FLORA OF AUSTRALIA
SUPPLEMENTARY SERIES

THE MARINE BENTHIC FLORA OF SOUTHERN AUSTRALIA
Vol. IIIA, IIIB & IIID

Published by the
AUSTRALIAN BIOLOGICAL RESOURCES STUDY (ABRS)
Canberra, Australian Capital Territory

Vol. IIID co-published with the State Herbarium of South Australia

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State Herbarium of South Australia
PO Box 2732
Kent Town SA 5071
Australia

Government of South Australia
Department of Environment, Water and Natural Resources

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

THE MARINE BENTHIC FLORA OF SOUTHERN AUSTRALIA

Part IIIB

by

H.B.S. WOMERSLEY



Flora of Australia Supplementary Series Number 5

AUSTRALIAN BIOLOGICAL RESOURCES STUDY



FLORA OF AUSTRALIA SUPPLEMENTARY SERIES
NUMBER 5

THE MARINE BENTHIC FLORA OF SOUTHERN AUSTRALIA

RHODOPHYTA — Part IIIB

Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales

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The Botanic Gardens of Adelaide and State Herbarium,
and the Department of Botany, University of Adelaide,
South Australia

Non-geniculate Corallinales by W.J. Woelkerling (with A.S. Harvey for Austrolithoideae) and D.L. Penrose (for certain genera of Mastophoroideae); geniculate taxa by H.B.S. Womersley & H.W. Johansen

Published by the
Australian Biological Resources Study, Canberra
with assistance from the State Herbarium of South Australia

PREVIOUS PARTS (I, II and IIIA)

Parts I and II of this Flora were published by the Flora and Fauna of South Australia Handbooks Committee and printed by the South Australian Government Printing Division.

Part IIIA was published by the Australian Biological Resources Study, Canberra.

Part I. (1984). Introduction; Collection and preservation; History of studies; Ecology; Biogeography; Seagrasses (by E.L. Robertson); Chlorophyta and Charophyta.

Part II. (1987). Phaeophyta and Chrysophyta (*Vaucheria*).

Part IIIA. (1994). Rhodophyta. Bangiophyceae and Florideophyceae (Acrochaetiales, Nemaliales, Gelidiales, Hildenbrandiales and Gigartinales *sensu lato*).

Womersley, H.B.S. (Hugh Bryan Spencer), 1922-
The marine benthic flora of southern Australia.
Rhodophyta. Part IIIB, Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales.

Bibliography.
Includes Index.
ISBN 0 642 24849 4.
ISBN 0 642 19806 3 (series).

1. Marine flora - South Australia. 2. Benthos - South Australia. I. Australian Biological Resources Study. II. State Herbarium of South Australia. III. Title. (Series: Flora of Australia supplementary series ; no. 5).

581.99423

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Published 28 June, 1996
Printed by Union Offset, Canberra

Cover photograph:
Sporolithon durum at Cape Northumberland, South Australia (LTB).
Photograph — T. Phillips.

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PREFACE

Part IIIB of this Marine Benthic Flora of southern Australia covers four orders of the Rhodophyta (red algae), leaving the large order Ceramiales to be covered in Parts IIIC and IIID.

Part IIIB is arranged similarly to previous parts. Part I should be referred to for general comments on the southern Australian marine flora. Part IIIA presented maps of the southern Australian coast showing most localities mentioned in the text; these maps should be referred to for localities in Part IIIB.

The following have authored or co-authored various groups in this account.

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ACKNOWLEDGEMENTS

The author expresses his gratitude to the Director of the Botanic Gardens and State Herbarium, and to the Chief Botanist of the State Herbarium, for providing facilities for research on the Rhodophyta since 1989; previous research was conducted in the Department of Botany, University of Adelaide.

The author's research has been supported by the Australian Research Grants Scheme (to 1988) and since then by the Australian Research Council. Grants provided have permitted assistance for research, since 1986 by Mrs Carolyn Ricci, and Ms Lindy Scott in 1995. Acknowledgements in Part II list other staff who have contributed to this research. Appreciation is expressed to Mrs Ricci and Ms Scott who have been responsible for photographic processing, inking of the author's line drawings, proof reading and general manuscript checking, as well as herbarium curation and processing of collections.

Dr W.J. Woelkerling acknowledges financial support from the Marine Sciences and Technologies Scheme, The Australian Research Grants Scheme and the Australian Research Council for work on the non-geniculate Corallinales. Sincere thanks also are due to Trevor Phillips (School of Botany, La Trobe University) for assistance with the photography, and to A.S. Harvey (School of Botany, La Trobe University) for preparation of the figures of non-geniculate corallines, and assisting with the proof reading and general manuscript checking.

Collections on which this Flora is based have been contributed by many researchers and SCUBA divers [especially by Dr S.A. Shepherd and Mr K. Branden of the State Department of Fisheries (now SARDI, Aquatic Sciences), Ms K.L. Gowlett-Holmes (Natural History Museum, Adelaide) and Dr G.E. Edgar (Department of Zoology, University of Tasmania).] Ms Gowlett-Holmes and Dr Edgar have also made available colour slides (see acknowledgements for figures in plates). Directors of the Australian Herbaria (especially MEL, MELU, NSW and HO) have permitted consultation of their algal collections, and Mrs Doris Sinkora (MEL) has given valued assistance as well as extensive collections. Dr G.T. Kraft (University of Melbourne) has made available for study numerous collections, and discussions with him have contributed to the authors knowledge of many species. Dr J.M. Huisman (Murdoch University) has also assisted with information on certain Rhodymeniales, as have Dr I.A. Abbott, Dr C. Bird, Dr M.H. Hommersand and Dr M. Steentoft on *Gracilaria*. Dr P.C. Silva has assisted on some nomenclatural matters.

The text of Part IIIB was set up on word-processor by Miss Tina Eadsforth (State Herbarium). Latin diagnoses were kindly provided by Dr S.A. Shepherd, and Dr G. Scott (University of Melbourne) for *Lomentaria pyramidalis*, and Dr John Jessop, Chief Botanist of the State Herbarium, kindly commented on the manuscript.

Illustrations have been used from the following journals: Transactions of the Royal Society of South Australia; Journal of Phycology; and Australian Systematic Botany. In each case permission has been obtained from the Editor, and the relevant captions refer to the original author(s) who are then given in the references with the journal concerned.

H.B.S. Womersley

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ABBREVIATIONS USED IN FIGURES (LINE DRAWINGS)

a	apical cell	*h*	hair
aux	auxiliary cell	*host co*	host cortical cell
aux i	auxiliary initial	*l*	longitudinal filament
ax	axial cell	*l c*	lateral connecting cell
b	basal cell	*m f*	medullary filament
c	carpogonium	*o*	ostiole
csp	carposporangium	*pa*	periaxial cell
c br	carpogonial branch	*pc*	pericarp
c br 1	(cells 1, 2, 3 and 4)	*s cell*	secretory cell
c br 2		*sp*	spermatangium
c br 3		*sp i*	spermatangium initial
c br 4		*st b*	sterile branch
co	cortical cell	*stel*	stellate cell
cyst	cystocarp	*su*	supporting cell
d	diaphragm	*t*	tetrasporangium
fu	fusion cell	*t i*	tetrasporangium initial
g f	gonimoblast filaments	*tr*	trichogyne
gl	gland cell		

INTRODUCTION

Part IIIB of the Rhodophyta continues Part IIIA, and covers the orders Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales, as listed in the Synopsis (pp. 7, 8). Parts IIIC and IIID will now cover the Ceramiales, which includes about half of the southern Australian species of the Rhodophyta.

The layout of Part IIIB is similar to that in Part IIIA, and comments in the previous introduction apply here.

References cited under species include those which give descriptions, comments or detailed localities; references listing the name only within generalised areas (e.g. in Lucas 1909, 1912) or in ecological accounts are not included, nor are the generic descriptions in Kylin (1956).

While most references in such papers are included, it is recognised that some have not been accounted for since it has not been possible to locate the relevant specimens.

References on non-geniculate Corallinaceae are by W.J. Woelkerling, as are terms in the glossary pertaining to this group.

Photographs in figures of the Gracilariales, Rhodymeniales, Corallinales (geniculate taxa, unless credited to H.W. Johansen) and Bonnemaisoniales are by H.B.S.W. Photographs of non-geniculate Corallinales are by W.J. Woelkerling.



Plate 1 figure 1. *Gracilaria ramulosa* (AD, A63002).
Photograph — H.B.S. Womersley.



Plate 1 figure 3. *Coelarthrum opuntia* (AD, A64473).
Photograph — K.L. Gowlett-Holmes.



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Plate 1 figure 4. *Rhodymenia leptophylla* (AD, A64238).
Photograph — G. Edgar.

PLATE 1



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Photograph — K.L. Gowlett-Holmes.

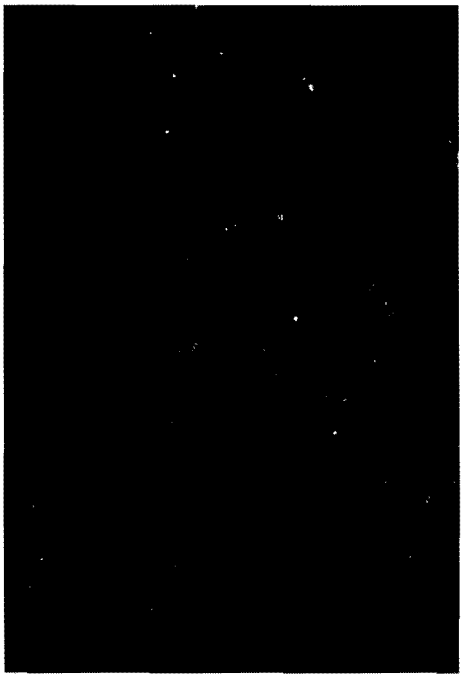


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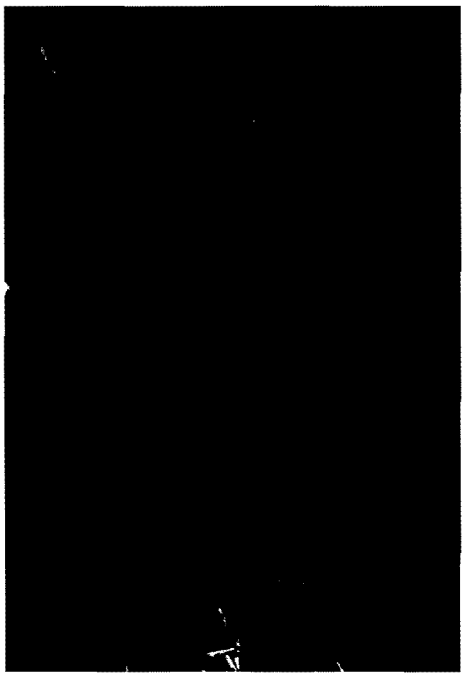


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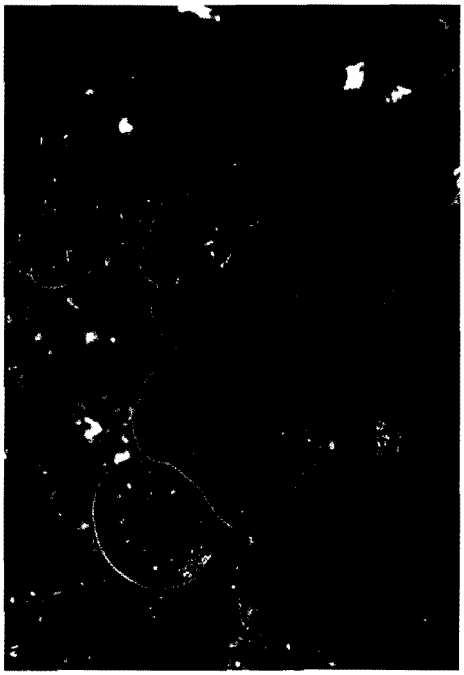


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Photograph — K.L. Gowlett-Holmes.



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Photograph — W.J. Woelkerling.

PLATE 3



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Photograph — H.B.S. Womersley.

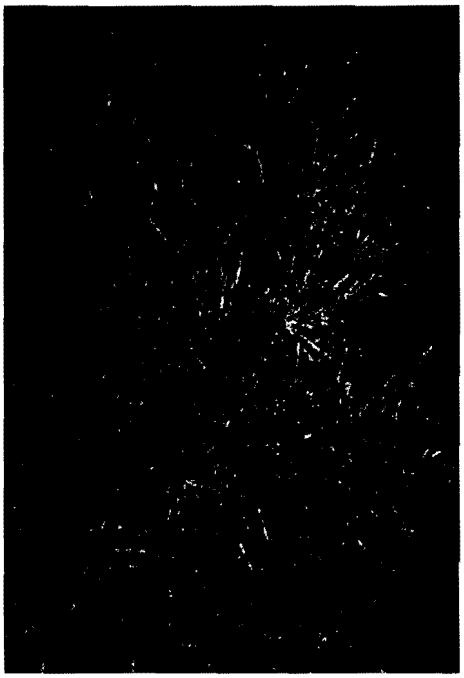


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Photograph — K.L. Gowlett-Holmes.



Plate 4 figure 2. *Corallina officinalis* (AD, A64460).
Photograph — K.L. Gowlett-Holmes.

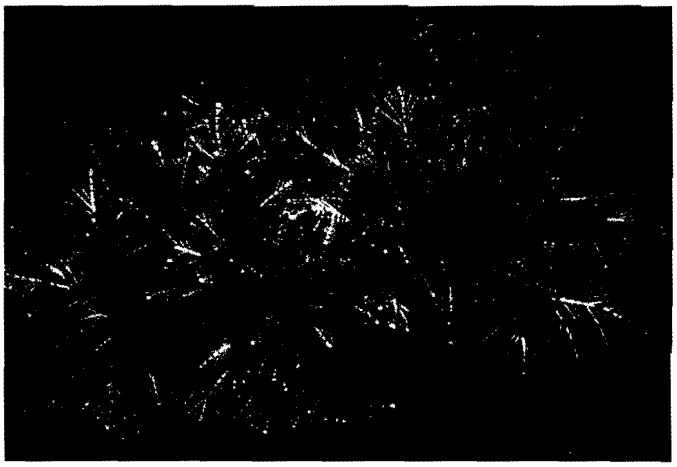


Plate 4 figure 4. *Haliptilon roseum* (AD, A64605).
Photograph — K.L. Gowlett-Holmes.

PLATE 4

RHODOPHYTA

CLASS FLORIDEOPHYCEAE Cronquist 1960: 438

ORDER GRACILARIALES Fredericq & Hommersand 1989a: 225

Thallus usually erect, branches terete to flat, radially or complanately branched; or parasitic and forming hemispherical pustules. Growth usually multiaxial (or uniaxial, but without an apparent central axis), pseudoparenchymatous, with a small-celled cortex grading to a large-celled medulla, with numerous secondary pit-connections. Apical and outer cortical cells dividing by oblique, longitudinal, concavo-convex walls followed by oblique or transverse division of the subterminal cell, with or without an apical cap of smaller cells. Cell walls containing agar; pit-plugs with one cap layer.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli usually dioecious; auxiliary cells absent. Carpogonial branches 2-celled, outwardly directed from an intercalary mid cortical multinucleate supporting cell which also bears two or more sterile branches; hypogynous cell binucleate to multinucleate, carpogonium uninucleate with a straight trichogyne. Auxiliary cells absent, cells of the sterile branches fusing with the fertilized carpogonium which forms a fusion cell developing laterally and outwardly multiple gonimoblast initials which establish secondary fusions with gametophytic cells in the cystocarp floor and the pericarp, then produce a dense, erect, tuft of filaments surmounted with chains or clusters of subspherical to ovoid carposporangia. Cystocarps protruding, hemispherical, with a thick walled ostiolate pericarp, or as slight bulges in pustular taxa. Spermatangia forming a surface layer or borne in conceptacle-like depressions or cavities.

Tetrasporangia (or bisporangia) scattered in the outer cortex or within a shallow nemathecium, cruciately divided.

The Gracilariales were distinguished at ordinal level by Fredericq & Hommersand (1989a), separated from the Gigartinales (where they were previously placed as a family) by lacking an auxiliary cell and in details of apical cell divisions, development of the carposporophyte and the spermatangia. Fredericq & Hommersand (1990a) also placed the family Pterocladiophilaceae, including 3 parasitic genera, in the Gracilariales.

KEY TO FAMILIES OF GRACILARIALES

1. Thallus parasitic, forming pale or pigmented pustules on the host branches (*Gracilaria* spp.)..... PTEROCLADIOPHILACEAE
1. Thallus free living, erect, many centimetres high.....GRACILARIACEAE

FAMILY PTEROCLADIOPHILACEAE Fan & Papenfuss 1959: 38

Thallus parasitic on Gelidiaceae or *Gracilaria*, forming small, white to pigmented, hemispherical to verrucose, pustules. *Structure* of branched, endophytic, rhizoidal filaments pit-connected to host cells, and the pustules of outer, anticlinal, cortical chains and inner larger-celled, multinucleate, medullary cells with numerous secondary pit-connections.

Life history triphasic with essentially isomorphic gametophytes and tetrasporophyte.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 2-celled, borne on a supporting cell in a cortical filament, with a straight trichogyne. Auxiliary cells absent; fertilized carpogonium possibly fusing with adjacent vegetative cells and developing the gonimoblast directly, consisting of horizontal filaments fusing with vegetative cells and clusters of erect filaments bearing chains of carposporangia, interspersed among cortical filaments; pericarp absent. Spermatangia formed in chains from surface cortical cells, cut off by intercalary divisions from initial cells.

Tetrasporangia scattered in the cortex or in pits, cruciately or zonately divided.

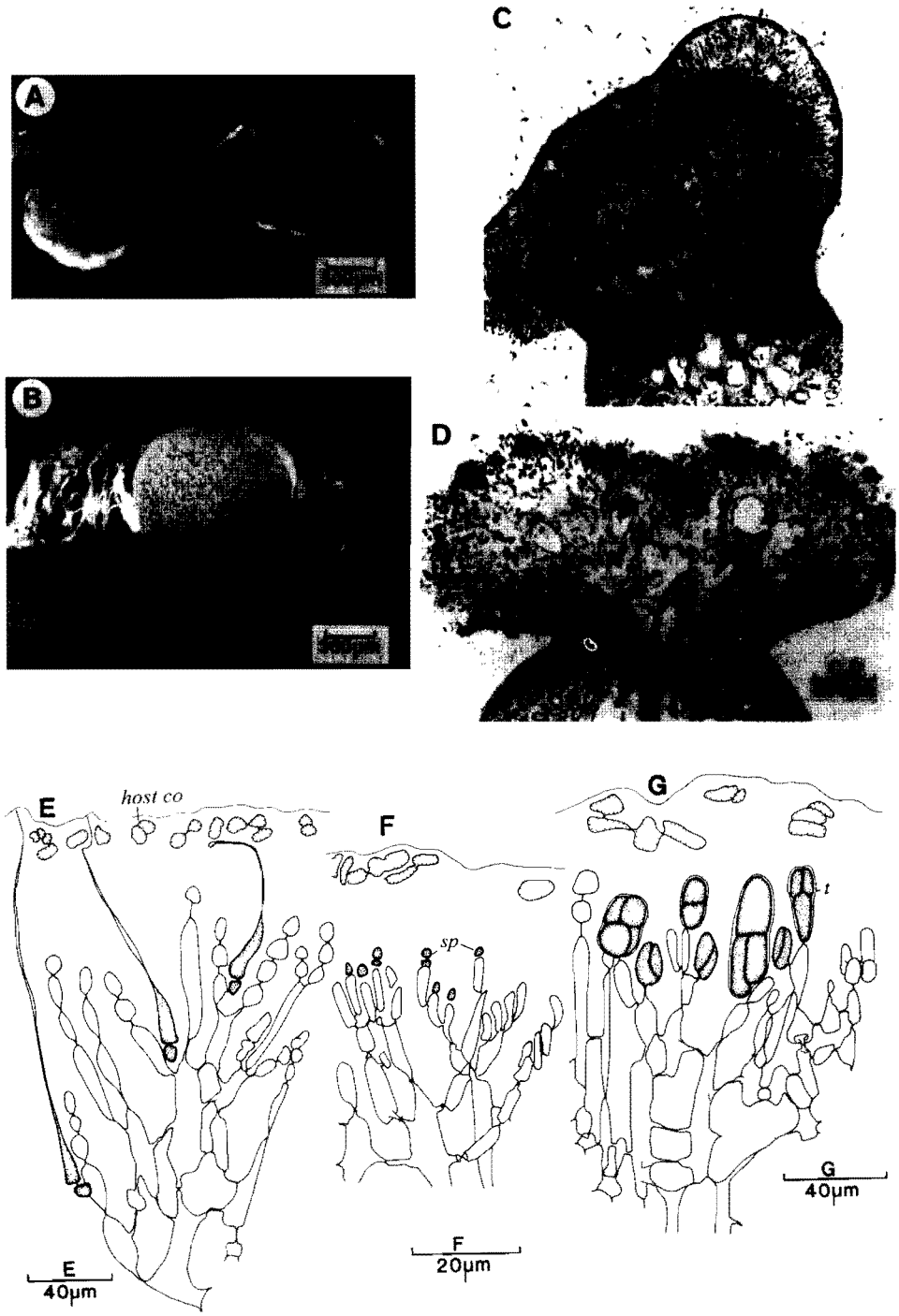


Fig. 1. *Holmsella australis* (**A, B,** MELU, K6230; **C, D,** AD, A63536). **A.** Two sexual thalli, each lobe containing a carposporophyte. **B.** A tetrasporangial thallus. **C.** Section through a female thallus with a mature carposporangial layer (arrow). **D.** Section of a tetrasporangial thallus. **E.** Section of female thallus with carpogonial branches. **F.** Section of male thallus with spermatangia. **G.** Section of tetrasporangial thallus. (In **E–G,** cells of the host are shown above.) **B, E–G,** after Noble & Kraft 1983.

