversed ovate, with the upper end the broader (attached at the narrower end). **obtuse:** blunt or rounded at the end.

oogametes: sperms and eggs.

oogamous: sexual reproduction where a sperm (usually small and motile) unites with a larger non-motile egg.

oogonia: female reproductive organs, each containing one or more eggs.

order: a taxonomic group between class and family, with the name ending in -ales. orthotropous: an erect ovule with a straight axis from the funicle to the micropyle.

ovary: the basal part of the carpel(s) enclosing the ovule(s).

ovate: egg-shaped in outline, with a broader basal end (a two-dimensional term).

ovoid: egg-shaped, broader basally (a three dimensional term).

ovule: the unfertilised seed in the ovary.

palisade: a row of elongate structures at right angles to the surface.

papillae: small, rounded or obtuse protuberances on an organ.

parietal: adjacent to the inner side of a cell or structure; ovules attached to the wall of an ovary or inward projections from it.

parthenogenesis: production of a new individual from a single, unfertilised gamete, usually an egg.

patent: spreading.

pedicel: the ultimate stalk or support for a reproductive organ.

peduncle: the stalk of an inflorescence.

peltate: having the stalk attached to about the middle of the lower surface of a shield-like structure.

penicillate: pencil-like; tufted as in an artist's brush.

percurrent: extending from base to apex of a thallus as one or more well-developed axes.

perennating organ: a vegetative part which assists a plant to remain alive for more than a year.

perennial: a plant or part which lasts for several years.

perianth: the outer 1 (or 2) sterile whorls of a flower.

pericarp: the fruit wall, developed from the ovary wall.

pericentral: elements surrounding the centre.

petal: a unit of the corolla.

petiole: the stalk of a leaf.

phenology: the study of periodic (seasonal) phenomena in relation to environmental factors.

phenotype: the observable characteristics of an organism, resulting from the interactions of the genotype and its environment.

phloem: the tissue which conducts the synthesized food in the vascular bundle.

photic zone: the illuminated zone of the sea or lakes within which plants can grow.

phragmoplast: an assemblage of microtubules parallel to the spindle axis at telophase of mitosis, across which the cell plate develops.

phycology: the study of algae, equivalent to and replacing the older term algology.

phycoplast: an assemblage of microtubules perpendicular to the spindle at the cell equator at telophase, between which the cell plate develops.

phylum: a major group of plants, equivalent to "division".

phytoplankton: the plant plankton.

pinnate: with leaflets or segments arranged along each side of an axis or branch.

placenta: the part of the ovary to which the ovules are attached.

placentation: the arrangement of the placentas in an ovary.

plankton: minute plants and animals freely suspended in the sea or lakes.

plano-convex: flat on one side and convex on the other side.

- plugs: wall thickenings of medullary filaments in some species of *Codium*, partially blocking the lumen.
- pluriseriate: with cells arranged in more than a single longitudinal series (c.f. uniseriate).
- pneumatophore: a vertical, aerial (at low tide) appendage to the roots of mangroves, through which gaseous exchange occurs.
- podogyne: the stalk of a fruit developed from an individual carpel.
- poikilohaline: varying in salinity.
- pole: one end of an elongate cell or structure.
- pollen (grain): the microspore of angiosperms and gymnosperms.
- pollen sac: see microsporangium.
- polychotomous: division at one point into several subequal branches.
- pompons: a woolly, ball-like tuft of filaments.
- prokaryotic: organisms lacking membrane-bound organelles in the cell (bacteria and blue-green algae).
- proliferous: bearing branches as irregularly placed offshoots.
- **propagule:** a small vegetative structure which can grow into a new plant when detached from the parent.
- prophyll: the first formed leaf of a shoot (often much modified).
- prostrate: lying flat on the substrate.
- protonema: a juvenile filamentous stage following germination of a spore or zygote.
- **province:** a major biogeographic division of a coast, with a marked difference in species composition from an adjacent province.
- **pseudodichotomous:** apparent dichotomous branching produced by stronger development of a lateral to resemble the original axis.
- pseudoflagella: immobile and non-functional flagella.
- **pseudoparenchymatous:** parenchyma-like due to lateral attachment or interweaving of filaments, but without cell divisions in all planes.
- **pyrenoid:** a differentiated region of a chloroplast, forming a centre for carbohydrate (e.g. starch) synthesis.
- **pyriform:** pear-shaped, with the narrower end the point of attachment. **pulvinate:** hemispherical or cushion shaped.
- quadriflagellate: with four flagella.
- radial: branching on any radius when viewed from above.
- ramuli: lesser or ultimate branchlets.
- refract: bent from the base backward.
- refractofalcate: refract and of falcate form.
- reniform: kidney shaped.
- reticulate: forming a net or reticulum.
- retinacule: a marginal outgrowth from a spadix (in Zosteraceae).
- rhizoid: a single or few-celled (without differentation) absorptive or attaching structure.
- rhizome: an underground, more or less horizontal stem of a vascular plant.
- robust: strongly developed, often thick, compared to related taxa.
- root: an absorptive and anchoring organ of vascular plants, with differentiated tissues and a root cap.
- rostrate: ending in a long often beak-like point.
- ruffled: with a strongly waved or undulate margin.
- saccate: in the form of a sac or cavity.
- samphire: members of the Chenopodiaceae with succulent, articulate stems and reduced leaves, often growing with their substrate and lower stems covered at high tide; genera such as *Sarcocornia* and *Halosarcia*.
- scale: a thin bract (frequently non-green).
- scalpelliform: shaped like a scalpel; with one side fairly straight and the other curved to the apex of the structure.