A family of 3 minute parasitic genera (*Pterocladiophila* Fan & Papenfuss and *Gelidiocolax* Gardner on Gelidiaceae and *Holmsella* Sturch on *Gracilaria*) which Fredericq & Hommersand (1990a) place in the Gracilariales. Only *Holmsella* has been recorded from southern Australia.

Genus HOLMSELLA Sturch 1926: 603

Thallus colourless, pulvinate to hemispherical, parasitic on *Gracilaria*. *Structure* multiaxial, with slender filaments penetrating between the host cells and pit-connecting with them, producing outwardly a mass of compact filaments of either slender or ovoid cells, with a cortex of anticlinal filaments.

Life history triphasic, with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 2-celled, borne on an intercalary cell of a cortical filament; fertilized carpogonium possibly fusing with adjacent vegetative cells. Carposporophyte spreading, with a basal layer of filaments and erect gonimoblast filaments producing chains of carposporangia; pericarp and ostiole absent. Spermatangia borne in chains on outer cortical cells.

Tetrasporangia developed from terminal cortical cells, ovoid, cruciately divided.

Holotype species: *H. pachyderma* (Reinsch)Sturch 1926: 603.

A genus of two species, the type from N. Europe and parasitic on *Gracilaria "verrucosa"*, and the southern Australian *H. australis*.

Holmsella australis Noble & Kraft 1983: 393, figs 1–15.

FIG. 1

Thallus (Fig. 1A, B) white, pulvinate, surface smooth (tetrasporangial) or verrucose (cystocarpic), 0.5–3 mm across, growing on *Gracilaria ramulosa* (or *G. flagelliformis*). *Structure* multiaxial, with slender filaments penetrating between the host cells and pit-connecting with them, externally with a mass of compact filaments forming the pustules with a thick gelatinous outer layer below 1–2 layers of host cortical cells raised up by the parasite.

Reproduction. Gametangial thalli dioecious. Carpogonial branches (Fig. 1E) 2-celled, borne on a supporting cell which is an intercalary cell of cortical filaments. Gonimoblast filaments radiating horizontally as a basal layer of hyaline filaments with frequent fusions with gametophytic cells, and erect clusters of gonimoblast filaments (Fig. 1C) which produce chains of carposporangia, 8–12 μm in diameter, amongst a lax palisade of cortical filaments. Spermatangia (Fig. 1F) borne on outer cortical cells in chains of 2–6, each about 4 μm in diameter.

Tetrasporangia (Fig. 1D, G) developed in terminal cortical cells scattered between sterile cortical filaments, ovoid, 30–40 μm long and 15–20 μm in diameter, decussately divided.

Type from Flinders, Vic., on *Gracilaria furcellata* (= *G. ramulosa*), 2–5 m deep (*Kraft*, 23.xi.1976); holotype and isotypes in MELU, K6230.

Distribution: Whitford Beach, Perth, W. Aust., and from Portland to San Remo, Vic.; Orford, Tasmania.

Selected specimens: Whitford Beach, Perth, W. Aust., 6 m deep on *Gracilaria flagelliformis* (*Cook*, 20.viii.1979; AD, A50580). Portland, Vic., drift at Whalers Point on *G. ramulosa* (*Muir*, 17.i.1950; AD, A63231) and drift in harbour on *G. ramulosa* (*Womersley*, 14.iv.1994; AD, A63536 — "Marine Algae of southern Australia" No. 376). Queenscliff, Vic., drift on *G. ramulosa* (*Womersley*, 8.iv.1959; AD, A22851). San Remo, Vic., drift on *G. ramulosa* on back beach (*Sinkora* A2017, 27.xi.–5.xii.1974; AD, A62465). Orford, Tas., 4–5 m deep on *G. ramulosa* (*Kraft* 9271, 15.xii.1992; MELU).

Holmsella australis is a small but distinctive parasite, mainly on *Gracilaria ramulosa* on Victorian coasts but also known on *G. flagelliformis* near Perth, Western Australia. It is probably more widespread in southern Australia.

FAMILY GRACILARIACEAE Nägeli 1847: 240, 254

Thallus erect and usually several to many centimetres high, or decumbent, or parasitic and pustular, when erect radially or complanately branched, branches terete to flat, usually firm and drying cartilaginous, usually on solid substrates. *Structure* uniaxial but axis not apparent, pseudoparenchymatous with a small-celled cortex often with anticlinal cell rows, and a large-celled medulla of multinucleate cells with numerous secondary pit-connections; cell walls containing agar.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 2-celled, flanked by two or more sterile filaments on a multinucleate intercalary supporting cell. Fertilized carpogonium fusing with adjacent cells of sterile filaments and developing gonimoblast filaments directly, with large cells thereof forming secondary pit-connections and terminal chains or clusters of carposporangia; secondary fusions of gonimoblast cells with vegetative cells in the floor of the cystocarp occur, and traversing nutritive cells or filaments ("tubular nutritive cells" or "traversing cells") from the gonimoblast to the pericarp may occur. Cystocarps protruding; pericarp thick, originating schizogenously, ostiolate. Spermatangia superficial as cortical sori or in cortical depressions or pits.

Tetrasporangia scattered in the cortex or in nemathecia, cruciately divided.

A family of 6 or 7 genera (see Fredericq & Hommersand 1990b), with 2 parasitic genera and 4 or 5 erect, free living, genera. *Hydropuntia* (syn. *Polycavernosa*), recognised by Fredericq & Hommersand (1990b), is often included within *Gracilaria* [e.g. Abbott *et al.* (1991)].

KEY TO GENERA OF GRACILARIACEAE

1. Thallus usually terete (in some species compressed); cystocarps on all sides of thallus, cavity not completely filled with carposporophyte, traversing nutritive cells present or absent in cystocarp floor and pericarp, carposporangia in clusters or short chains; spermatangia in pits (conceptacles) or superficial on the cortex; tetrasporangia usually scattered in outer cortex 2
1. Thallus compressed (rarely subterete) to flat; cystocarps usually on or near the margins, cavity completely filled with carposporophyte, traversing nutritive cells absent, carposporangia in long chains; spermatangia in surface sori; tetrasporangia in nemathecia, between paraphyses 3

2. Cystocarps with traversing nutritive cells between the carposporophyte and pericarp; spermatangia in pits or conceptacles ..... GRACILARIA
2. Cystocarps without traversing nutritive cells; spermatangia superficial, cut off from outer cortical initials ..... GRACILARIOPSIS

3. Branching subdichotomous, branches linear, compressed (1–4 mm broad) or subterete, branch apices with a thickened cap; cystocarps with thick-walled sterile gonimoblast tissue ..... MELANTHALIA
3. Branching irregular, branches flat, varying in width (4–50 mm broad), branch apices without a thickened cap; cystocarps lacking thick-walled sterile gonimoblast tissue ..... CURDIEA

Genus GRACILARIA Greville 1830: liv, 121

Thallus erect or decumbent, usually much branched subdichotomously, laterally, secundly or irregularly, radially or complanately, branches terete to flattened; holdfast usually discoid, epilithic or in sandy mud or occasionally loose lying. *Structure* uniaxial but appearing multiaxial, pseudoparenchymatous with a small-celled cortex grading or changing abruptly to a large-celled medulla, cells usually with numerous pit-connections.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli monoecious or dioecious. Carpogonial branches 2-celled, borne on an inner cortical (supporting) cell which also bears two adjacent filaments, the fertilized carpogonium fusing with cells of these filaments to form a fusion cell producing a dense gonimoblast of ovoid to elongate cells with clusters or chains of terminal carposporangia; traversing nutritive cells or filaments from gonimoblast to upper and/or lower pericarp usually present, either as single elongate cells or involving also several, fused, inner stellate cells of the pericarp. Cystocarps prominent, sessile and hemispherical to globular and basally constricted, with a thick pericarp, ostiolate; in some species an inner pericarp occurs by cell proliferation at the base of the carposporophyte. Spermatangia formed in pits or cavities, cut off from basal cells or cells of branched filaments lining the cavities.

Tetrasporangia scattered in the outer (often slightly thickened) cortex, basally pit-connected, cruciately divided.

Suggested lectotype species: *G. compressa* (C. Agardh)Greville 1830: 125 [= *G. bursa-pastoris* (S. Gmelin)Silva 1952: 265] – see Steentoft, Irvine & Bird 1991: 663.

The previously accepted lectotype species of *Gracilaria, G. confervoides* (Stackhouse)Greville (1830: liv, 121), has been shown by Steentoft *et al.* (1991, p. 663) to be, on the basis of the type specimen, a species of *Gracilariopsis*. To obviate numerous name changes in an economically important genus, they suggest that *G. compressa* (C. Agardh)Greville should be considered the lectotype species. They also show that synonymy of *G. confervoides* with *G. verrucosa* (Hudson)Papenfuss (1950, p. 195) is incorrect, and Irvine & Steentoft (1995) propose rejection of the name *Fucus verrucosus*. There now appears no reason to record *G. verrucosa* from southern Australia, and this taxon is probably confined to European coasts.

Much of the confusion between *Gracilaria* and *Gracilariopsis* Dawson has been clarified by Fredericq & Hommersand (1989b) who show that the latter genus is characterised by superficial spermatangial sori, absence of traversing nutritive cells from the gonimoblast to the pericarp, and a fertile layer of carposporangia in relatively straight chains. Steentoft *et al.* (1995) clarify the relationships of the two terete species (*Gracilaria gracilis* and *Gracilariopsis longissima*) in Britain.

There is still considerable doubt concerning many species of *Gracilaria* [see papers in Abbott & Norris (1985), and Abbott (1988, 1992)], and further studies are needed on the species described below. Australian species were described by May (1948) before modern classification concepts developed, and all her specimens need re-interpretation. Some species have been monographed recently by Withell *et al.* (1994). Identifications (e.g. as *G. confervoides*) based on non-sexual collections (where the male is essential) are usually dubious, and as far as possible the collections cited below include male plants. There is also doubt as to identification of some plants from Victorian and Tasmanian coasts which have secund branching. These are mostly interpreted as secund forms of *G. ramulosa* since they are distinctly less robust with thinner branches than the N.S.W. *G. secundata*.

KEY TO SPECIES OF *GRACILARIA*

1. Thallus complanately branched, branches compressed, 2–4 (-5) mm broad ..... 1. *G. preissiana*
1. Thallus irregularly to subdichotomously or secundly branched, branches terete, mostly 0.5–2 (-3.5) mm in diameter 2

    2. Thallus 5–25 cm high, densely tufted, branching subdichotomous or somewhat secund, most branches of similar height ..... 2. *G. ramulosa*
    2. Thallus 10–60 cm high, branching irregular or secund, dense to relatively sparse with long main branches and laterals of varying length 3

3. Branches with markedly secund laterals, mostly relatively short ..... 3. *G. secundata*
3. Branching irregular, with long laterals 4

4. Thallus slender, apical cell visible, branches 0.4–1 mm in diameter, cortex not thickened on lower branches; spermatangial pits shallow with basal spermatangia ("*textorii*" type) and with clavate outer cortical cells surrounding them ..... 4. *G. chilensis*
4. Thallus robust, apical cell not visible, most branches (1-) 2–3.5 mm in diameter, cortex thickened or not near base; spermatangial pits ovoid ("*verrucosa*" type) to deeply sunken ("*polycavernosa*" type) 5

5. Thallus branches 1–3.5 mm in diameter, thicker near the base where the cortex is thickened; medulla (15-) 20–30 cells broad ..... 5. *G. flagelliformis*
5. Thallus branches 1.3–1.8 mm in diameter from base to upper parts, cortex not thickened below; medulla 4–8 cells across, inner cells 150–400 µm in diameter ..... 6. *G.* sp.

1. **Gracilaria preissiana** (Sonder)Womersley *in* Min-Thein & Womersley 1976: 109. Huisman & Walker 1990: 417. Lewis 1984: 26. Withell *et al.* 1994: 294, figs 11–13.
Rhodomenia preissiana Sonder 1845: 56; 1848: 191. J. Agardh 1852: 622.
Rhodophyllis preissiana (Sonder)Kützing 1849: 786. Sonder 1871: 62(?).
Calliblepharis preissiana (Sonder)Harvey 1859a: pl. 106. Sonder 1881: 22.
Calliblepharis pannosa Harvey 1855a: 550. J. Agardh 1876: 434.
Gracilaria pannosa (Harvey)J. Agardh 1885: 62. De Toni 1900b: 450. Lewis 1984: 26. May 1948: 44, pl. 10 fig. 1; 1965: 392.

FIG. 2

Thallus (Fig. 2A) medium to dark red-brown, fading to grey-red, 3–10 (-24) cm high, irregularly and profusely but essentially complanately branched, often proliferous from the margins, lower branches flat, 2–4 (-5) mm broad and 300–700 µm thick, upper branches compressed, 200–500 µm broad and 200–300 µm thick. Holdfast discoid or divided, 2–5 mm across, with one to several fronds from short stipes; epilithic or on calcareous substrates. *Structure* apparently multiaxial, pseudoparenchymatous throughout (Fig. 2B), with a cortex 2–3 cells thick, outer cells 5–8 (-14) µm in diameter and L/D 1–1.5, changing fairly abruptly to the medulla 4–8 cells broad, cells subspherical to ovoid, 50–180 µm in diameter, walls 4–8 µm thick; refractive cells (gland like) often present in the cortex. Rhodoplasts discoid, in chains in medullary cells.

Reproduction. Gametangial thalli dioecious or monoecious. Carpogonial branches 2-celled. Carposporophytes (Fig. 2D) with a basal mass of gonimoblast cells and upper gonimoblast filaments producing short chains of ovoid carposporangia maturing terminally, 12–22 µm in diameter, with occasional traversing nutritive filaments; such filaments fuse with several pericarp cells forming elongate, darkly staining, fused filaments (Fig. 2D, arrow) with lateral projections derived from lateral pit-connections, found mainly on the sides and base of the carposporophyte. Cystocarps (Fig. 2C) ovoid, 1–2 mm across, slightly basally constricted; pericarp massive, with anticlinal filaments of cells 10–20 µm across with numerous lateral pit-connections and with a prominent ostiole; inner pericarp absent. Spermatangia in deep lobed pits (Fig. 2E) 115–200 µm broad and 100–250 µm deep, with a small opening.

Tetrasporangia sparsely scattered in the cortex, basally pit-connected to inner cortical cells, ovoid, 30–45 µm long and 15–22 (-30) µm in diameter, cruciately divided.

Type from "Occid. Nov. Holl." (*Preiss*); lectotype (Womersley *in* Min-Thein & Womersley 1976, p. 109) with Sonder's drawings in MEL, 45104 (with fragments under 44988).

Distribution: Houtman Abrolhos and Champion Bay, W. Aust., to Wittelbee Point, S. Aust. Also recorded from Cape York, Qld, by Sonder (1871).

Selected specimens: Pelsaert Group, Houtman Abrolhos, 20–24 m deep (*Kraft* 8608 & *Huisman*, 14.x.1990; MELU, 40691). Champion Bay, W. Aust. (Alg. Muell.; MEL, 44990). Point Leander reef, Port Denison, W. Aust., upper sublittoral pool sides (*Kraft*, 14.xii.1971; AD, A41233). Point Phillip, Rottnest I., W. Aust., 7 m deep (*Borowitzka*, 6.xii.1984; AD, A56649). Garden I., W. Aust., upper sublittoral on reef (*Mitchell*, 21.ix.1966; AD, A31207). Cowaramup Bay, W. Aust., 2–3 m deep (*Clarke & Engler*, 1.ix.1979; AD, A50649). Scott Bay (6 km W of Fowler Bay), S. Aust., shaded pools

(*Womersley*, 27.i.1951; AD, A13843). Wittelbee Point (near Ceduna), S. Aust., upper sublittoral (*Womersley*, 22.i.1951; AD, A13605 and A15150).

G. preissiana is a western species reaching to Wittelbee Point, near Ceduna, in South Australia, where it was common just below low tide level.

The lectotype in TCD of *G. pannosa*, from King George Sound, W. Aust. (*Harvey*, Trav. Set 98) is identical with *R. preissiana* Sonder.

Sonder's (1871) record of *Rhodophyllis preissiana* from Cape York, Qld (*Daemel*) is in MEL (45106) and is doubtfully *G. preissiana*.

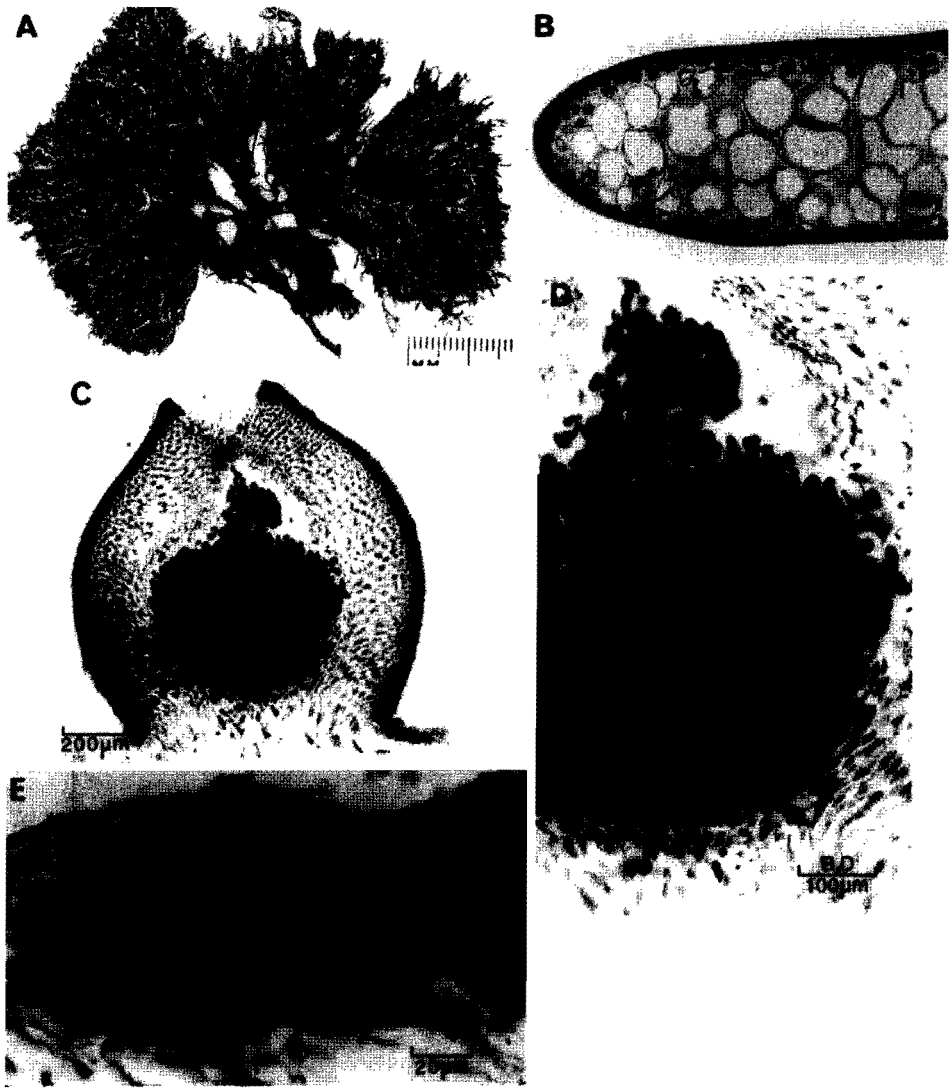


Fig. 2. *Gracilaria preissiana* (**A**, AD, A13605; **B**, AD, A13843; **C–E**, AD, A41233). **A.** Habit. **B.** Transverse section of thallus. **C.** Section of cystocarp. **D.** Section of carposporophyte with traversing nutritive cells (arrow). **E.** Transverse section of male thallus with elongate spermatangial pits.

2. **Gracilaria ramulosa** J. Agardh 1876: 417. De Toni 1900b: 439. Sonder 1881: 22.
Gracilaria furcellata Harvey 1863: pl. 286. J. Agardh 1876: 419; 1901: 60. Chapman 1979: 301, pl. 109. De Toni 1900b: 441. May 1948: 53, fig. 9, pl. 14 fig. 2; 1965: 392. Sonder 1881: 22. Tisdall 1898: 508. Wilson 1892: 176. Womersley 1950: 169; 1966: 147.
NON *G. furcellata* (Montagne)Zanardini 1858: 266 [= *Sarconema filiforme* (Sonder)Kylin].
Gracilaria furcellata f. *ramulosa* (J. Agardh)May 1948: 56, pl. 14 fig. 2.
Gracilaria sp. Harvey 1855a: 551; 1863, synop.: xxxiv.
Gracilaria cliftonii Withell, Millar & Kraft 1994: 285, figs 4, 5.
Gracilaria secundata sensu Womersley 1966: 147.

PLATE 1, fig. 1; FIG. 3

Thallus (Fig. 3A) medium to dark red-brown, fading to yellow-red, cartilaginous, usually densely tufted, 5–25 cm high, mostly subdichotomously branched and often more or less of even height, sometimes with longer, laterally (slightly secundly) branched, extended branches, more rarely with occasional to plentiful short lateral branches; branch apices sometimes shortly multifid (following grazing?). Branches terete to slightly compressed (when dry), 400–700 µm in diameter near apices, (600-) 800–1300 µm in mid to lower parts of most plants, becoming thickened and 1–2 mm in diameter near bases of single axis plants (second year?). Holdfast discoid, with one to (usually) several fronds, 4–12 mm across; epilithic. *Structure* pseudoparenchymatous (Fig. 3E), grading in cell size from the outer cortex to the large inner medullary cells, cortex 2–4 cells thick, outer cells rounded to angular in surface view and 5–12 µm across, L/D 1–1.5 in section of thallus, in young parts with elongate-ovoid to conical hair basal cells 10–15 µm in diameter; medulla 8–15 (-30) cells across, inner medullary cells ovoid, usually 100–200 µm in diameter, with numerous prominent secondary pit-connections; walls of inner cells 8–20 (-30) µm thick. Base of single axes thickened, with the outer cortical cells becoming meristematic to form long, tightly packed, filaments of small cells. Rhodoplasts discoid, sometimes in chains or ribbon like in medullary cells.

Reproduction. Gametangial thalli usually dioecious. Carpogonial branches (Fig. 3B) 2-celled, borne on an inner cortical (supporting) cell bearing also two 2-celled filaments. Carposporophytes (Fig. 3C) with a small rounded to lobed basal fusion cell, a dense pseudoparenchymatous mass of large-celled gonimoblast filaments (cells ovoid, 20–50 µm in diameter, L/D 1.5–3) which when well developed may have 2–4 deep lobes, bearing an upper zone of slender, small-celled, filaments producing terminal, subspherical to ovoid, carposporangia 15–35 µm in diameter, subterminal cells later maturing as carposporangia; traversing nutritive cells rare to common, mainly at the base of the carposporophyte where they may be single celled or involve fusion of several pericarp cells, often also from the upper gonimoblast to the pericarp. Cystocarps sessile and hemispherical when young, becoming subspherical and basally constricted, 1–2 mm in diameter; pericarp (Fig. 3C) massive, 200–400 µm thick with anticlinal rows of 10–15 (-20) cells with lateral pit-connections (becoming stellate), ostiolate and sometimes beaked; a slight inner pericarp of small cells usually present. Spermatangia (Fig. 3D) in ovoid pits 22–60 µm in diameter, cut off from lining cells, 2–5 µm in diameter.

Tetrasporangia (Fig. 3E) scattered, usually densely, in the cortex, basally pit-connected 2–5 cells deep, ovoid, 30–60 µm long and 20–50 µm in diameter, cruciately or decussately divided.

Type from King George Sound, W. Aust. (*Harvey*, Alg. Aust. Exsicc. 324B); holotype in Herb. Agardh, LD, 29286; isotype in MEL, 629924 (excl. right hand specimen).

Distribution: Cottesloe, W. Aust., to Walkerville, Vic., and around Tasmania.

Selected specimens: Cottesloe, W. Aust., drift (*Smith*, April 1945; AD, A2136). Point Peron, W. Aust., reef pools (*Mitchell*, 22.ix.1966; AD, A30743). Ward I., S. Aust., 25–30 m deep (*Shepherd*, 31.iii.1982; AD, A53125). Elliston, S. Aust., 10–12 m deep in bay (*Shepherd*, 23.x.1969; AD, A34943). Kellidie Bay, Coffin Bay, S. Aust., 3–4 m deep (*Womersley*, 12.i.1987; AD, A57366). Wanna, S. Aust., upper sublittoral pools (*Ricci*, 13.ii.1994; AD, A63369). O'Sullivan Beach, S. Aust.,

upper sublittoral (*Clarke & Engler*, 21.xi.1978; AD, A54854). Hallett Cove–Port Stanvac, S. Aust., lower eulittoral pool (*Clarke*, 10.i.1978; AD, A53939). Port Noarlunga, S. Aust., 3–5 m deep (*Owen*, 2.xi.1970; AD, A37421) and 24 m deep, 5 km offshore (*Ottaway*, 3.ii.1981; AD, A52089). Port Elliot, S. Aust., drift (*Womersley*, 10.viii.1957; AD, A21126). Vivonne Bay, Kangaroo I., S. Aust., 1.5–6 m deep (*Mitchell*, 21.viii.1963; AD, A26962). Pennington Bay, Kangaroo I., S. Aust., low eulittoral pool (*Womersley*, 23.viii.1950; AD, A13392). Ballast Head, Kangaroo I., S. Aust., lower eulittoral (*Womersley*, 31.x.1947; AD, A6100). Robe, S. Aust., upper sublittoral pools W of jetty (*Womersley*, 17.ix.1993; AD, A63024 — "Marine Algae of southern Australia" No. 374). Cape Lannes, S. Aust., upper sublittoral sandy pools (*Womersley*, 17.ix.1993; AD, A63002). Dutton Bay, Portland, Vic., drift (*Womersley*, 13.iv.1959; AD, A22689). Portarlington, Port Phillip Bay, Vic., just below low tide

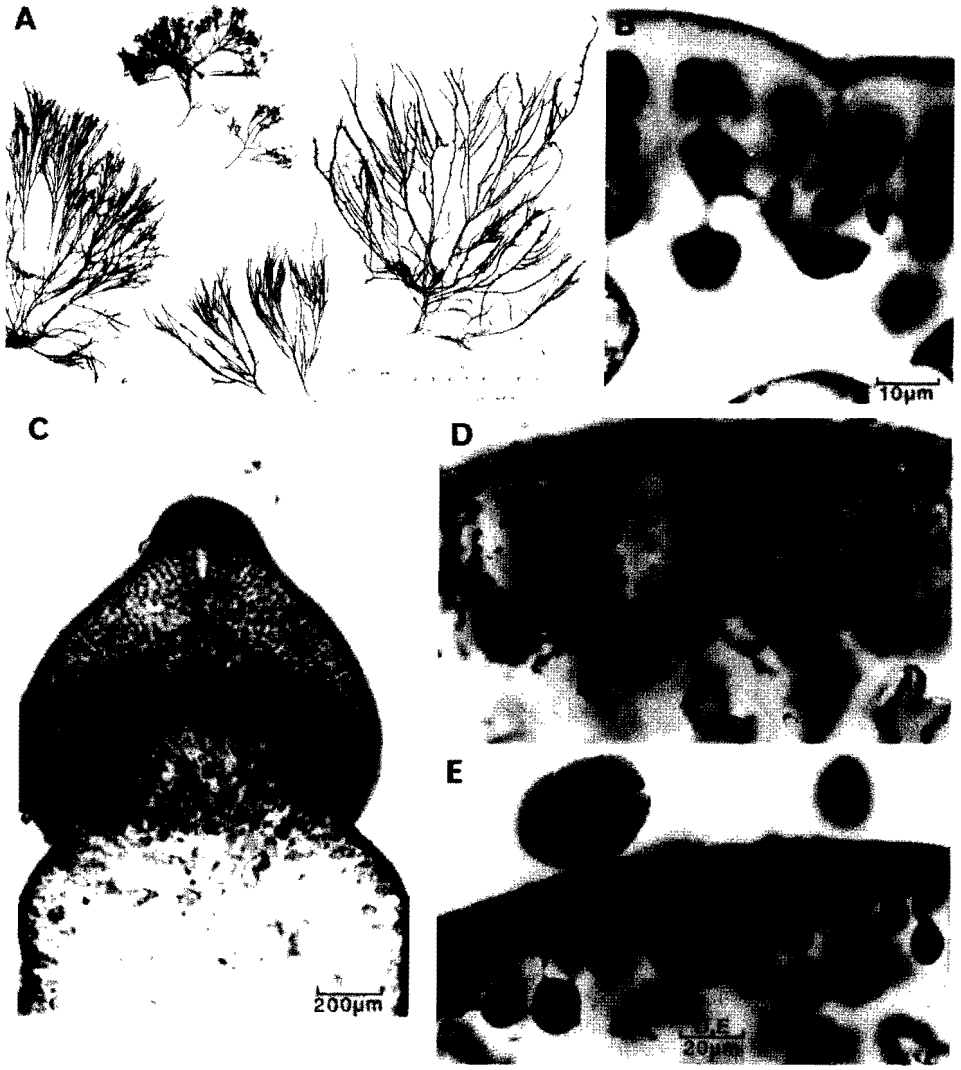


Fig. 3. *Gracilaria ramulosa* (**A–C, E,** AD, A63024; **D,** AD, A63002). **A.** Habit. **B.** Transverse section of thallus with a 2-celled carpogonial branch and adjacent 2-celled filaments on the supporting cell. **C.** Section of a near-mature cystocarp. **D.** Transverse section of male thallus with spermatangial pits. **E.** Transverse section of thallus with tetrasporangia.

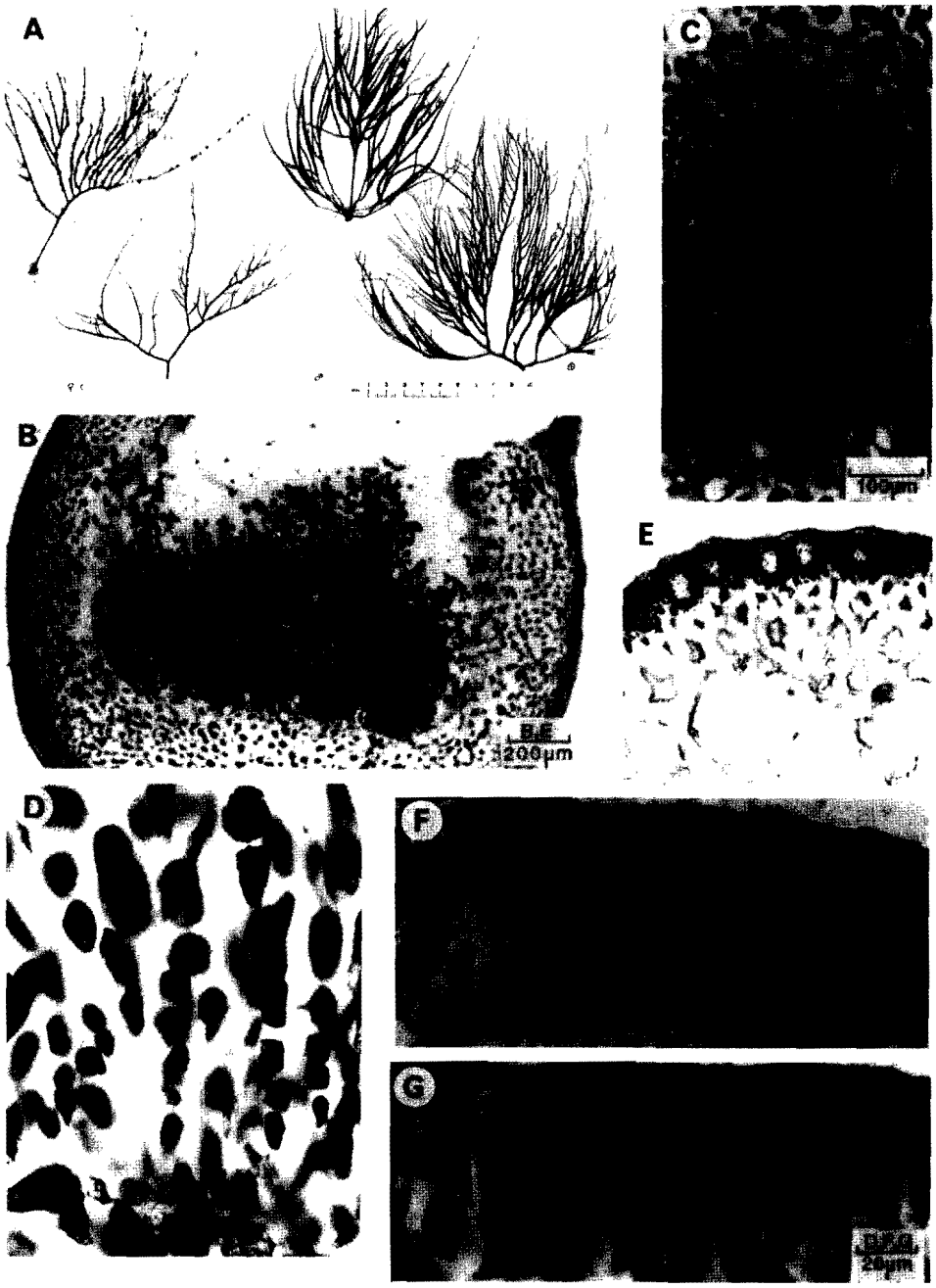


Fig. 4. *Gracilaria secundata* (AD, A64488). **A.** Habit. **B.** Section of cystocarp. **C.** Section of carposporophyte with slight basal inner pericarp and upper chains of carposporangia. **D.** Chains of carposporangia. **E.** Transverse section of male branch with spermatangial pits. **F.** Section with spermatangial pits. **G.** Transverse section of cortex with tetrasporangia.

(*Sinkora* A1476, 1477, 29.xi.1971; AD, A43117, A43120). Queenscliff, Vic., drift (*Norris*, 21.i.1963; AD, A27483). Red Rocks, Phillip I., Vic., 4–6 m deep (*Riddle*, 12.ii.1990; AD, A60165). Walkerville, Vic., just below low tide level (*Sinkora* A2141, 2.iii.1975; AD, A48306).Guyton Point, Robbins I., Tas., upper sublittoral (*Wollaston & Mitchell*, 23.ii.1964; AD, A27617). Greens Beach, N Tas., rock pool (*Wollaston & Mitchell*, 4.iii.1964; AD, A27573). Georgetown, Tas., upper sublittoral (*Womersley*, 29.i.1949; AD, A10294). Bluestone Bay, Freycinet Pen., Tas., 10–13 m deep (*Brown, McGeary & Womersley*, 4.xi.1982; AD, A56260). Crayfish Point, Taroona, Tas., 5 m deep (*Brown*, 24.x.1982; AD, A55779).

Gracilaria ramulosa is based on a specimen of Harvey's Alg. Aust. Exsicc. 324B, doubtfully referred to *Gracilaria* by Harvey and named by J. Agardh after the numerous lateral ramuli. Most specimens form densely branched tufts with an even height and vary greatly in number of lateral ramuli; the type specimen has a relatively large number of lateral ramuli but is otherwise not distinct from the common species previously known as *G. furcellata* Harvey. There appears to be only the one species with this habit on the coast at King George Sound.

Within one or adjacent populations, plants may be flat-topped, with all the subdichotomous branches reaching an even height, or may have occasional longer, partly secund branches within the tuft; structurally and reproductively such plants appear identical, the carposporophytes being uniform in structure. Plants from Victoria and Tasmania appear more variable in habit with a greater tendency to secund forms. They do not, however, have the robust and thick branches of *G. secundata*.

The type of *G. furcellata* Harvey was from Fremantle, W. Aust. (Alg. Aust. Exsicc. 323A), and the lectotype (see Withell *et al.* 1994, p. 285) is in Herb. Harvey, TCD, with an isolectotype in MEL, 629923.

Renaming of this species as *G. cliftonii* by Withell *et al.* (1994, p. 285) was unnecessary in view of the variation in habit which encompasses *G. ramulosa* J. Agardh. Possible relationships with the earlier *G. dura* (C. Agardh)J. Agardh, as pointed out by Withell *et al.*, need further investigation.

3. **Gracilaria secundata** Harvey 1863, synop.: xxxv. J. Agardh 1876: 418; 1901: 72. Chapman 1929: 297, pl. 104. De Toni 1900b: 440. May 1948: 46, fig. 8, pl. 11; 1965: 393. Millar & Kraft 1993: 28. Nelson 1987: 88, figs 1–5. Withell *et al.* 1994: 293, 348.

FIG. 4

Thallus (Fig. 4A) medium to dark red, upper branches often fading to yellow in high light situations, cartilaginous, loosely to densely tufted, 10–30 (-50) cm high, with few to numerous secundly and irregularly branched axes of variable length. Branches terete, secund branches basally slightly constricted, larger branches not or slightly constricted, 1.5–2 mm in diameter below, lesser branchlets 0.4–0.8 mm in diameter, apices rounded-conical. Holdfast discoid, relatively thin, 2–6 (-10) mm across, with one to several axes. *Structure* pseudoparenchymatous, grading evenly (Fig. 4G) in cell size from the outer cortex to the medulla, cortex 3–5 cells thick with 2–3 small, ovoid, outer cells 5–6 (-8) µm in diameter and L/D (1.5-) 2–3 (-6), with frequent ovoid hair basal cells 10–20 µm in diameter; medulla 5–10 (-15) cells across, cells ovoid and 150–350 µm in diameter with numerous prominent secondary pit-connections; walls of inner cells 15–25 (-40) µm thick. Rhodoplasts discoid to laminate.

Reproduction. Gametangial thalli dioecious. Carpogonial branches not observed. Carposporophytes (Fig. 4B, C) with a small basal fusion cell, a dense pseudoparenchymatous mass (sometimes lobed) of gonimoblast filaments (lower cells elongate-ovoid and 40–90 µm in diameter, upper cells elongate and 10–15 µm in diameter) bearing a sharply defined outer zone of chains (Fig. 4D) of ovoid to clavate carposporangia 10–18 µm in diameter; traversing nutritive cells slender, occasional to frequent. Cystocarps prominent, scattered along branches and often clustered, sessile, hemispherical or slightly to distinctly basally constricted, 1–3 mm in diameter; pericarp 200–300 µm thick, with anticlinal rows of 8–15 (-20) cells, inner cells stellate, ostiolate; inner pericarp absent to slight. Spermatangia

(Fig. 4E, F) in subspherical to ovoid pits 16–25 μm in diameter, cut off from lining cells, ovoid and 3–4 μm in diameter.

Tetrasporangia (Fig. 4G) scattered in the slightly thickened cortex, basally pit-connected to inner cortical cells, ovoid, 35–90 μm long and 20–50 μm in diameter, decussately divided.

Type from Kiama, N.S.W. (*Harvey*); holotype in Herb. Harvey, TCD. Syntypes (from Newcastle, N.S.W.) in Alg. Aust. Exsicc. 325.

Distribution: Bales Beach, Kangaroo I., S. Aust., to SE Tasmania and Newcastle, N.S.W.

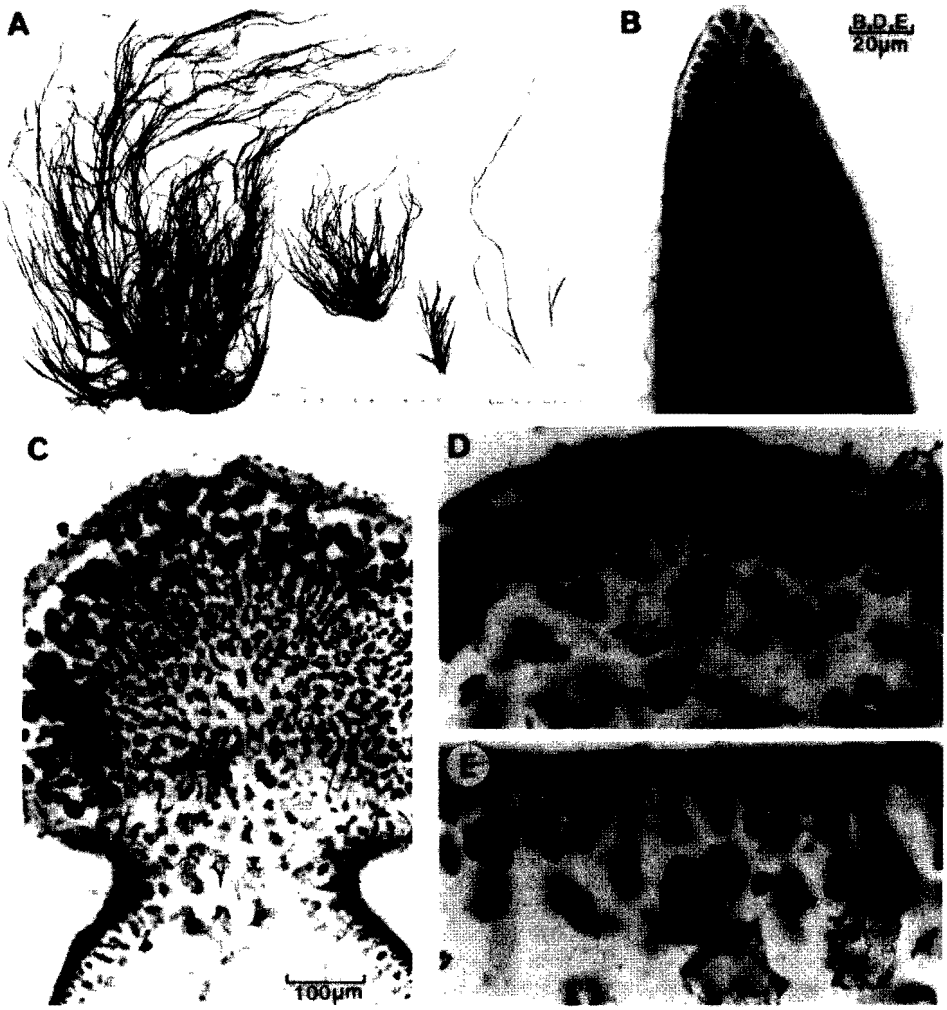


Fig. 5. *Gracilaria chilensis* (**A–C, E,** AD, A63419; **D,** AD, A63232). **A.** Habit, male plants on right. **B.** Apex of a branch. **C.** Section of a cystocarp. **D.** Transverse section of a male thallus with shallow spermatangial pits. **E.** Transverse section with displaced tetrasporangia.