scarious: thin, dry and membranous.

sclerenchymatous: having thick-walled cells.

seagrass: a marine monocotyledon growing submerged at least at high tide.

segment: a division of an axis or branch; a large cell of a series.

segregative division: cell formation where the protoplast cleaves into separate masses which expand and develop walls (order Siphonocladales).

semicarpous: carpels partially or loosely joined.

sepal: a unit of the calyx.

septate: with cross walls to the cells or filaments.

septum: a cross wall.

serially arranged: disposed in a row, one behind the other.

serrate: toothed with teeth pointing forwards.

serrulate: serrate with very small teeth.

sessile: attached directly to the substrate without a distinct holdfast and stipe; not stalked. setae: stiff hairs or bristles.

sheath: leaf base surrounding the stem, may be open or closed.

shield cells: the outer cells of the male organ of Charophyta.

simple: unbranched or undivided.

siphonein: a carotenoid pigment found in chloroplasts of certain coenocytic green algae (e.g. Caulerpales).

siphonoxanthin: a carotenoid pigment (related to siphonein) found in chloroplasts of certain coenocytic green algae (e.g. Caulerpales).

spadix: a spike-like structure with a modified axis usually enclosed in a spathe.

spathe: a large bract or pair of bracts, surrounding an inflorescence.

spathulate: elongate with the basal end narrower, as in a spatula or spoon.

sphaeroid: almost spherical.

spike: an elongated inflorescence with flowers sessile on the axis; a condensed branch system with lateral branches and gametangia (Charophyta).

spine: a stiff, sharp-pointed projection on a cell or tissue.

sporangia: spore producing cells or structures (mitosporangia or meiosporangia).

spore: a one-celled reproductive cell derived by mitosis (mitospore) or meiosis (meiospore) and capable of growth directly.

sporophyte: the diploid (2N), spore producing multicellular phase of a life history.

sporulation: the process of spore formation.

spur: a horn-like extension to an organ.

squamules: small scales within the sheathing base of the leaf.

stamen: the organ of a flower consisting of an anther and a filament.

stellate: with the form of a star, having numerous projections from a central region.

stephanokontic: with a ring or crown of flagella on the zoospore.

stigma: the terminal receptive part of a carpel, to which the pollen adheres.

stipe: the stalk, lying between the holdfast and the blade or frond of the thallus.

stipitate: with a lower, stipe-like region to the thallus; stalked.

stipulode: 1-celled appendages at the axial nodes of Charophyta, beneath the branchlets.

stolon: a prostrate or creeping stem with roots and shoots at the nodes (e.g. *Halophila*); a prostrate axis, lying on or in the substrate, from which erect branches arise (e.g. *Caulerpa*).

striations: more or less parallel longitudinal markings.

style: the more or less elongate portion of a carpel between the ovary and stigma.

sublittoral: the photic zone below the eulittoral region; from about mean low tide level down and usually marked by the upper limit of kelps or other large brown algae.