Selected specimens: Bales Beach, S coast Kangaroo I., S. Aust., in uppermost sublittoral sandy inshore pools (*Womersley*, 25.x.1995; AD, A64488). B.P. Refinery Pier, Westernport Bay, Vic., 1 m deep (*Millar*, 22.iii.1979; MELU, 23879). Ninepin Point, Tas., 10–13 m deep (*Sanderson & Kraft*, 22.xii.1992; MELU, 40687). Coalcliff, N.S.W., at low tide level (*Harada*, 28.xi.1976; AD, A52464). N. Bondi, N.S.W., upper sublittoral and pools (*Womersley*, 27.xii.1962; AD, A26368). Tamarama, N.S.W., upper sublittoral (*Madgwick*, April 1969; AD, A35086).

Harvey (1863, synop.: xxxv) originally recorded *G. secundata* only from Kiama, N.S.W. Most of his Alg. Aust. Exsicc. 325 sheets however appear to be from Newcastle, north of Sydney. May (1948, p. 46) recorded her failure to locate this species at Kiama, though finding it at Newcastle.

G. secundata appears to be of sporadic occurrence on southern Australian coasts, though common at Bales Beach, Kangaroo I., in October 1995, where plants in the field were readily distinguishable from typical *G. ramulosa*. The former is a robust species with frequent strongly secund branches on each plant. It is, however, closely related to *G. ramulosa*, which in some plants does have occasional secund branches. These species differ in habit (*G. ramulosa* having branches of even height), in thickness of main branches (*G. secundata* usually broader), in size of inner medullary cells, in apparent lack of secondary cortex in *G. secundata*, and in the carposporophyte becoming deeply lobed in *G. ramulosa*. Further study of authentic *G. secundata* from the N.S.W. coast is, however, clearly needed since N.S.W. specimens are more robust than those from southern Australia.

4. **Gracilaria chilensis** Bird, McLachlan & Oliveira 1986: 2928, figs 2–13. Adams 1994: 178, pl. 56 upper centre. Bird *et al.* 1990: 375, figs 1–5.
Gracilaria sordida Nelson 1987: 90, figs 6–9.

FIG. 5

Thallus (Fig. 5A) dark red-brown, 10–60 cm high, irregularly branched with long main branches and numerous laterals of varying length, apices acute, branches terete, 0.4–0.8 (-1) mm in diameter for most of their length, 0.2–0.4 mm in diameter close to the apices, not basally constricted. Holdfast discoid, 2–3 mm across, with one to a few fronds; epilithic or loose lying. *Structure* uniaxial, with a slightly protruding apical cell (Fig. 5B), soon becoming pseudoparenchymatous, grading in cell size from the outer cortex to inner medullary cells, cortex 2–3 cells thick, outer cells ovoid (often slightly palisade like) and 4–7 µm across in surface view, L/D 1.5–2.5 in section, with larger hair basal cells (15–20 µm long and 6–8 µm in diameter); medulla 6–12 cells across, inner medullary cells ovoid, 40–100 (-180) µm in diameter, developing thick walls (10–30 µm) and numerous secondary pit-connections; secondary thickening of lower branches not present. Rhodoplasts discoid.

Reproduction. Gametangial thalli dioecious. Carpogonial branches unreported. Carposporophytes (Fig. 5C) with a small basal fusion cell and dense pseudoparenchymatous gonimoblast cells with numerous pit-connections, producing chains of carposporangia, when mature ovoid to clavate and 16–30 µm in diameter; traversing nutritive cells usually present between lower gonimoblast cells and basal tissue of the cystocarp. Cystocarps scattered, sessile, hemispherical, conical to globular and basally constricted, 500–800 µm in diameter; pericarp 80–100 µm thick, with anticlinal rows of 6–9 cells, ostiolate; inner pericarp absent. Male plants usually small (5–10 cm high); spermatangia (Fig. 5D) formed at the base of relatively shallow pits, 12–20 µm across, surrounded by clavate cells 15–20 µm high and 4–6 µm in diameter; spermatangia 2–3 µm across.

Tetrasporangia (Fig. 5E) scattered in the cortex, basally pit-connected, ovoid, 40–55 µm long and 25–40 µm in diameter, cruciately to almost tetrahedrally divided.

Type from Penco, Bahía Concepción, Chile (*Romo*, 1.ix.1982); holotype and isotypes in NRCC, 9131(a) and (b).

Distribution: Chile, from Bahía Herradura to Río Maullin. New Zealand.

In southern Australia, from Cowell, Eyre Pen., S. Aust., to Hobsons Bay, Vic., and probably Port Arthur, Tasmania (male specimens not seen).

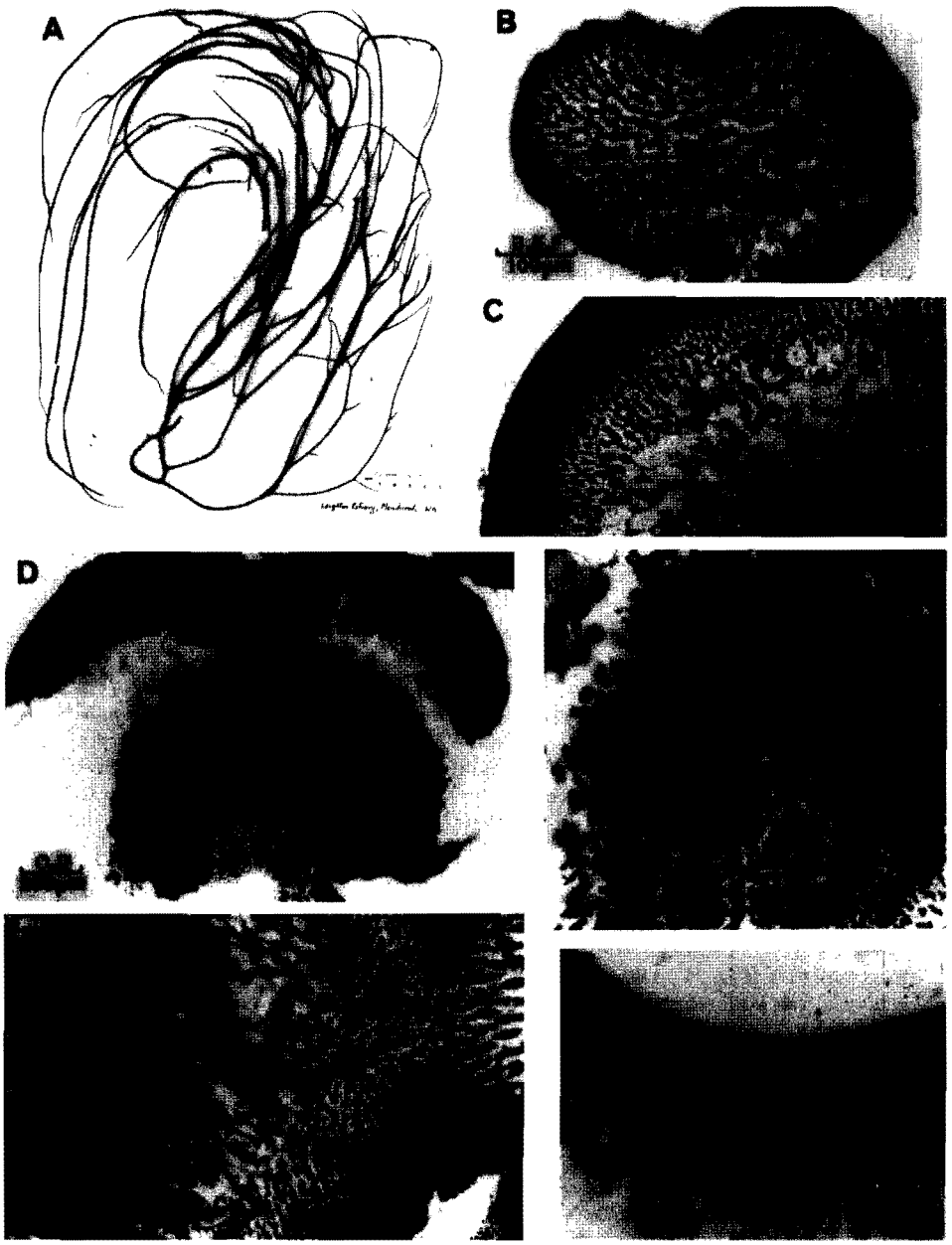


Fig. 6. *Gracilaria flagelliformis* (**A, B,** AD, A22113; **C–E,** AD, A14146; **F,** AD, A50580; **G,** AD, A59736). **A.** Habit. **B.** Transverse section of young branch. **C.** Transverse section of old branch with secondary cortical thickening. **D.** Section of a (broken) cystocarp. **E.** Section of a carposporophyte with carposporangia on left and a small fusion cell on lower right. **F.** Section near base of a cystocarp with traversing nutritive cells from carposporophyte to pericarp. **G.** Section of thallus with young tetrasporangia.

Selected specimens: Cowell, S. Aust., floating in Salt Creek (*Hone & Clark*, 24.viii.1993; AD, A62991). Port Wakefield, S. Aust., mid eulittoral pools in mangroves (*Womersley*, 26.iii.1950; AD, A13017). Onkaparinga R. estuary, S. Aust., about 40 cm deep just within mouth (*Inns & Thomas*, 13.viii.1973; AD, A43893 and *Womersley*, 12.xii.1993; AD, A63232). Beacon 19 Boat Ramp, Sir Richard Pen., The Coorong, S. Aust., drift (*Womersley*, 14.ii.1994; AD, A63338). American River inlet, Kangaroo I., S. Aust., on tidal flats (*Womersley*, 1.ii.1946; AD, A3153). Glenelg R. Est., (Nelson), Vic., near low water just inside mouth (*Womersley*, 14.iv.1994; AD, A63419 —"Marine Algae of southern Australia" No. 377). Hobsons Bay, Port Phillip, Vic., 0–0.5 m deep at Power Station outfall (*Watson*, 1.v.1972; AD, A42342). Crawfish Rock, Westernport Bay, Vic., 6 m deep (*Watson*, 28.v.1974; AD, A45421). Long Bay, Port Arthur, Tas., littoral sand-mud bank (*Cribb* 115.1, 22.i.1951; AD, A16195).

G. chilensis appears to be largely confined to river mouths or estuaries, as in Chile and New Zealand. It is a slender species with long main branches and laterals of irregular lengths, with a single apical cell usually visible in the acute branch tips. It is distinguished in particular by the spermatangial pits (of the "*textorii*" type) with relatively long clavate cells surrounding them and spermatangia cut off from cells in the relatively flat base.

Identity of the Australian material with the Chilean species has been checked by Dr Carolyn Bird (pers. comm.).

5. **Gracilaria flagelliformis** (Sonder)Womersley, *comb. nov.*

Polyides flagelliformis Sonder 1845: 55.

Gigartina flagelliformis (Sonder)Sonder 1848: 176. J. Agardh 1851: 283. De Toni 1897: 227. Kützing 1849: 751; 1869: 7, pl. 18c, d.

Gracilaria harveyana J. Agardh 1885: 59; 1901: 65. De Toni 1900b: 441; 1924: 257. May 1948: 56, pl. 15 fig. 1; 1965: 393. Withell *et al.* 1994: 291, figs. 9, 10.

Gracilaria paradoxa J. Agardh 1901: 67. De Toni 1924: 257. May 1948: 59.

FIG. 6

Thallus (Fig. 6A) dark red-brown, 20–60 cm high, irregularly laterally branched at intervals of 1–6 cm below, upper parts often unbranched for many centimetres, branches terete, 0.5–1 mm in diameter above, usually markedly thicker (2–3.5 mm in diameter) near the base where the cortex is thickened. Holdfast discoid, 2–6 mm across, with one to several stipes; epilithic. *Structure* appearing multiaxial, pseudoparenchymatous (Fig. 6B, C) throughout, with an even gradation over many cells from small outer cortical cells 4–6 (-8) µm in diameter and L/D (1-) 2–4, arranged in anticlinal rows which extend to many cells long in older basal parts (Fig. 6C), through radially elongate cells (L/D 2–4) of the inner cortex and outer medulla, to the inner medulla of large and small cells intermixed, the larger cells ovoid, 50–120 (-160) µm in diameter, with very numerous secondary pit-connections and walls becoming 10–20 µm thick; medulla (15-) 20–30 cells broad. Rhodoplasts discoid.

Reproduction. Gametangial thalli dioecious. Carpogonial branches not observed. Carposporophytes (Fig. 6D) with a basal mass of gonimoblast cells and probably a small basal fusion cell, and upper gonimoblast filaments producing short chains of ovoid carposporangia (Fig. 6E) maturing terminally, 15–25 µm in diameter, with traversing nutritive filaments (Fig. 6F). Cystocarps ovoid, 1–1.6 mm across, slightly basally constricted; pericarp massive, with anticlinal chains of cells mostly 10–25 µm across with prominent lateral secondary pit-connections, and with an ostiole lined with chains of short cells cut off from pericarp cells; inner pericarp prominent. Spermatangia in deep pits, some becoming compound, 40–150 µm broad and up to 175 µm deep (Withell *et al.* 1994, p. 292, fig. 9C, D).

Tetrasporangia (Fig. 6G) in surface sori around the branches, in a slightly thickened cortex, basally pit-connected to mid cortical cells, elongate-ovoid, 30–55 (-70) µm long and 12–25 (-40) µm in diameter, cruciately divided.

Type from "Occid. Nov. Holl." (*Preiss*); holotype in MEL, 652097.

Distribution: Geraldton to Geographe Bay, W. Aust. (doubtfully further south).

Selected specimens: Lancelin, W. Aust., 14 m deep on "2 mile reef" (AIMS-NCI, Q66C 2733-M, 18.iii.1989; AD, A59736). Yanchep, W. Aust., drift (*Kraft* 8524, 20.ix.1990; MELU, 40688). Ocean

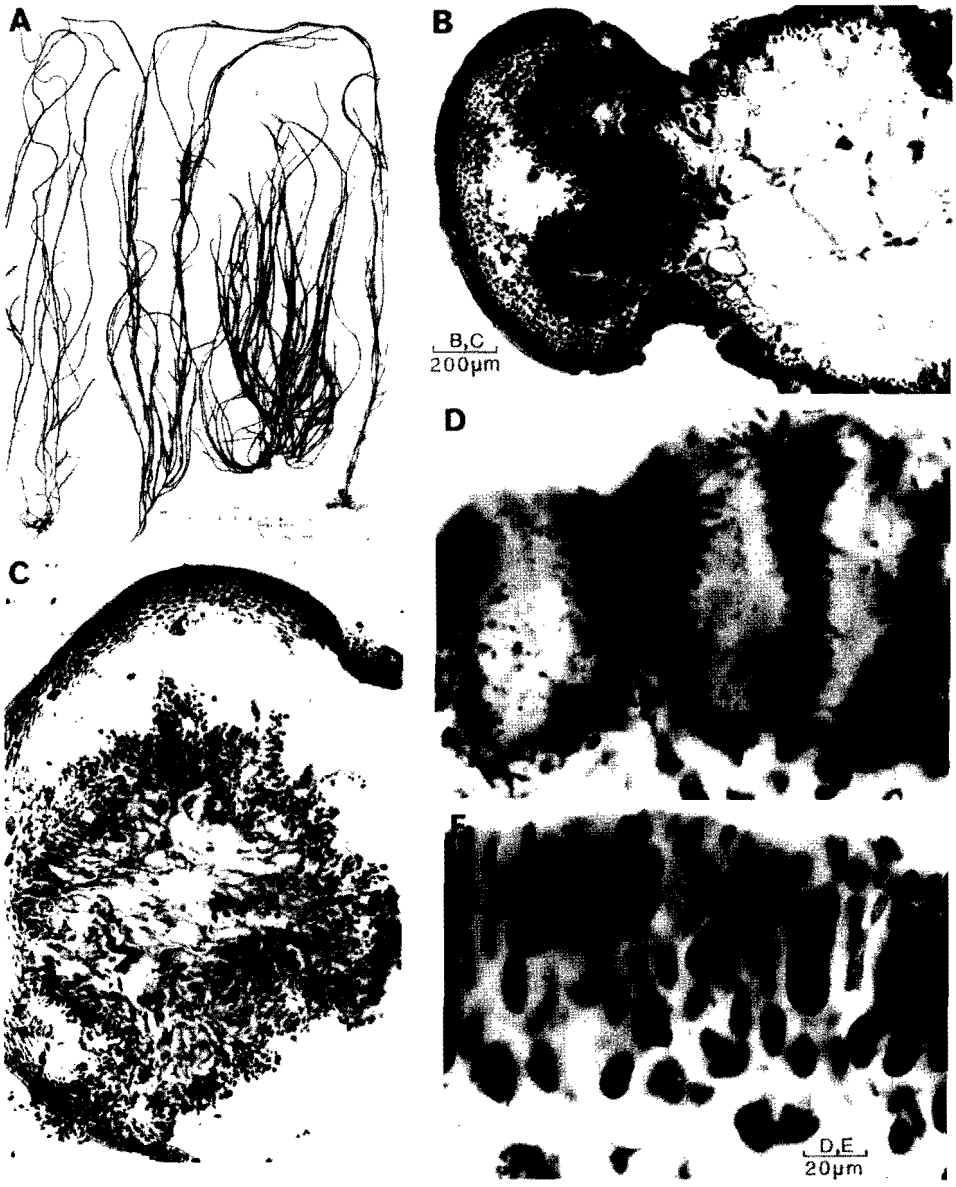


Fig. 7. *Gracilaria* sp. (AD, A62811). **A.** Habit. **B.** Transverse section of monoecious thallus with a cystocarp (left) and spermatangial pits (right). **C.** Section of a cystocarp. **D.** Section of male thallus with deep spermatangial pits. **E.** Section of tetrasporangial thallus.

Reef Marina, Perth, W. Aust., 6 m deep (*O'Brien & Millar*, 9.xii.1980; MELU, 24325). Whitford Beach, Perth, W. Aust., 6 m deep (*Cook* CS14, 20.viii.1979; AD, A50580). Leighton Estuary, Mandurah, W. Aust., drift (*Wollaston*, 4.ii.1957; AD, A22113). Capel Beach, W. Aust., on rocks below low water (*Royce* 361, 17.ix.1949; AD, A14146). West Beach, Bunbury, W. Aust., upper sublittoral (*Wollaston*, 6.ii.1957; AD, A23971). Geographe Bay, W. Aust. (Feb. 1880; MEL, 501401–501403).

The above description is based on dried herbarium specimens in AD, which indicate that *G. flagelliformis* is distinctive in form, in having thick lower branches with an expanding cortex and in the relatively dense sori of tetrasporangia. Further studies on good liquid preserved material are needed.

The type of *G. flagelliformis* in MEL is accompanied by Sonder's drawings of sections with tetrasporangia, showing the thick cortex; Kützing's pl. 18 fig. c is a near mirror image of the left of three pieces. Both *G. harveyana* J. Agardh and *G. paradoxa* J. Agardh appear to be based on Harvey's ms name of *Chondria paradoxa* given to Clifton specimens from Swan R., W. Aust. Apparently J. Agardh first gave it the name *G. harveyana* and later reverted to Harvey's name *paradoxa*. The same type (LD, 29255) applies to both names in Herb. Agardh.

Polyides flagelliformis Sonder 1845 is the earliest valid name for this species, which is here transferred to *Gracilaria*. However, there are two previous but invalid mentions of the name *Gracilaria flagelliformis* Suhr mscr in J. Agardh (1852, p. 588) as a synonym of *G. tuberculosa*, and of *G. flagelliformis* J. Agardh (nomen) in Mueller (1874, p. 209), a species which was validly published as *G. flagellifera* J. Agardh (1876, p. 412) (Dr Paul Silva, pers. comm.).

G. flagelliformis may not occur south of Cape Naturaliste. The Fowler Bay, S. Aust. (*Richards*) record (May 1948, p. 58), based on specimens in MEL (629941, 629942) are more likely robust *G. ramulosa*, and the records of Reinbold (1848, p. 46) and Lucas (1929b, p. 49) are doubtful. Nelson (1987, p. 96) rejects *G. harveyana* from the New Zealand flora.

Withell *et al.* (1994, p. 293) prefer to recommend conservation of the name *G. harveyana* J. Agardh (1885) over the much earlier (*P.*) *flagelliformis* Sonder (1845), as under Art. 14 of the Tokyo code of the I.C.B.N. The Article commences "In order to avoid disadvantageous changes in nomenclature ..." and "aims at retention of those names which best serve stability of nomenclature". There are five references to *flagelliformis* (mainly as *Gigartina*) after the original description, those of J. Agardh (1852) and Kützing (1869, with illustrations) involving further taxonomic study in that they elaborate on Sonder's original description. There are six references to Australian *G. harveyana* following the original one of J. Agardh (1885), but this name is scarcely "well documented" as Withell *et al.* claim. Conservation of species' names may be justified for very well-known species (such as *Ceramium rubrum*) but conservation of names of little known Australian species, rather than following the rule of priority that has applied in the past and is still basic to the ICBN, will surely lead to a chaotic situation. Adoption of the name *flagelliformis* for this *Gracilaria* is in accord with the ICBN rules for a little-known species, and conservation of the epithet *harveyana* is here rejected.

6. **Gracilaria** sp.

FIG. 7

Thallus (Fig. 7A) dark red-brown, 20–50 cm high, irregularly and often relatively sparsely branched, most branches long with apices slightly tapering, proliferous laterals often common. Branches terete, 1.3–1.8 mm in diameter from base to upper parts, smaller laterals 0.7–1.2 mm in diameter near their apices, not or only slightly basally constricted. Holdfast discoid, 2–4 mm across, with one to a few fronds; epilithic on pebbles or on shells, in a sandy-mud substrate, or loose-lying. *Structure* pseudoparenchymatous, grading in cell size from the outer cortex to inner medullary cells, cortex 3–5 cells thick, outer cells rounded to angular in surface view and 5–12 μm across, L/D (1-) 1.5–2 in section, with few hair basal cells; medulla (Fig. 7B) 4–8 cells across, inner medullary cells ovoid, 150–400 μm in

diameter, developing thick walls [15–30 (-40) μm] and very numerous secondary pit-connections; secondary thickening of lower axes not present. Rhodoplasts discoid.

Reproduction. Gametangial thalli monoecious. Carpogonial branches 2-celled, borne on an inner cortical (supporting) cell bearing also two lateral filaments. Carposporophytes (Fig. 7C) with a small basal fusion cell and numerous erect gonimoblast filaments with relatively loosely packed, elongate-ovoid, cells 40–90 μm in diameter with many secondary pit-connections, the upper cells producing branched chains of 4–8 cells with terminal subspherical to ovoid carposporangia 10–24 μm in diameter, subterminal cells maturing later, surface of carposporophyte crenulate; traversing nutritive cells present to both lower and upper parts of pericarp, sometimes involving fusion of several inner pericarp cells. Cystocarps sessile, hemispherical when young, becoming subspherical and basally slightly constricted, (1-) 1.5–2 mm in diameter; pericarp (Fig. 7C) 130–220 μm thick, with anticlinal rows of 10–15 cells, inner cells becoming stellate with lateral pit-connections, with a small ostiole; a slight to prominent inner pericarp present. Spermatangia (Fig. 7D) originally in ovoid pits 60–85 μm in diameter, cut off from cells of lining filaments, ovoid and 2–3 μm in diameter; cortical filaments adjacent to the pits 3–5 cells long; pits later fusing and extending deeper ("*polycavernosa*" type).

Tetrasporangia (Fig. 7E) scattered in the slightly extended outer cortex of 2–5 elongate cells, basally pit-connected, elongate-ovoid, 40–55 μm long and 20–28 μm in diameter, cruciately divided, adjacent filaments slightly nemathecial.

Distribution: In southern Australia, only known from Torrens I., South Australia.

Selected specimens: Point Grey, N end Torrens I., S. Aust., low eulittoral on mud flat (*Hone & Clark*, 19.viii.1993; AD, A62811 —"Marine Algae of southern Australia" No. 375) and (*Hone*, 4.i.1995; AD, A63948). Barker Inlet, Torrens I., S. Aust., 1–1.5 m deep (*Wellbourne*, 9.ix.1993; AD, A63005).

This unnamed species appears in March or April following early rains, reaches its main growth in May to September, and disappears in mid summer (December/January) – pers. comm. P. Hone. Its locality near Port Adelaide suggests it may be an adventive, but it has not been possible to identify it with any of the numerous named species of *Gracilaria*, most of which are not adequately described for detailed comparisons.

The Torrens Island species has spermatangial pits varying from ovoid to deep and chambered (the "polycavernosa" type). It shows similarities with *G. subtilis* (Xia & Abbott)Xia & Abbott (1991, p. 23) from Malaysia in habit and thallus dimensions, in the medulla of few, large, cells (but thin walled in *G. subtilis*), in having basal and often robust traversing cells or filaments, large central cells in the carposporophyte, and in size of tetrasporangia. However, the cortex/medulla transition is described as abrupt in *G. subtilis*. There are also similarities with *G. asiatica* Zhang & Xia (1985, pp. 175, 179) from China, which is described as a more robust species, with the cortex/medulla grading. However, descriptions of both species are inadequate for detailed comparisons, and the Torrens I. species is also monoecious whereas the two Asian species are apparently dioecious.

Genus **GRACILARIOPSIS** Dawson 1949: 40

Thallus erect, irregularly branched, branches terete or compressed; holdfast discoid, epilithic. *Structure* uniaxial but central axis not apparent, pseudoparenchymatous with a small-celled cortex grading to a large-celled medulla, cells with numerous secondary pit-connections.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 2-celled, borne on an inner cortical (supporting) cell which also bears two adjacent filaments, the fertilized carpogonium fusing with cells of these filaments, then producing a dense gonimoblast of relatively small ovoid cells with terminal chains of carposporangia; traversing nutritive cells absent, but lower gonimoblast cells becoming pit-connected to cells in the floor of the cystocarp. Cystocarps prominent, sessile, hemispherical to conical, not or very slightly

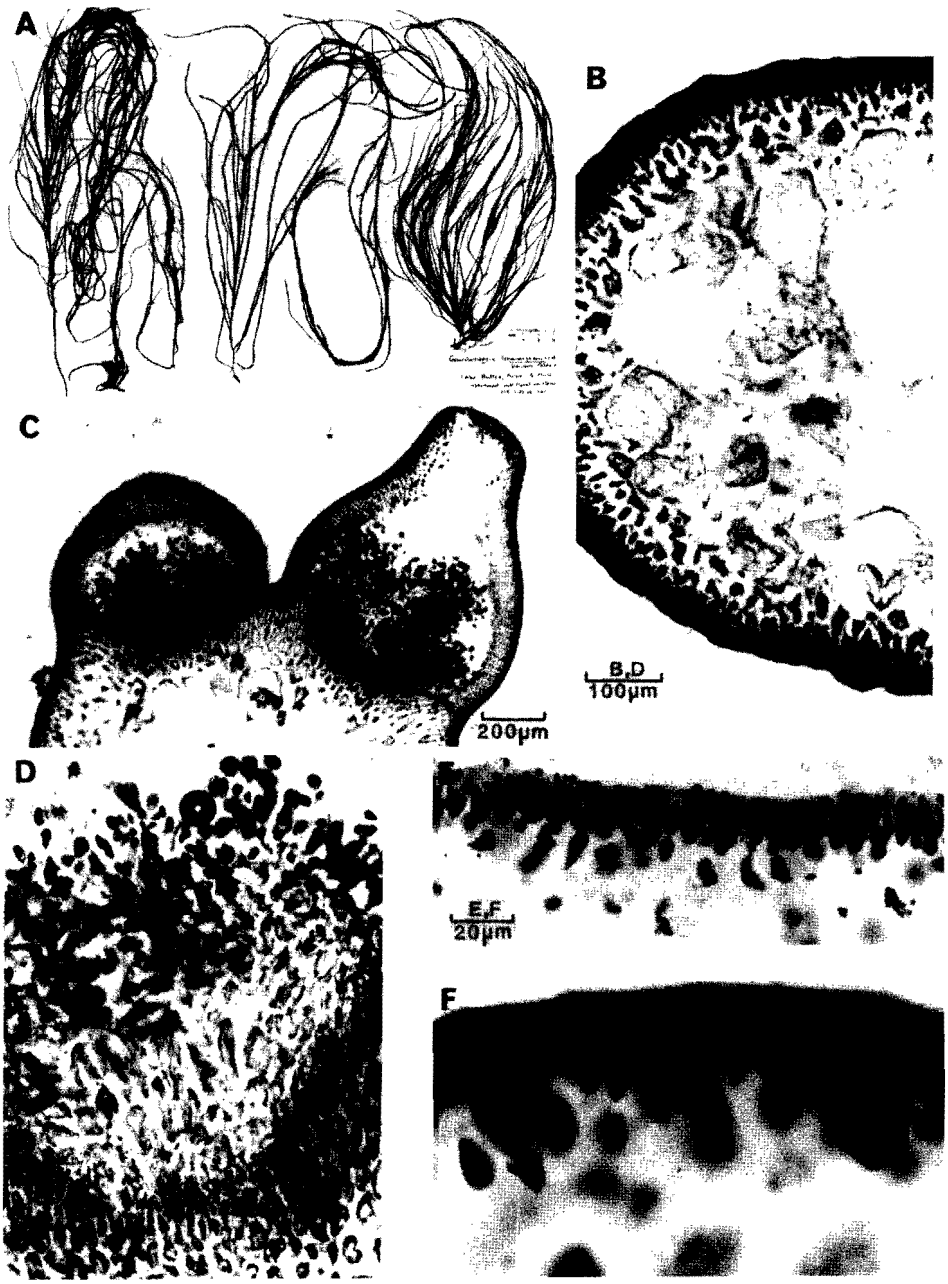


Fig. 8. *Gracilariopsis lemaneiformis* (AD, A63430). **A.** Habit. **B.** Transverse section of thallus. **C.** Section of thallus with two cystocarps. **D.** Section of a carposporophyte. **E.** Transverse section of thallus through a spermatangial sorus. **F.** Transverse section with tetrasporangia.

basally constricted, pericarp thick, ostiolate. Spermatangia scattered, cut off by transverse divisions from surface cortical cells via elongate initials.

Tetrasporangia scattered, basally pit-connected to mid cortical cells, decussately divided.

Type species: *G. sjoestedtii* (Kylin)Dawson (1949, p. 40) [= *G. lemanaeformis** (Bory)Dawson, Acleto & Foldvik (1964, p. 59)].

A genus of about 4 species, the type species clarified by Fredericq & Hommersand (1989b) who consider *Gracilariopsis* generically distinct from *Gracilaria* rather than a subgenus of the latter. Steentoft *et al.* (1995) clarify the occurrence of *Gracilariopsis longissima* and *Gracilaria gracilis* on coasts of the British Isles.

Gracilariopsis lemaneiformis (Bory)Dawson, Acleto & Foldvik 1964: 59, pl. 56 fig. A. Fredericq & Hommersand 1989: 228, figs 1–49.
Gigartina lemanaeformis Bory 1828: 151.
Cordylecladia lemanaeformis (Bory)Howe 1914: 128, pl. 52.
Gracilaria lemanaeformis (Bory)Weber-van Bosse 1928: 435, fig. 176. Bird & Oliveira 1986: 318, figs 11, 14. Etcheverry 1986: 237, pl. 15.
Gracilaria sjoestedtii Kylin 1930: 55, figs 40E, F, 41, 43.
Gracilariopsis sjoestedtii (Kylin)Dawson 1949: 40, pl. 15 fig. 10, pl. 16 figs 5–8, pl. 17, pl. 18 fig. 4.

FIG. 8

Thallus (Fig. 8A) medium red to dark red-brown, 20–120 cm high, moderately to much branched irregularly at varying intervals, branches terete to very slightly compressed, main branches 0.7–1.4 mm in diameter, laterals usually slenderer and 300–600 μm in diameter, decreasing to 150–200 μm in lesser branchlets, laterals not or slightly constricted basally, apices rounded, apical cell unclear. Holdfast discoid, 1–3 mm across; epilithic or adherent to sponge. *Structure* uniaxial but axial filament not apparent, becoming pseudoparenchymatous (Fig. 8B) with a cortex 2–4 cells thick, outer cells sub-palisade like, 4–7 μm in diameter, L/D 1.5–2.5, grading over 3–5 cells to large, ovoid to isodiametric (in both transverse and longitudinal section) medullary cells 200–500 μm in diameter, with numerous secondary pit-connections, walls 10–20 μm thick; medulla 3–5 cells across. Hairs frequent, with larger basal cells in the outer cortex. Rhodoplasts discoid to elongate, becoming ribbon like.

Reproduction. Gametangial thalli dioecious. Carpogonial branches not observed (in Robe material). Carposporophytes (Fig. 8D) broad-based, with a small fusion cell, lower gonimoblast cells not enlarged, ovoid, 20–40 μm in diameter, developing slightly branched chains of more or less ovoid carposporangia 20–30 μm in diameter; lower gonimoblast cells pit-connected to inner pericarp cells in floor of cystocarp, traversing nutritive cells absent. Cystocarps (Fig. 8C) irregularly radially placed, hemispherical to conical, broad-based and not or only slightly basally constricted, 1–1.5 mm in basal diameter and 0.8–1.5 mm high, with or without a slight beak; pericarp 100–200 μm and 8–14 cells thick, cells isodiametric, in anticlinal chains, with secondary lateral pit-connections; ostiolate. Spermatangia (Fig. 8E) scattered over the cortex, cut off from elongate initials by transverse walls, ovoid, 2–3 μm in diameter.

Tetrasporangia (Fig. 8F) scattered in the outer cortex, basally pit-connected to inner cortical cells, ovoid, 40–55 μm long and 15–35 μm in diameter, decussately divided. The cortex is slightly thicker and less smooth where tetrasporangia are dense.

Type from Paita, Peru; type sheet [lectotype left specimen (Fredericq & Hommersand 1989, p. 228)] in Herb. Bory, PC.

Distribution: Pacific N. and S. America; China; India (see Bird & Oliveira 1986, fig. 1); western Europe (Fredericq & Hommersand 1989, p. 240).

In southern Australia, known only from Robe, S. Aust.

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* Spelling corrected to *lemaneiformis* by Abbott (1983, p. 561).

Known specimens: Lake Butler, Robe, S. Aust., uppermost sublittoral on stones (*Womersley*, 15.iv.1994; AD, A63430 — "Marine Algae of southern Australia" No. 373, and 3.iii.1995; AD, A64282).

These collections, both of numerous plants, are the only record of *G. lemaneiformis* from Australia, and "completes the circum-Pacific distribution of the species." The plants agree well with descriptions of this species but DNA sequencing is needed to support the determination which is regarded as likely by Dr Carolyn Bird (pers. comm.).

Lake Butler at Robe is a small lake used as a harbour for the fishing fleet. This species may be an adventive and should be searched for elsewhere on the southern Australian coast.

Genus MELANTHALIA Montagne 1843: 296

Thallus erect, 10–40 cm high, cartilaginous, subdichotomously branched, branches linear, compressed, 0.5–4 mm broad, dark red-brown and drying darker to almost black; holdfast discoid. *Structure* multiaxial, pseudoparenchymatous throughout, cells usually with refractive globules; branch apices with a dome-shaped cap of rows of relatively small, cytoplasm-dense, cells surmounting the core of larger, less dense, medullary cells. Outer cortical cells dividing by obliquely longitudinal divisions followed by transverse division of subapical cells.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli probably dioecious. Carpogonial branches 2-celled, borne on supporting cells in the mid cortex, probably with adjacent sterile branches. Carposporophyte with a small basal fusion cell, erect, densely tufted, gonimoblast filaments with straight terminal chains of numerous subspherical carposporangia, maturing apically, largely filling the cystocarp cavity. Cystocarps marginal, with a thick pericarp of dense filaments of short cells, ostiolate. Spermatangia probably in surface sori of anticlinal cell rows from outer cortical cells.

Tetrasporangia in shallow and usually inconspicuous nemathecia below branch apices, basally pit-connected to outer cortical cells which also bear a slender 2–3 celled paraphysis, elongate-ovoid to clavate, cruciately divided.

Type species: *M. obtusata* (Labillardière)J. Agardh 1852: 614.

A genus of about 6 species, three from southern Australia, one (*M. polydactylis* J. Agardh 1885, p. 58) from the NSW coast (Millar 1990, p. 342, fig. 20C–E), and two from New Caledonia (*M. vieillardii* Kützing 1869, p. 16, pl. 42c, d and *M. fastigiata* Kützing 1869, p. 16, pl. 44a, b), both of which need further study.

Melanthalia is a distinctive genus with its subdichotomous, linear, compressed branches each with a terminal cap of smaller cells, cystocarps with a very thick ostiolate pericarp and carposporangia borne in long, straight chains, and tetrasporangia borne in nemathecia. *M. abscissa* (as *M. obtusata* var. *abscissa*) has been investigated by Fredericq & Hommersand (1990c).

The three species recognised below are closely similar in their structure and reproduction, differing essentially in branch width and whether compressed or not. While they could be regarded as varieties of one species, virtually all specimens can be separated on these features and it thus seems best to regard them as species.

KEY TO SPECIES OF *MELANTHALIA*

1. Branches (1.5-) 2–3 (-4) mm broad, strongly compressed ..... 1. *M. obtusata*
1. Branches 0.3–1.3 mm broad, terete to compressed 2

2. Branches distinctly compressed, mostly 0.7–1.3 mm broad ..... 2. *M. abscissa*
2. Branches terete to slightly compressed, mostly 0.3–0.8 mm broad ..... 3. *M. concinna*

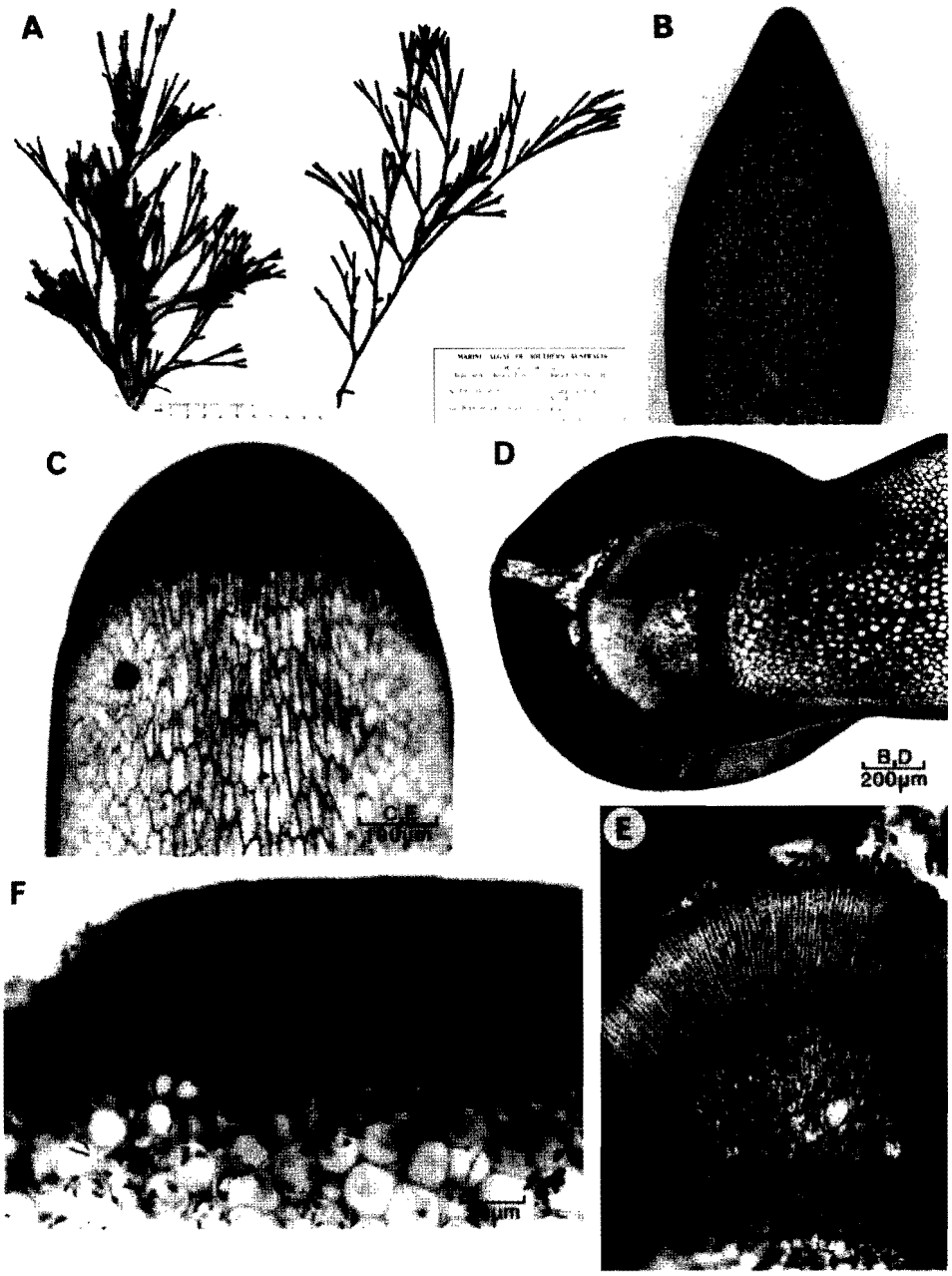


Fig. 9. *Melanthalia obtusata* (**A–D,** AD, A57039; **E, F,** AD, A56507). **A.** Habit. **B.** Transverse section of thallus. **C.** Longitudinal section of branch apex showing meristematic cap. **D.** Longitudinal median section of a cystocarp. **E.** Longitudinal section of carposporophyte with chains of carposporangia. **F.** Transverse section of thallus with a tetrasporangial nemathecium.