sublittoral fringe: a distinctive fringe zone which is sometimes characteristic of the region just below the eulittoral, e.g. in the suck-back of waves at low tide.

subsessile: almost sessile, with only a slight stipe or stalk present.

substrate: the place (rock, mud, sand or a host) where an organism is attached.

subtend: to be positioned at the base of another organ.

subterminal: occurring or attached just below the terminal part of an organ, filament or cell.

subtruncate: almost or partially truncate.

subulate: long and more or less terete but tapering to a point.

superior: above some other organ, e.g. a superior ovary situated above the petals and sepals. supralittoral: the region above the eulittoral (or about high tide level) with organisms of marine affinites; the spray zone.

sympodial: development of an axis by repeated replacement of the growing apex by a lateral growing point from below.

synonym: a superseded name, replaced by the correct one, for a taxon.

tannin cell: a cell with dark polyphenolic inclusions.

taxon (plural-taxa): a group of organisms, at any level, in the classification of plants or animals.

taxonomy: the study of taxa.

tenacula: minute, lobed, hapteroid cells.

tepal: a perianth-like segment.

terete: cylindrical and usually slightly tapering.

testa: the seed-coat, developed from the integuments.

tetrasporangium: a meio-sporangium containing four spores, usually in a distinctive arrangement. thallus: the relatively simple plant body of a non-vascular plant.

thylakoid: a flattened sac-like membranous structure associated with photosynthetic pigments, within the choroplasts.

tomentose: densely covered with short, often matted hairs.

torulose: cylindrical but with numerous rounded excrescences.

trabeculae: slender, internal, strands of wall material, extending across the lumen in *Caulerpa* or projecting inwards from the utricle wall in *Codium*.

transection: a cross-section of the thallus or any part of a plant.

trapezoid: an unsymmetrical four-sided shape.

triquetrous: a three-sided structure, triangular in cross section.

truncate: with the end abruptly flattened as if cut off.

- turion: a specialised swollen shoot (or part thereof), stored with food material, which acts as a perennating organ.
- type: the specimen on which a species (or lesser category) is based, or the species name which provides the basis of the genus; similarly for higher taxa.

ultrastructure: the submicroscope structure of cells as shown in the electron microscope. umbilicate: depressed in the centre, navel-like.

umbo: a boss or projection in the centre of a structure.

undulate: wavy.

unicellular: single-celled.

unilateral: with lateral branches on one side only.

uninucleate: with a single nucleus per cell.

uniseriate: with cells arranged in a single row, not more than one cell broad.

unisexual: with only one sex on any one individual.

upwelling: movement to the surface of oceans of colder, usually nutrient rich, deeper water, usually on coastlines and due to wind and rotational effects of the earth.

utricle: the swollen, terminal ends of cortical branches in *Codium* and some Udoteaceae, forming a palisade-like surface layer.

vacuole: the central, liquid, region of a plant cell within the cytoplasm.

vascular bundle: a strand of conducting tissue composed of xylem and phloem elements.

vegetative: to do with cells or tissues produced by mitosis and not associated with any form of reproduction.

veins: strands of larger cells within a (usually flattened) tissue; or vascular tissue in a leaf. venation: the pattern of veins or vascular strands (e.g. in a leaf).

verrucose: covered with wart-like outgrowths.

vesiculate: forming a vesicle or small sac-like structure.

viviparous: a seed which germinates while still attached to the parent plant.

voucher specimen: a herbarium specimen kept as the basis for an identification reported in the literature.

whorls: structures arranged in a circle or verticil around an axis.

xylan: a polysaccharide wall component (e.g. of Caulerpales) which yields xylose on hydrolysis. xylem: the tissue which conducts water and mineral salts in the vascular bundle.

zonate: banding or zoning of a thallus (usually due to concentric growth), or parallel division of a tetrasporangium (in certain Rhodophyta).

zonation: the horizontal banding or zoning of organisms in the intertidal or subtidal regions, dependent on environmental and biotic factors.

zooidangia: the structure producing or containing zooids.

zooids: motile reproductive cells, either spores or gametes.

zoospore: a motile reproductive cell not involved in sexual reproduction, resulting from mitosis (mitospore) or meiosis (meiospore).

zygote: the cell resulting from gametic fusion.

zygotic meiosis: meiosis which occurs during zygote maturation or germination.

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