1. **Melanthalia obtusata** (Labillardière)J. Agardh 1852: 614; 1876: 404. De Toni 1900b: 422. Guiler 1952: 89. Harvey 1858: pl. 25; 1859b: 313. Kylin 1932: 58. Lucas 1929b: 49. Lucas & Perrin 1947: 183, fig. 51. May 1965: 391. Reinbold 1897: 51. Sonder 1853: 689; 1881: 22. Tisdall 1898: 508. Wilson 1892: 176. Womersley 1950: 169; 1966: 147.
Fucus obtusatus Labillardière 1807: 111, pl. 255. Turner 1811: 26, pl. 145.
Rhodomela obtusata (Labillardière)C. Agardh 1822: 383; 1824: 200.
Melanthalia billardieri Montagne 1843: 298. Kützing 1849: 784; 1869: 15, pl. 42a, b. Sonder 1855: 522.

FIG. 9

Thallus (Fig. 9A) dark red-brown, drying darker to almost black, 10–40 cm high, subdichotomously and complanately branched from the margins, usually at intervals of 1–3 cm, branches strongly compressed (Fig. 9B), (1.5-) 2–3 (-4) mm broad, linear or with occasional marginal irregularities or constrictions (associated with new growth), raised centrally in surface view (elliptic to biconvex in transverse section), branch apices (Fig. 9C) with a distinct, broad, cap and 2–3 mm wide just below apex. Holdfast discoid, 5–15 mm across, bearing one to a few terete stipes; epilithic. *Structure* multiaxial, with sudden transition from densely protoplasmic cap cells (Fig. 9C) to clearer and larger medullary cells, pseudoparenchymatous throughout with small outer cortical cells, 3–5 µm in diameter and L/D 1–1.5, in anticlinal rows, the outer cells dividing obliquely longitudinally and then transversely, secondary pit-connections abundant, globules within the cells frequent; medullary cells 20–35 µm in diameter, walls 2–4 µm thick. Rhodoplasts discoid.

Reproduction. Female plants with 2-celled carpogonial branches borne near the branch margins on mid cortical supporting cells with closely adjacent cortical branches. Carposporophytes with a dense gonimoblast reticulum involving a small basal fusion cell and cell fusions with gametophytic cells, producing a dense tuft of erect gonimoblast filaments terminating in straight chains (Fig. 9E) of numerous ovoid to subspherical carposporangia 8–11 µm in diameter, maturing apically. Cystocarps (Fig. 9D) marginal or submarginal, often subopposite or clustered, hemispherical, 1–1.5 mm across; pericarp massive, with inner tangentially elongate cells and outer anticlinal cell rows 2–4 µm in diameter, with a prominent ostiole produced by breakdown of pericarp tissue. Spermatangia not observed.

Tetrasporangial nemathecia (Fig. 9F) shallow, inconspicuous, on upper branches below apices; tetrasporangia basally pit-connected to outer cortical cells among dense 2–4-celled paraphyses 30–40 µm long and 3–6 µm in diameter, sporangia elongate-ovoid to clavate, 25–30 µm long and 8–12 µm in diameter, irregularly cruciately divided.

Type from SE Tasmania *(Labillardière);* holotype in FI. Syntype in Herb. Montagne, PC.

Distribution: Pennington Bay, Kangaroo I., S. Aust., to Port Phillip Heads, Vic. and Deal I., Bass Strait, and around Tasmania.

Selected specimens: Pennington Bay, Kangaroo I., S. Aust., upper sublittoral, shaded (*Womersley*, 22.i.1948; AD, A6439). Toad Head, West I., S. Aust., 6–9 m deep (*Shepherd*, 15.i.1966; AD, A30169). 1.3 km off Middle Point, Cape Northumberland, S. Aust., 13 m deep (*Shepherd*, 19.iii.1974; AD, A44943). Nora Creina, S. Aust., upper sublittoral pool (*Womersley*, 26.i.1967; AD, A31644). Lady Julia Percy I., Vic., 19 m deep (*Shepherd*, 4.i.1968; AD, A32418). Point Roadknight, Vic., drift (*Womersley*, 6.vi.1953; AD, A18810). Port Phillip Heads, Vic., 10 m deep (*Watson*, 8.iii.1985; AD, A57039 —"Marine Algae of southern Australia" No. 306). Little Squally Cove, Deal I., Bass Strait, 21 m deep (*Houridis*, 14.iii.1993; AD, A63281). Lady Bay, Southport, Tas., 3–5 m deep (*Brown & Womersley*, 28.x.1982; AD, A56507).

M. obtusata is a deep-water species found on rough-water coasts.

Harvey (1858, pl. 25) distinguished var. *intermedia*, giving as synonyms *M. abscissa* as in Hooker & Harvey (1845, p. 548) and *M. jaubertiana* (as in Sonder 1853, p. 689). These names are here considered to apply to *M. abscissa* (Turner)Hooker & Harvey. *M. obtusata* has been recorded from New Zealand as varieties which are *M. abscissa*. May (1966, p. 18) also recorded it from New Caledonia, but this record is more likely to apply to one of the two New Caledonian species described by Kützing, both of which need investigation.

2. **Melanthalia abscissa** (Turner)Hooker & Harvey 1845: 548; 1847: 406. Adams 1994: 180, pl. 56 lower. J. Agardh 1852: 613; 1876: 404. De Toni 1900b: 421. Kylin 1932: 59, fig. 17D. Papenfuss 1935: 1, figs 1–10.
Fucus abscissus Turner 1819: 66, pl. 223.
Sphaerococcus abscissus (Turner)C. Agardh 1822: 252.
Chondrococcus abscissus (Turner)Kützing 1849: 752; 1867: 29, pl. 96c, d.
Melanthalia jaubertiana Montagne 1843: 299, pl. 13. J. Agardh 1852: 613. Kützing 1849: 784; 1869: 16, pl. 43b, c(?). Sonder 1853: 689.
Melanthalia obtusata var. *intermedia* Harvey 1858: pl. 25 fig. 2.
Melanthalia intermedia (Harvey)J. Agardh 1879: 127, pl. 23 figs 10, 11. Tisdall 1898: 508.
Melanthalia billardieri var. *angustata* Sonder 1855: 522.
Melanthalia muelleri Kützing 1869: 16, pl. 43a.
Melanthalia obtusata var. *abscissa* (Turner)Chapman 1979: 309, fig. 84, pls 118, 119. Fredericq & Hommersand 1990c: 4, figs 1–22.
Melanthalia obtusata var. *jaubertiana* (Montagne)Chapman 1979: 311, pl. 120.

FIG. 10

Thallus (Fig. 10A) dark red-brown, 10–40 cm high, subdichotomously and essentially complanately branched from the margins, mostly at intervals of 0.5–2 cm, branches compressed, 0.7–1.3 mm broad, linear, ovate to elliptic in transverse section, branch apices with a distinct thickened cap and 0.7–1 mm broad just below apex. Holdfast discoid, 3–25 mm across, bearing few to numerous terete stipes; epilithic. *Structure* multiaxial (Fig. 10B), with sudden transition from densely protoplasmic cap cells to clearer and larger medullary cells, pseudoparenchymatous throughout with small outer cortical cells 3–4 µm in diameter and L/D 1–1.5 (-2), in anticlinal rows, the apical cells dividing obliquely longitudinally and then transversely, secondary pit-connections and cell globules frequent; medullary cells 10–25 (-40) µm in diameter, walls 2–3 µm thick. Rhodoplasts discoid to lobed.

Reproduction. Female plants with 2-celled carpogonial branches borne near the branch margins on mid cortical supporting cells with closely adjacent cortical branches. Carposporophytes (Fig. 10C) with a dense gonimoblast reticulum involving a small basal fusion cell and other fusion centres, and fusions between gonimoblast and gametophyte cells, and with a dense tuft of erect gonimoblast filaments terminating in straight chains of numerous ovoid to subspherical carposporangia (Fig. 10D) 8–12 µm in diameter, maturing apically. Cystocarps marginal or submarginal, hemispherical, 1–1.5 mm across; pericarp massive, with inner tangentially elongate cells and outer anticlinal rows 6–8 µm in diameter, with a prominent ostiole. Spermatangia not observed.

Tetrasporangial nemathecia (Fig. 10E) shallow, inconspicuous, on upper branches; tetrasporangia pit-connected to basal cells within the dense layer of 2–3-celled paraphyses 30–45 µm long and 3–5 µm in diameter, sporangia ovoid, 20–25 µm long and 7–10 µm in diameter, cruciately divided.

Type from New Zealand (*Banks*); lectotype (?) in BM.

Distribution: New Zealand.

In southern Australia, from Wedge I., S. Aust., to Wilsons Prom., Vic. (Sonder) and around Tasmania.

Selected specimens: 7 km SE of Wedge I., S. Aust., 22–35 m deep (*Baldock*, 4.i.1964; AD, A27188). Althorpe I., S. Aust., 9–13 m deep N side (*Baldock*, 4.i.1964; AD, A27217). Toad Head, West I., S. Aust., 6–9 m deep (*Shepherd*, 15.i.1966; AD, A30170). Port Elliot, S. Aust., drift (*Womersley*, 24.vii.1949; AD, A11141). Robe, S. Aust., drift (*Womersley*, 29.viii.1949; AD, A11011). Lawrence Rock, Portland, Vic., 24–30 m deep 1.6 km W of Rock (*Owen*, 2.ix.1971; AD, A39670). Warrnambool, Vic., drift (*Womersley*, 13.iv.1959; AD, A22918). Little Squally Cove, Deal I., Bass Strait, 5 m deep (*Shepherd & R. Lewis*, 3.v.1974; AD, A45202). Port Arthur, Tas. (*Perrin* 506 & *Lucas*; BM).

M. abscissa has usually been placed as a variety of *M. obtusata* but they appear to be quite distinct in branch width, although very similar structurally and reproductively. The type of *M. jaubertiana* was from SE Tasmania, Montagne (1843, p. 299) stating "Hab. cum

priori" which was "littora Van-Dieman" for *M. billardieri*. In transferring *F. abscissus* to *Melanthalia*, Hooker & Harvey (1845, p. 549) commented on the similarity between this species and *M. jaubertiana* Montagne. The lectotype of var. *intermedia* of *M. obtusata* is Alg. Aust. Exsicc. 319D from Port Fairy, Vic., in Herb. Harvey, TCD. Harvey (1858, pl. 25) commented that var. *intermedia* was "frequently found growing from the same base as the normal form" (i.e. *M. obtusata*), but this has never been observed by the present author. The holotype of *M. muelleri* Kützing is from Belfast, Vic. (*Mueller*) and is in L, 941, 149 ... 65.

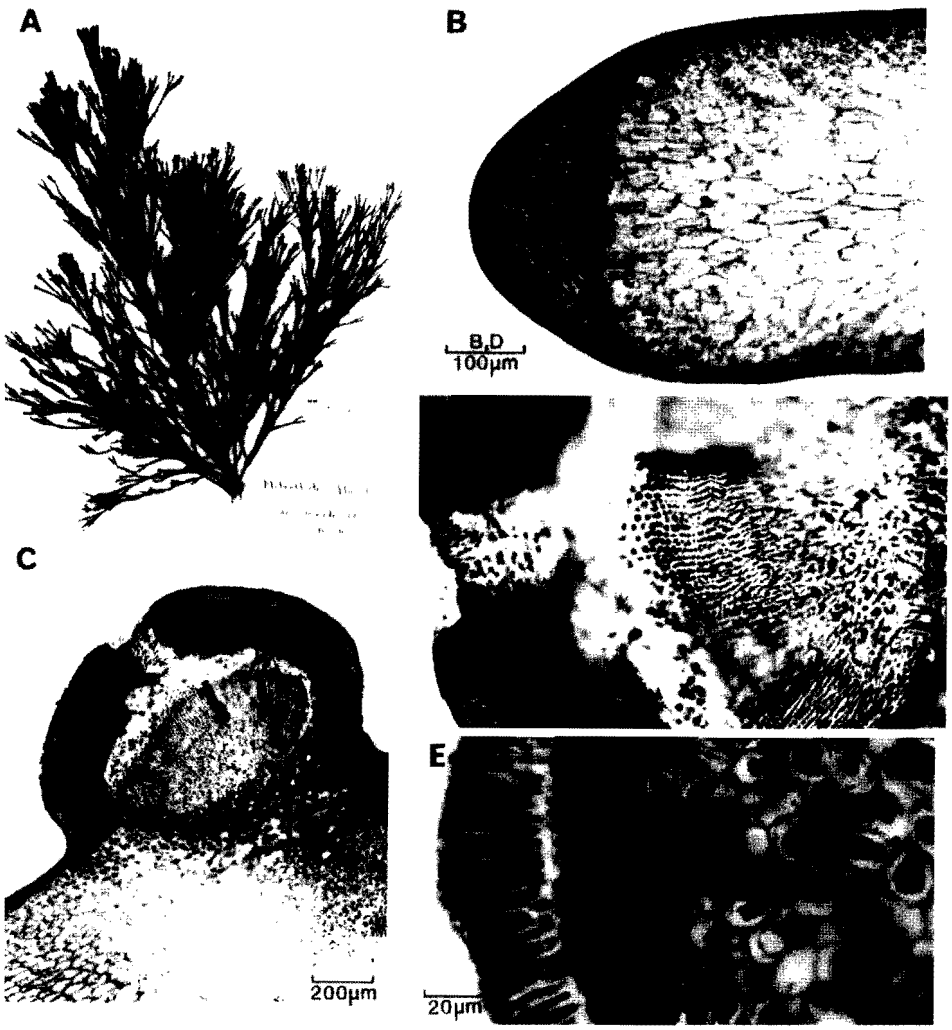


Fig. 10. *Melanthalia abscissa* (**A–D,** AD, A11141; **E,** AD, A30170). **A.** Habit. **B.** Longitudinal section through apical cap. **C.** Longitudinal section through a cystocarp. **D.** Section of cystocarp with chains of carposporangia. **E.** Transverse section of thallus with a tetrasporangial sorus.

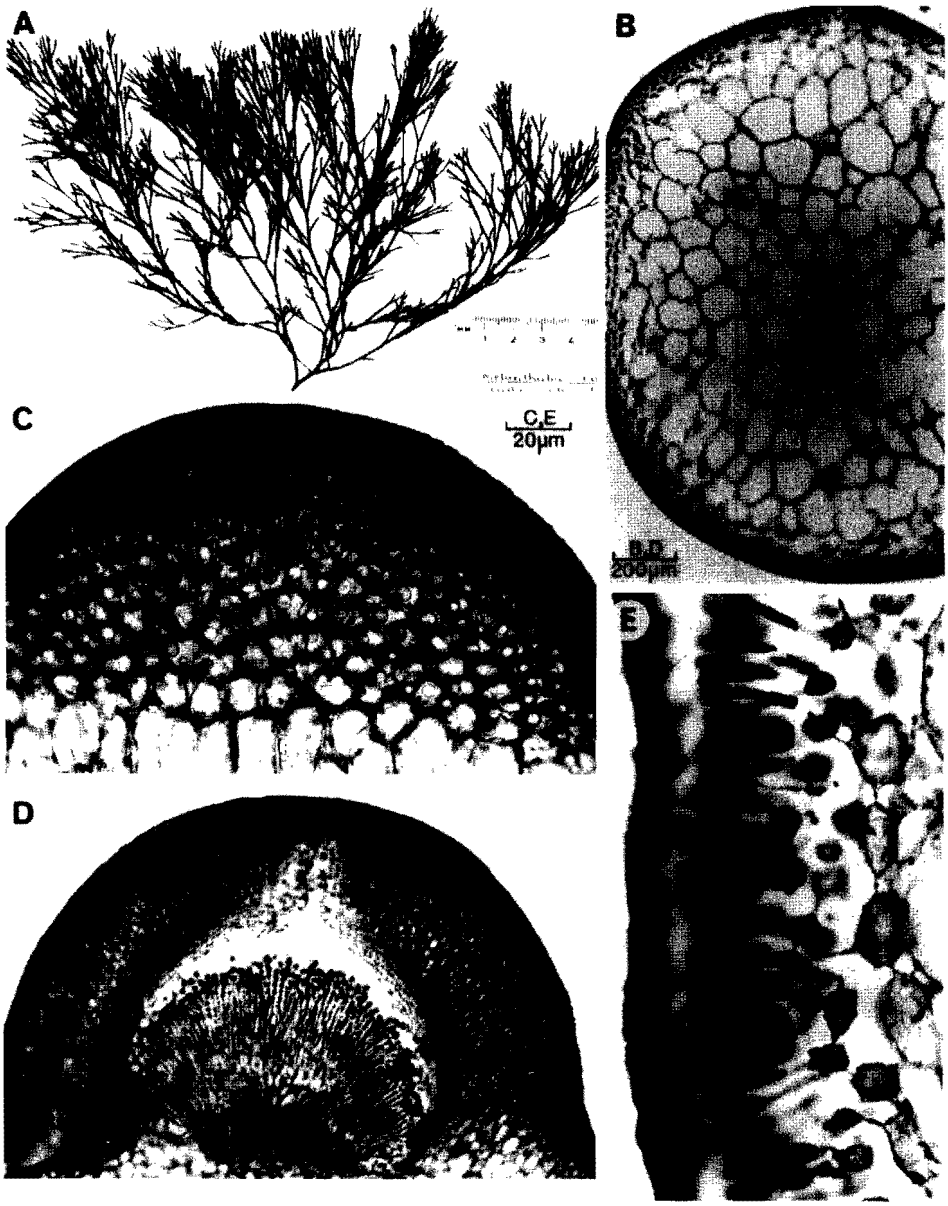


Fig. 11. *Melanthalia concinna* (**A**, AD, A32471; **B, E,** AD, A30612; **C, D,** AD, A24401). **A.** Habit. **B.** Transverse section of a branch. **C.** Longitudinal section through apical cap. **D.** Section of cystocarp with chains of carposporangia. **E.** Transverse section with tetrasporangia.

3. **Melanthalia concinna** J. Agardh 1876: 404. De Toni 1900b: 421. Chapman 1979: 312, pl. 117(?). Kylin 1932: 58. Lucas 1929b: 49. May 1965: 391(?). Reinbold 1897: 51. Sonder 1881: 22. Tisdall 1898: 508. Womersley 1950: 169.

FIG. 11

Thallus (Fig. 11A) dark red-brown, 10–30 cm high, subdichotomously and complanately branched especially in upper parts, mostly at intervals of 5–20 mm, branches terete (Fig. 11B) to slightly compressed, linear, 0.3–0.7 (-1.0) mm broad, only slightly thicker below, branch apices with a thickened cap and 0.3–0.6 mm broad just below apex. Holdfast discoid, 2–10 mm across, bearing few to numerous stipes; epilithic. *Structure* multiaxial, with rapid transition (Fig. 11C) from smaller cap cells to larger medullary cells, pseudoparenchymatous throughout with the outer cortex 2–3 cells thick (not in distinct rows), outermost cells 3–7 μm in diameter and L/D 1–1.5, with a secondary cortex developing below; secondary pit-connections and cell globules common (Fig. 11C), the latter especially in cap cells, pericarp cells and cells of nemathecial paraphyses; medullary cells (20-) 40–90 μm in diameter, walls 2–3 μm thick. Rhodoplasts discoid.

Reproduction. Carpogonial branches not observed. Carposporophyte (Fig. 11D) with a dense gonimoblast reticulum involving a small basal fusion cell, fusions between gonimoblast and gametophyte cells, and other fusion centres, with a dense tuft of erect gonimoblast filaments terminating in straight chains of numerous ovoid to subspherical carposporangia 8–15 μm in diameter, maturing apically. Cystocarps scattered on upper branches, radial, hemispherical to globular, 0.7–1 mm across; pericarp (Fig. 11D) massive, with inner tangentially elongate cells and outer anticlinal rows 5–8 μm in diameter, with an ostiole. Possible spermatangial sori scattered on upper branches, with anticlinal cell rows releasing terminal cells as spermatia(?).

Tetrasporangial nemathecia (Fig. 11E) surrounding branches below apices, distinct, 45–90 μm thick, paraphyses elongate-clavate, 3–5 cells long, 4–6 μm in diameter, with prominent globules; tetrasporangia basally pit-connected to upper cells of paraphyses, 20–25 μm long and 8–11 μm in diameter, cruciately divided.

Type from Queenscliff, Vic. (*Mueller*); lectotype (here designated) in Herb. Agardh, LD, 28642.

Distribution: Isles of St Francis, S. Aust., to Walkerville, Vic., and Erith I., Bass Strait. New Zealand?

Selected specimens: Near Isles of St Francis, S. Aust., 37 m deep (*Symonds*, 23.x.1973; AD, A44256). Elliston, S. Aust., 10–12 m deep outside bar (*Shepherd*, 25.x.1971; AD, A42669). Wanna, S. Aust., drift (*Womersley*, 19.ii.1959; AD, A22363). Oedipus Point, West I., S. Aust., 10 m deep (*Shepherd*, Dec. 1966; AD, A31129). Whale Point, West I., S. Aust., 26 m deep (*Shepherd*, June 1966; AD, A30612). Vivonne Bay, Kangaroo I., S. Aust., drift (*Womersley*, 2.i.1949; AD, A10655). Robe, S. Aust., drift (*Womersley*, 15.iv.1959; AD, A23009 and 24.viii.1960; AD, A24401). 1.35 km off Middle Point, Cape Northumberland, S. Aust., 15 m deep (*Johnson*, 13.vii.1974; AD, A45455). Lady Julia Percy I., Vic., 8–11 m deep (*Shepherd*, 3.i.1968; AD, A32471). Walkerville, Vic., drift (*Sinkora* A2593, 29.iii.1979; AD, A61004). Erith I., Bass Strait, 5–7 m deep (*Riddle*, 20.ii.1990; AD, A60456).

Melanthalia concinna is essentially a deep water species on rough-water coasts.

There has been some confusion with *Fucus concinnus* R. Brown *ex* Turner [= *Trematocarpus concinnus* (R. Brown *ex* Turner)De Toni], based on Brown specimens from Kent I., Bass Strait, but all Brown specimens in BM appear to be *Trematocarpus*, and *Melanthalia concinna* J. Agardh was based on other southern Australian material.

It is doubtful if Chapman's (1979, p. 312, pl. 117) description of *M. concinna* from New Zealand does apply to this Australian species.

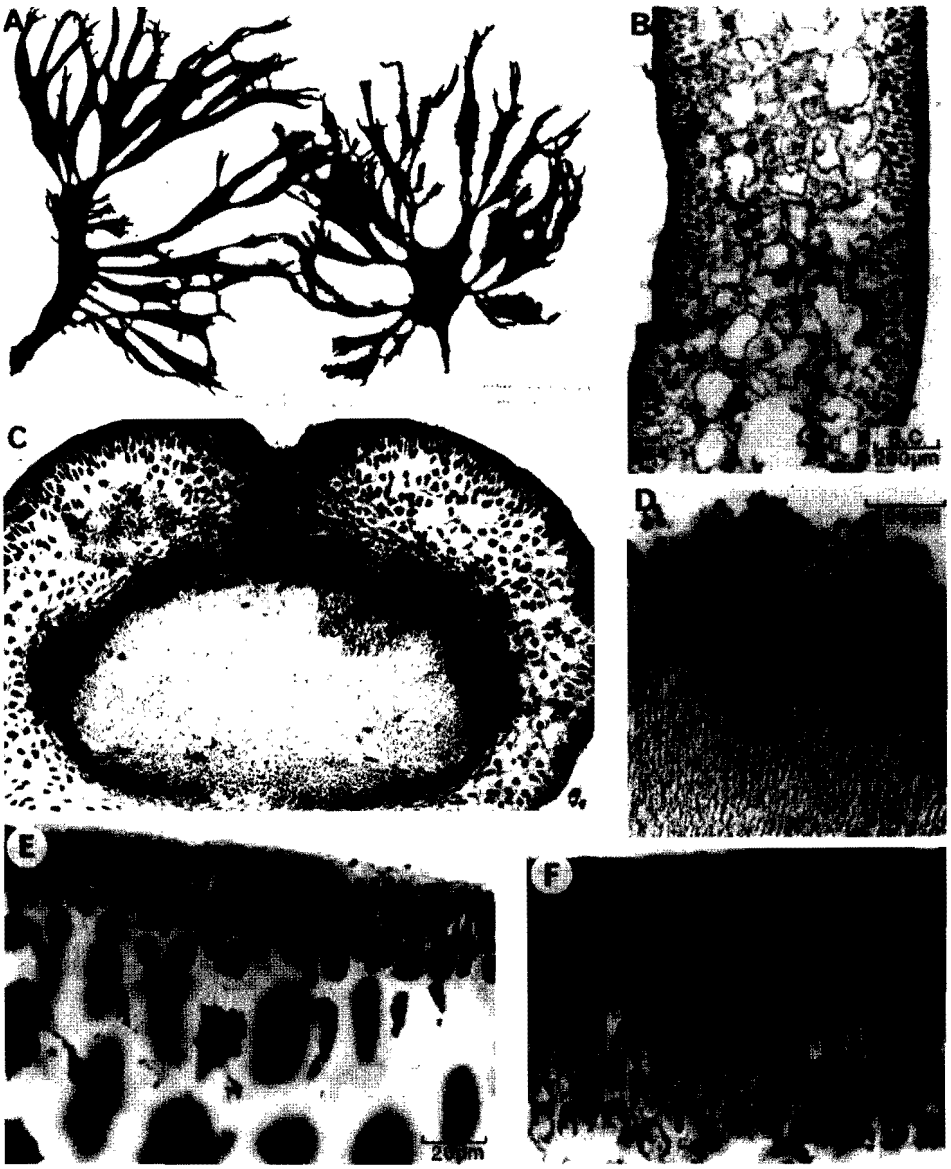


Fig. 12. *Curdiea angustata* (**A–C, E,** AD, A63260; **D,** AD, A63540; **F,** AD, A39533). **A.** Habit. **B.** Transverse section of thallus. **C.** Section of cystocarp. **D.** Section of carposporophyte with carposporangial chains. **E.** Section of male thallus with a spermatangial sorus. **F.** Section of tetrasporangial thallus.

Genus CURDIEA Harvey 1855b: 333

Thallus erect or decumbent, 5–50 cm high or long, coriaceous, variously and irregularly complanately branched with branches strongly compressed and of varying width; holdfast discoid. *Structure* multiaxial, pseudoparenchymatous throughout, branch apices without distinct caps, outer cortical cells small, in short anticlinal chains, medullary cells large with numerous secondary pit-connections.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli probably dioecious. Carpogonial branches 2-celled, borne on supporting cells in the mid cortex with adjacent sterile branches. Carposporophyte with a small basal fusion cell producing slight sterile gonimoblast tissue and densely tufted, erect, simple or basally branched, straight chains of numerous subspherical carposporangia maturing apically and largely filling the cystocarp cavity. Cystocarps largely marginal, large and conspicuous, with a thick pericarp of dense filaments of short cells, ostiolate. Spermatangia unknown.

Tetrasporangia in shallow and inconspicuous nemathecia, basally pit-connected to the basal or mid cells of short, 2–5-celled paraphyses, ovoid, cruciately divided.

Type species: *C. laciniata* Harvey 1855b: 333. [= *C. angustata* (Sonder)Millar]

A genus of about 8 species, from southern and warm temperate Australia, New Zealand, Subantarctic Islands and Chile.

As Millar (1990, p. 340) has noted, *Sarcocladia* Harvey (1855a, p. 550), with type species *S. obesa* Harvey, was probably published prior to *Curdiea*. The former has usually been considered a synonym of *Curdiea* and there is justification for conserving *Curdiea* Harvey if dates of publication can be clarified.

A New Zealand species, *C. flabellata* Chapman, has been investigated in detail by Fredericq & Hommersand (1989c). Southern Australian species include the common and morphologically variable *C. angustata*, the western, partly erect, *C. obesa*, and the eastern, decumbent, *C. crassa*. *C. irvineae* J. Agardh (1894, p. 135) from Western Australia appears distinct from southern species, having more or less linear branches 3–6 mm broad, usually curved longitudinally with cystocarps on the convex surface, but further comparisons with *C. obesa* are needed.

KEY TO SPECIES OF *CURDIEA*

1. Thallus erect, much branched irregularly, with similar cortices on both sides; cystocarps marginal ..... 1. *C. angustata*
1. Thallus decumbent to partly erect, moderately to slightly branched, with distinct upper and lower cortices; cystocarps on the thallus surface or submarginal 2
    2. Thallus moderately branched and partly erect, 0.5–1.0 mm thick in young parts, 1–1.5 mm thick in older parts; cystocarps usually submarginal ..... 2. *C. obesa*
    2. Thallus irregularly lobed, decumbent, 1–1.5 mm thick in young parts, 3–4 mm thick in older parts; cystocarps mostly on the surface ..... 3. *C. crassa*

1. **Curdiea angustata** (Sonder)Millar 1990: 342. Millar & Kraft 1993: 27.
    Epymenia angustata Sonder 1853: 677. J. Agardh 1892: 94. De Toni 1900b: 529. Harvey 1863, synop.: xlv. Wilson 1892: 178.
    Gracilaria callophyllis Areschoug 1854: 350.
    Curdiea callophyllis (Areschoug)Fredericq *in* Fredericq & Hommersand 1989a: 224.
    Curdiea laciniata Harvey 1855b: 333; 1858: pl. 39. J. Agardh 1876: 402. Chapman 1979: 306, pl. 114(?). De Toni 1900b: 424. Guiler 1952: 89. Kützing 1869: 12, pl. 33c, d. Kylin 1932: 60. Levring 1945: 17. Lucas 1929a: 18; 1929b: 49. May 1965:

408. Reinbold 1897: 52. Tisdall 1898: 508. Wilson 1892: 176. Womersley 1950: 169.

Curdiea meredithiae J. Agardh 1876: 403. De Toni 1900b: 425. Guiler 1952: 89. Kylin 1932: 60, pl. 23 fig. 57. Lucas 1929a: 18. May 1965: 408.

Curdiea kuetzingiana J. Agardh 1896: 95. Kylin 1932: 60, pl. 23 fig. 58. May 1965: 408.

Curdiea engelhartii J. Agardh 1901: 105. De Toni 1924: 248. Kylin 1932: 60, pl. 24 fig. 59. Levring 1945: 17. Lucas & Perrin 1947: 186. May 1965: 408.

FIG. 12

Thallus (Fig. 12A) medium to dark red-brown, 20–60 cm high, drying cartilaginous, 0.5–1 (-1.5) mm thick, complanately, marginally and irregularly branched, often with marginal proliferations (sometimes mostly unilateral), main branches 5–30 (-50) mm broad, lesser branches and proliferations usually 2–10 mm broad and 1–4 (-8) cm long, usually basally constricted. Holdfast discoid, 2–10 mm across, with one to a few stipes; epilithic. *Structure* multiaxial, pseudoparenchymatous (Fig. 12B) throughout, with a cortex 2–4 cells thick, outer cells 3–6 µm in diameter and L/D 1–2, becoming thicker below with anticlinal rows of elongate cells, grading inwards to a medulla of large ovoid cells 80–150 µm in diameter with thick walls (becoming 15–25 µm thick) and numerous, prominent, secondary pit-connections. Rhodoplasts discoid, numerous per cell.

Reproduction. Gametangial thalli dioecious. Female plants with 2-celled carpogonial branches borne near branch margins on mid cortical supporting cells with closely adjacent cortical filaments. Carposporophytes (Fig. 12C) with a dense gonimoblast reticulum and small basal fusion cell(s), producing a dense upper mass of erect gonimoblast filaments terminating in straight chains (Fig. 12D) of numerous subspherical to ovoid carposporangia 10–14 µm in diameter, maturing apically. Cystocarps marginal, usually in long series, prominent, globose, sessile or slightly basally constricted, 1–1.5 mm across; pericarp (Fig. 12C) massive, with inner tangentially elongate cells (continuing around base of the carposporophyte) and a medulla and cortex similar to the vegetative tissue, with a small ostiole lined by short cells cut off from the medullary pericarp cells. Spermatangia (Fig. 12E) in surface sori, cut off via elongate initials from outer cortical cells.

Tetrasporangial nemathecia (Fig. 12F) shallow, inconspicuous, on upper branches; tetrasporangia basally pit-connected to subapical cells of 4–5-celled paraphyses 100–140 µm long, end cells clavate and 3–8 µm in diameter, sporangia clavate to ovoid, 20–25 µm long and 10–15 µm in diameter, cruciately divided.

Type from Gulf St Vincent, S. Aust. (*Mueller*); holotype in MEL, 670225.

Distribution: Hamelin Bay, W. Aust., to Collaroy, N.S.W. (Millar & Kraft 1993, p. 27) and around Tasmania.

New Zealand? (Chapman 1979: 306).

Selected specimens: Hamelin Bay, W. Aust., drift (*Royce* 712, 21.vi.1950; AD, A15490). Elliston, S. Aust., 20 m deep outside bar (*Shepherd*, 14.v.1971; AD, A38696). Port Elliot, S. Aust., drift (*Womersley*, 24.vii.1949; AD, A11102). Middleton, S. Aust., drift (*Womersley*, 14.xi.1965; AD, A29684). 13 km S of Vivonne Bay, Kangaroo I., S. Aust., 50–70 m deep (*Latz*, 24.xi.1968; AD, A32998). Robe, S. Aust., drift (*Womersley*, 15.iv.1994; AD, A63540). Cape Lannes, S. Aust., drift (*Womersley*, 31.x.1993; AD, A63260). Stinky Bay, Nora Creina, S. Aust., drift (*Womersley*, 25.v.1963; AD, A26519). 400 m off Cape Buffon, S. Aust., 5 m deep (*Collings*, 25.i.1991; AD, A61239). 1.3 km off Middle Point, Cape Northumberland, S. Aust., 15 m deep (*Shepherd*, 13.ii.1976; AD, A47003). Warrnambool, Vic., drift (*Womersley*, 1.ix.1971; AD, A39533). Queenscliff, Vic., drift (*Womersley*, 8.iv.1959; AD, A22833). Swansea, Tas., drift (*Womersley*, 19.i.1949; AD, A10223). Port Arthur, Tas., 10–12 m deep (*McCauley*, 2.iii.1990; AD, A60466). Fluted Cape, Bruny I., Tas., 10 m deep (*Shepherd*, 11.ii.1972; AD, A41804).

Curdiea angustata is very variable in habit, especially in branch width and marginal proliferations. It has been commonly known as *C. laciniata* Harvey [lectotype from Port Fairy, Vic. (*Eddington*); in Herb. Harvey, TCD] and includes *C. meredithiae* J. Agardh [lectotype from Orford, Tas. (*Meredith*); in Herb. Agardh, LD, 28569], *C. kuetzingiana* J. Agardh [holotype from Encounter Bay, S. Aust. (*Hussey*); in Herb. Agardh, LD, 28587]

and *C. engelhartii* J. Agardh [holotype from Lacepede Bay, S. Aust. (*Engelhart*); in Herb. Agardh, LD, 28582; isotype in MEL, 66734].

The likely identity of *Epymenia angustata* Sonder and *Curdiea laciniata* Harvey was first suggested by Harvey (1863, synop.: xlv), followed by De Toni (1900b, p. 529), and made formally by Millar (1990, p. 677). *C. angustata* is most common on south-east Australian coasts, usually in deep water on rough-water coasts; plants to the west of this region and the N.S.W. record are smaller and slenderer than the robust Victorian – S. Australian plants.

Chapman (1979, p. 306), following other authors, recorded *C. laciniata* [= *C. angustata*] from New Zealand and referred to marginal, spherical, cystocarps. This contrasts with *C. flabellata* Chapman (1979, p. 304) in which cystocarps occur scattered over the thallus surface and partly sunken, and most erect, irregularly branched, New Zealand specimens appear to be *C. flabellata*. Whether *C. angustata* does occur in New Zealand remains to be verified.

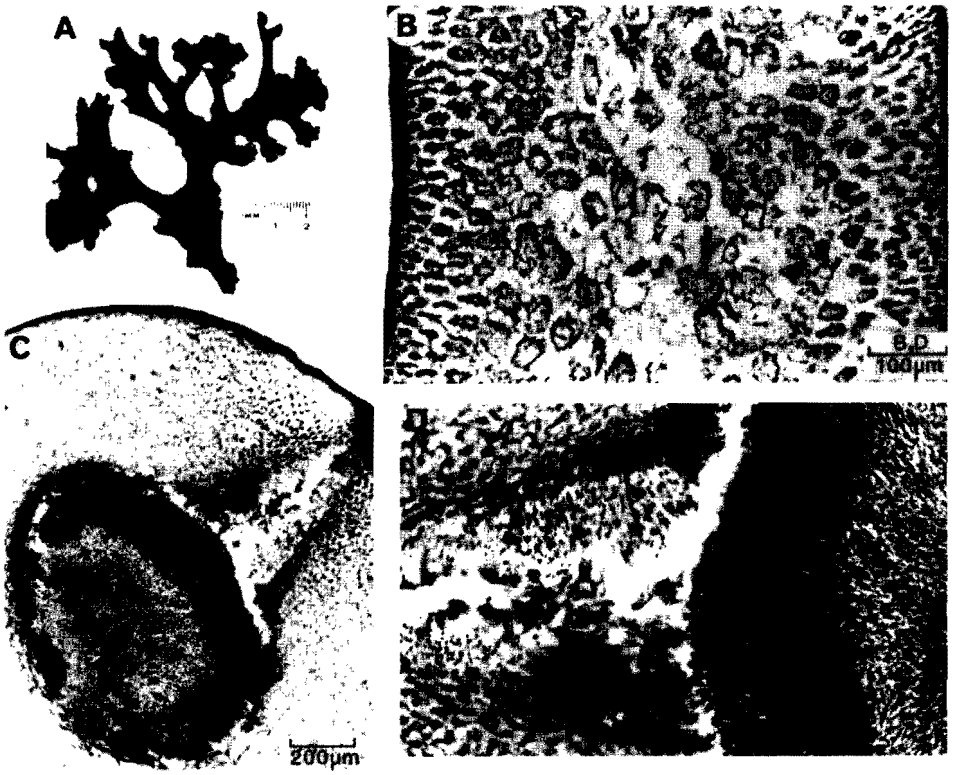


Fig. 13. *Curdiea obesa* (**A, B,** AD, A51996; **C, D,** AD, A19880). **A.** Habit. **B.** Transverse section of thallus. **C.** Section of cystocarp. **D.** Section of cystocarp showing ostiole and dense chains of carposporangia.

2. **Curdiea obesa** (Harvey)Kylin 1932: 61. Huisman & Walker 1990: 417. Womersley 1950: 169.

Sarcocladia obesa Harvey 1855a: 550; 1862: pl. 217. J. Agardh 1876: 427. De Toni 1900b: 426. De Toni & Forti 1923: 25, pl. III fig. 4. May 1965: 408.

FIG. 13

Thallus (Fig. 13A) dark red-brown, decumbent but free of the substrate above the holdfast, 5–10 (-15) cm long, cartilaginous, more or less complanately and irregularly branched from the margins, branches (3-) 5–15 (-25) mm broad but irregular in width and often undulate, apices rounded, 0.5–1.0 mm thick just below apices, 1–1.5 mm thick below, with distinct upper and lower surfaces, the latter usually covered by sponge. Holdfast discoid, 2–10 mm across, with one to a few stipes; epilithic. *Structure* multiaxial, pseudoparenchymatous throughout (Fig. 13B), with a cortex 2–3 cells thick on the lower surface, becoming 4–6 cells thick on the upper surface, outer cells 3–7 (-11) µm in diameter and L/D 1–2, grading inwards to a medulla of large ovoid cells 50–100 µm in diameter, with walls 5–10 µm thick and numerous secondary pit-connections. Rhodoplasts discoid, numerous per cell.

Reproduction. Female plants with 2-celled carpogonial branches borne inside branch margins on mid cortical supporting cells. Carposporophytes (Fig. 13C) with a dense gonimoblast reticulum and a small basal fusion cell, producing a dense upper mass of erect gonimoblast filaments terminating in straight chains (Fig. 13D) of numerous subspherical to ovoid carposporangia 10–14 µm in diameter, maturing apically. Cystocarps on the branch surface but often near the margins, scattered, globose and usually sessile, (1-) 1.5–3 (-4) mm across; pericarp (Fig. 13C) massive, with inner tangentially elongate cells (continuing around base of the carposporophyte) and a medulla and cortex similar to the vegetative tissue, with an ostiole lined by branched filaments of short cells cut off from medullary pericarp cells. Spermatangia not observed.

Tetrasporangia not observed.

Type from Rottnest I., W. Aust. (*Harvey*); lectotype (Millar 1990, p. 341) in Herb. Harvey, TCD (Trav. Set 280).

Distribution: Geraldton, W. Aust. (De Toni & Forti 1923, p. 25), to Nora Creina, S. Aust., on rough-water coasts from shaded shallow depths to deep water.

Selected specimens: Port Denison, W. Aust., drift (*Parsons*, 8.xi.1968; AD, A33210). Safety Bay, W. Aust., drift (*Womersley*, 23.viii.1947; AD, A5844). Hamelin Bay, W. Aust., 1–2 m deep (*Clarke & Engler*, 1.ix.1979; AD, A50616). Point Valliant, Two People Bay, W. Aust., in large pool (*Womersley*, 30.viii.1979; AD, A50956). Elliston, S. Aust., 17 m deep outside bar (*Shepherd*, 12.v.1971; AD, A38676). Thistle I., S. Aust., 16 m deep (*Baldock*, 2.i.1964; AD, A27176). Pondalowie Bay, S. Aust., 4 m deep (*Clarke*, 14.ii.1981; AD, A51996) and drift (*Womersley*, 24.iv.1955; AD, A19880). Victor Harbor, S. Aust., drift (*Womersley*, 23.v.1953; AD, A18744). Sou'West R., Kangaroo I., S. Aust., 6 m deep (*Mitchell*, 24.viii.1963; AD, A26825). Baudin Rocks, Guichen Bay, S. Aust., 2–3 m deep (*Shepherd*, 15.ii.1975; AD, A46115). Nora Creina, S. Aust., 5–6 m deep (*R. Lewis & Kraft*, 13.v.1972; AD, A42219).

C. obesa is characterized by its decumbent habit, resulting in a slightly thicker cortex on the upper surface and commonly a covering of sponge on the lower (shaded) surface. It is essentially of western distribution, reaching east to Nora Creina in South Australia.

3. **Curdiea crassa** Millar 1990: 341, fig. 19A–C. Millar & Kraft 1993: 27.

FIG. 14

Thallus (Fig. 14A) very dark red-brown, complanate, 5–20 cm long, cartilaginous, (1-) 2–4 mm thick, decumbent with distinct upper and lower surfaces, irregularly lobed and divided with lobes 2–5 cm broad, apically rounded and usually narrower below, the underside usually covered with sponge or bryozoans. Holdfast discoid, usually at one end of the thallus, 0.5–2 cm across, thallus flat immediately above; epilithic. *Structure* multiaxial, pseudoparenchymatous throughout, with the cortex on the lower surface (Fig. 14B) 2–3 cells thick, outer cells 10–12 µm in diameter and L/D 1–1.5, and on the upper surface 4–15 (-20) cells thick (Fig. 14C) with anticlinal chains, outer cells 5–10 µm in diameter and L/D 1–2,

grading inwards to a medulla of large ovoid cells 50–120 (-140) μm in diameter with walls 12–30 μm thick and numerous secondary pit-connections. Rhodoplasts discoid, numerous per cell.

Reproduction. Female plants with 2-celled carpogonial branches borne on mid cortical supporting cells. Carposporophytes (Fig. 14D) with a dense gonimoblast reticulum and small basal fusion cell(s), producing a dense upper mass of erect gonimoblast filaments terminating in straight chains (Fig. 14E) of numerous subspherical to ovoid carposporangia 8–14 μm in diameter, maturing apically. Cystocarps scattered over the surface, globular, sessile, 2–3 mm across; pericarp massive, with inner tangentially elongate cells (continuing partly around the base of the carposporophyte, with more ovoid cells at the base) and a medulla and cortex similar to the upper surface of the thallus with an ostiole lined with branched filaments of short cells cut off from medullary pericarp cells. Spermatangia not observed.

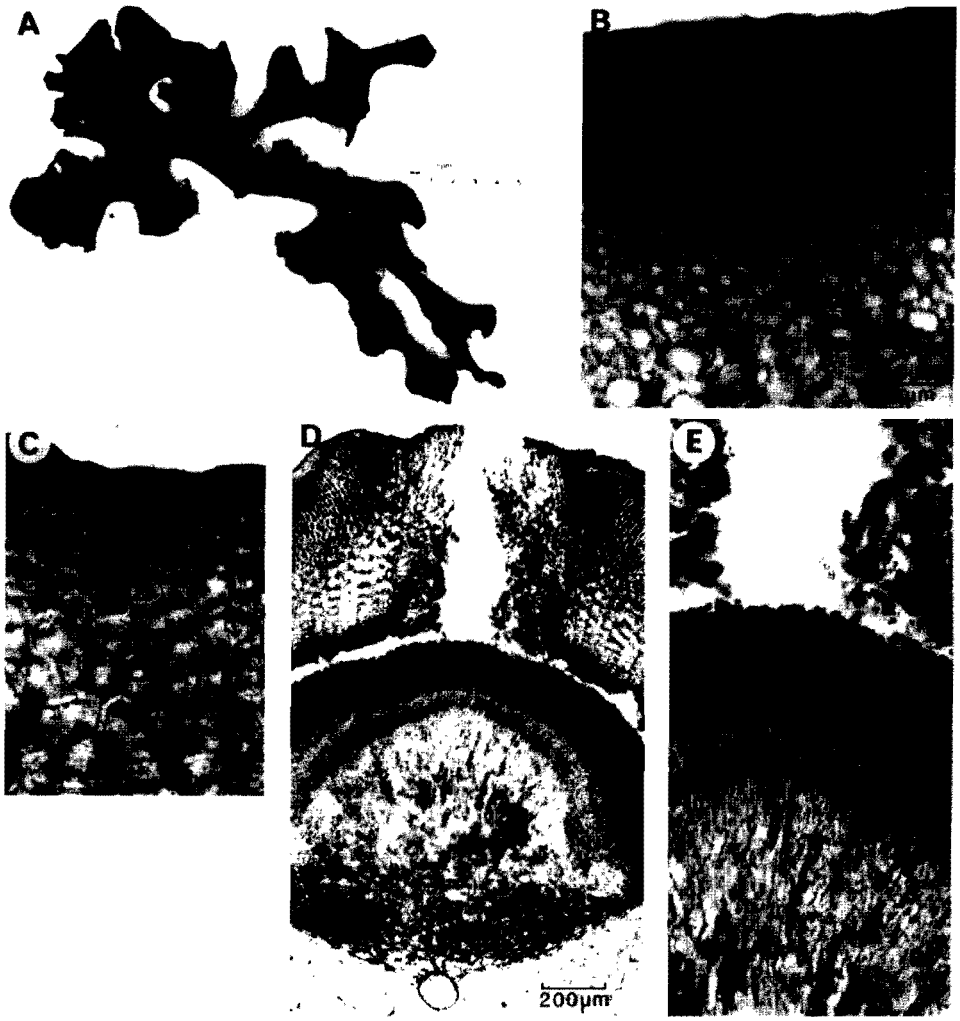


Fig. 14. *Curdiea crassa* (**A**, AD, A57393; **B–E**, AD, A60291). **A.** Habit. **B.** Section of thallus, upper surface. **C.** Section of thallus, lower surface. **D.** Section of cystocarp (air bubble near base). **E.** Section of carposporophyte and ostiole.

Tetrasporangia not observed.

Type from Muttonbird I., Coffs Harbour, N.S.W. (*Millar & Chidgey*, 15.vii.1981); holotype in MELU, AM563.

Distribution: Known from Split Solitary I. to Jervis Bay, N.S.W. and Point Lonsdale to Gabo I., Vic., and E Tasmania.

Selected specimens: Glaneuse Reef, Point Lonsdale, Vic., 2–3 m deep (*Kraft* 5789, *Lewis & O'Brien*, 19.ii.1976; MELU, 23244). Queenscliff, Vic., 8 m deep (*Ramm & Rankin*, 5.ix.1976; MELU). Cape Woolamai, Vic., 15–18 m deep S side (*Goldsworthy & Berthold*, 16.ii.1990; AD, A60187). Gabo I., Vic., 2–5 m deep (*Shepherd*, 16.ii.1973; AD, A43370). Eddystone Point, Tas., 30 m deep (*Riddle*, 24.ii.1990; AD, A60406). S of Eddystone Rock, Tas., 25 m deep (AIMS-NCI, Q66C 3670–G, 24.ii.1990; AD, A60291). Waterfall Bay, Tasman Pen., Tas., 13–19 m deep (*McGeary-Brown*, 29.x.1986; AD, A57393). Bicheno, Tas., 20–22 m deep (*Kraft* 9379a, 18.xii.1993; MELU, 42054).

Millar (1990, p. 341) records *C. crassa* as iridescent and 2–6 mm thick. The south-eastern Australian specimens agree well with Millar's description but are usually only 1–3 mm thick.

ORDER **RHODYMENIALES** Schmitz *in* Engler 1892: 19

Thallus usually erect, foliose to complanately or radially branched, branches terete to compressed or flat, solid or hollow and often segmented; some genera parasitic, minute, pulvinate or lobed. *Structure* multiaxial, pseudoparenchymatous, developing a small-celled cortex and larger-celled medulla, often with secretory cells on inner cells; hollow genera often with longitudinal filaments within the medulla, in some families with transverse diaphragms or partitions. Pit-plugs without cap layers.

Life history triphasic, with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli usually dioecious, procarpic. Carpogonial branches 3- or 4-celled, borne on inner cortical cells together with 2- (or 3-) celled auxiliary cell branches, with the auxiliary initial often being a cortical cell; auxiliary cells produced before fertilization but usually maturing afterwards, often containing a spherical proteinaceous globule; diploid nucleus transferred to auxiliary cell directly or via a connecting cell. Carposporophyte developing outwards, with a basal, erect, fusion cell(s) and with most gonimoblast cells, or only the terminal ones, becoming carposporangia; basal nutritive tissue present or not, with numerous connections to the auxiliary initial cell or supporting cell, with erect filaments of cells from the nutritive tissue to the pericarp remaining as the "tela arachnoidea" of slender elongate cells, or as more or less separated stellate cells around the developing carposporophyte, or in many genera disintegrating. Cystocarps protuberant or largely immersed, with a well-developed pericarp, usually ostiolate. Spermatangia cut off from surface cortical cells via initials.

Tetrasporangia cut off laterally or terminally from mid cortical cells, or transformed from cortical cells, cruciately, decussately or tetrahedrally divided (polysporangia in *Coeloseira*).

The order is usually recognised to include three families and some 38 genera (Kraft 1981), of which 17 genera occur on southern Australian coasts. The families and genera of the Rhodymeniales have been reviewed by Guiry & Irvine (1981) and Irvine & Guiry (1986), and Hawkes & Scagel (1986) monograph and discuss this order on the coast of British Columbia and northern Washington, U.S.A.

KEY TO FAMILIES OF RHODYMENIALES

1. Thallus solid, or hollow but without regular longitudinal filaments bordering the cavity. Tetrasporangia cruciately or decussately divided (but tetrahedral in *Hymenocladia*) ..... RHODYMENIACEAE
1. Thallus hollow, segmented and usually regularly partitioned, with longitudinal or irregular medullary filaments within the mucilage filled cavity and extending back from the branch apices. Tetrasporangia tetrahedrally divided, scattered or in small sori..... 2

    2. Branches with regularly arranged transverse monostromatic diaphragms, with longitudinal filaments either peripheral or scattered between the diaphragms. Carposporangia terminal on gonimoblast filaments or formed directly from the fusion cell. Tetrasporangia scattered, transformed from cortical cells ..... CHAMPIACEAE
    2. Branches with polystromatic partitions or irregular filamentous plugs separating the segments. Carposporangia formed from all or most gonimoblast cells. Tetrasporangia in small depressed sori, borne terminally on cortical cells ..... LOMENTARIACEAE

FAMILY RHODYMENIACEAE Harvey 1849b: 75, 120

Thallus erect, encrusting or minute and parasitic, branches terete to flat or segmented, solid or hollow to varying degrees but lacking regular longitudinal filaments in the medulla, branching alternate, di- to polychotomous, or irregular, radial or complanate, often proliferous. *Structure* multiaxial, cortex 1–3 (-5) cells thick, outer cells often in anticlinal rows, older parts often with a secondary cortex; medulla usually 2–8 (-20) cells across, cells ovoid, with or without small accessory cells or secondary filaments, with secretory cells in some genera; longitudinal filaments bordering the inner medulla absent.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli usually dioecious; procarpic. Carpogonial branches 3- or 4-celled, auxiliary cell branches 2- or 3-celled, borne on inner cortical cells. Carposporophyte developing outwards, with basal fusion cell(s) and nearly all gonimoblast cells becoming carposporangia. Basal nutritive tissue present, with numerous pit-connections to the supporting cell and auxiliary initial cell, erect filaments slender ("tela arachnoidea") or coarse or non persistent. Cystocarps prominent, protuberant or immersed, with a thick pericarp, ostiolate. Spermatangia cut off from outer cortical cells via initials.

Tetrasporangia scattered in the cortex or in nemathecia or sori and lying between sterile cortical filaments, terminal on inner cortical cells or transformed from inner cells, cruciately or decussately divided (tetrahedrally in *Hymenocladia*).

The Rhodymeniaceae is the largest family of the order, with some 30 genera. The habit varies considerably between the genera but reproductive features are similar, with virtually all gonimoblast cells forming carposporangia. The "tela arachnoidea" (J. Agardh 1876, p. 290), used by Kylin (1931) and other authors is, as Sparling (1957, p. 373) found, a variable feature though usually consistent for the genus. All genera have a basal nutritive tissue of branched chains of darkly staining cells, connected to the supporting cell and auxiliary initial cell by numerous pit-connections, and above connected to slender, erect, elongate (often stretched) cells (the "tela arachnoidea") around the developing carposporophyte and thence to pericarp cells around the ostiole; the elongate cells may be relatively coarse or may consist of stellate inner pericarp cells which may disintegrate to varying extents as the cystocarp develops. This variation makes use of the term "tela arachnoidea" of little value, and this account refers instead to the basal nutritive tissue, with erect filaments which may be persistent or may disintegrate and may be slender or relatively prominent.

KEY TO GENERA OF RHODYMENIACEAE

1'. Thallus minute (1–4 mm high), parasitic on *Rhodymenia*.....RHODYMENIOCOLAX
1. Thallus erect, usually 2–40 cm high, not parasitic 2

2. Thallus terete or saccate, segmented or not, laterals at least saccate..... 3
2'. Thallus not saccate, foliose or branched, branches terete to flat..... 7

3. Axes terete, solid, with clavate to ovoid saccate laterals, firm and not mucilaginous..... 4
3'. Axes absent or very short, branches hollow, simple or constricted at intervals; soft and mucilaginous 5

4. Laterals ovoid to obovoid, 3–10 (-14) mm in diameter, borne irregularly on the axes ..... BOTRYOCLADIA
4'. Laterals 1–2 mm in diameter, produced only near apices when fertile, bearing reproductive structures..... CORDYLECLADIA

5. Thallus simple or occasionally basally branched, clavate, 5–30 mm in diameter; tetrasporangia transformed from intercalary cortical cells ..... GLOIOSACCION
5'. Thallus simple or much branched usually polychotomously, with ovoid to elongate segments and regular constrictions; tetrasporangia transformed or lateral on inner cortical cells 6

6. Cortex with a single layer of outer cells; cystocarps protuberant, erect filaments absent around the carposporophyte; tetrasporangia scattered, transformed from inner cortical cells..... COELARTHRUM
6'. Cortex with outer, short, anticlinal filaments of 2–3 cells; cystocarps immersed, erect filaments around the carposporophyte present or absent; tetrasporangia in nemathecia, cut off from inner cortical cells or lower cells of paraphyses ..... WEBERVANBOSSEA

7. Thallus firm, cartilaginous, simple to complanately and furcately to irregularly branched; tetrasporangia cut off from cortical cells, cruciately or decussately divided ... 8
7'. Thallus soft to moderately firm, foliose to complanately branched; tetrasporangia cut off from cortical cells and cruciately or decussately divided, or transformed from inner cells and tetrahedrally divided 9

8. Thallus simple, ovate, relatively thick with a cortex of anticlinal rows of cells and medulla with small cells intermixed with larger cells; tetrasporangia in scattered sori over the blade surface, transformed from intercalary cells ..... ERYTHRYMENIA
8'. Thallus simple and ovate (with proliferations) or much branched largely complanately, furcately or laterally or proliferously, cortex 2–5 cells thick, with rows only in the secondary cortex, medulla of large cells only; tetrasporangia scattered or in sori or nemathecia below branch apices, cut off laterally or terminally from cortical cells or intercalary ..... RHODYMENIA

9. Cortex with anticlinal rows of small cells 10
9'. Cortex one to a few cells thick, not in anticlinal rows 11

10. Cortex compact, of dense anticlinal, mostly unbranched, filaments; medullary cells thick-walled, without secondary pit-connections, with layers (1–4 cells thick) of rhizoidal filaments between the large cells. Cystocarps smooth, becoming horned when mature..... FAUCHEOPSIS
10'. Cortex of lax, dichotomous filaments, medulla with occasional slender rhizoidal filaments and frequent secondary pit-connections. Cystocarps horned ..... GLOIOCLADIA

11. Thallus foliose, simple or branched, medulla 2–4 cells thick, of large ovoid cells bordering a central space within which rhizoids develop, at first sparsely then later filling the space. Cystocarps largely immersed, erect filaments non-persistent; tetrasporangia cut off from cortical cells, cruciately divided, small (20–45 μm in diameter) ..... LEPTOSOMIA

11. Thallus much branched, pinnately to irregularly, medulla 3–20 cells thick, of large and small cells intermixed. Cystocarps protruding; tetrasporangia transformed from inner cells, tetrahedrally divided, large (60–140 μm in diameter)..... HYMENOCLADIA

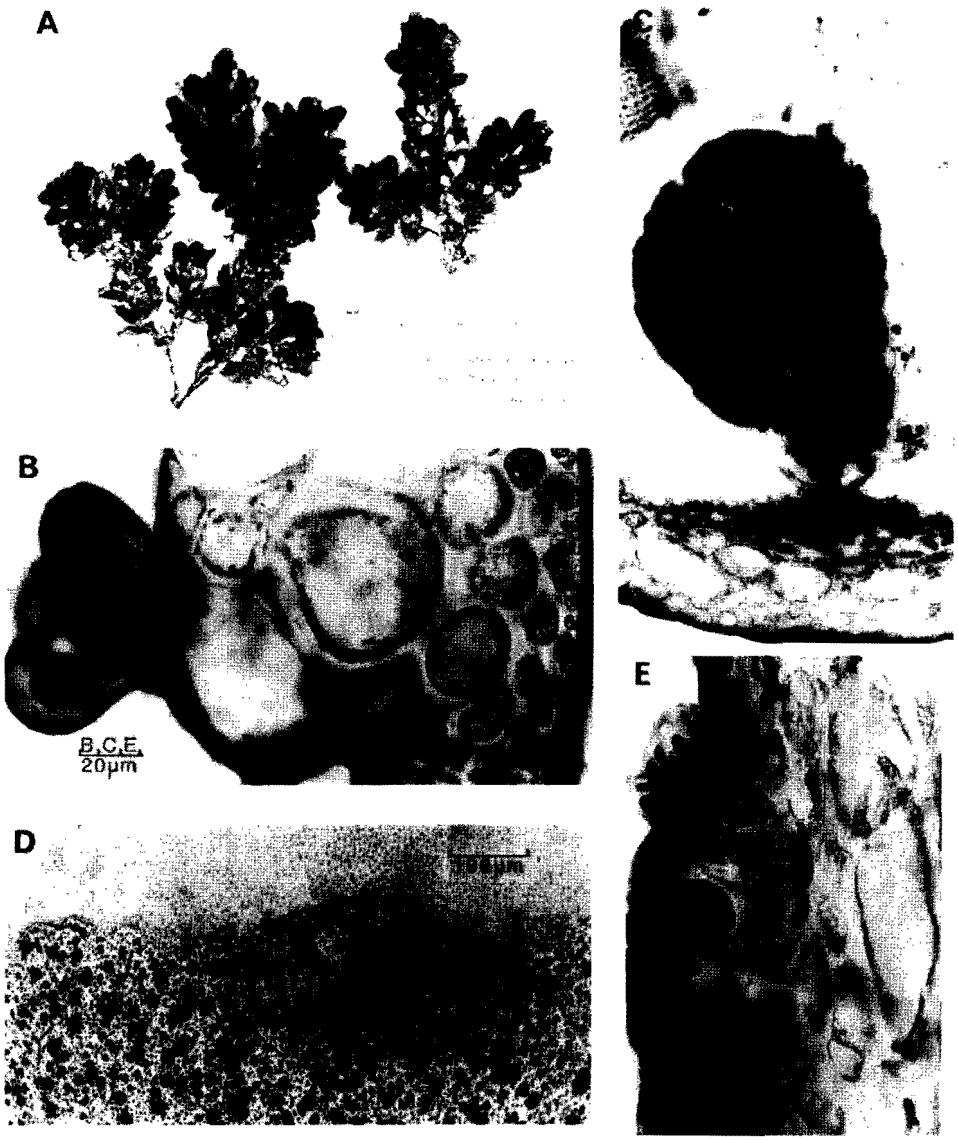


Fig. 15. *Botryocladia sonderi* (**A–C**, AD, A59848; **D**, AD, A63569; **E**, AD, A34914). **A.** Habit. **B.** Section of thallus with internal secretory cells. **C.** Section of cystocarp. **D.** Surface view of margin of tetrasporangial nemathecium. **E.** Section of tetrasporangial nemathecium.

Genus BOTRYOCLADIA (J. Agardh)Kylin 1931: 17, *nom. cons.*

Thallus erect, with sparsely branched, more or less terete, solid, branches bearing hollow, inflated, ovoid to pyriform, usually simple, vesicular laterals, radially or distichously arranged; holdfast discoid or stoloniferous. *Structure* multiaxial, the solid branches with a small-celled cortex grading to a medulla of compact larger cells. Vesicles not or only slightly mucilaginous, with a cortex 2–3 (-6) cells thick, outer layer of small cells continuous or forming rosettes, grading to a medulla 2–3 cells thick, inner cells larger, with or without rosettes of smaller cells developed inwardly between the larger cells; secretory cells single or in groups, borne on the larger medullary cells.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 4-celled, borne on inner cortical (supporting) cells together with a 2-celled auxiliary cell branch; carposporophyte erect, with a basal fusion cell producing lobes with all cells forming carposporangia. Basal nutritive tissue present, erect filaments slender and tending to disintegrate. Cystocarps protruding both inwards and outwards, smooth, ostiolate with a thick pericarp. Spermatangia in scattered sori, cut off from elongate initials on cortical cells of the vesicles.

Tetrasporangia scattered or in shallow nemathecia on the vesicles, transformed from intercalary cortical cells but with slight and unclear pit-connections to outer cortical cells, cruciately or decussately divided.

Type species: *B. uvaria* Kylin (see Silva 1980a, p. 124). [= *B. botryoides* (Wulfen) J. Feldmann].

Botryocladia was first established as a subgenus of *Chrysymenia* by J. Agardh (1851, p. 214) and elevated to a genus by Kylin (1931, p. 17).

A distinctive genus of some 30 species, mainly in tropical to warm temperate waters. Brodie & Guiry (1988a) have given a thorough account of *B. ardreana* from Portugal.

Botryocladia sonderi Silva*

Chrysymenia obovata Sonder 1848: 176; 1853: 677; 1881: 18. J. Agardh 1872: 19; 1876: 324. De Toni 1900b: 544. Harvey 1849a: 77; 1855a: 556; 1858, pl. 10; 1859b: 327. Lucas & Perrin 1947: 203, fig. 67. Tisdall 1898: 506. Wilson 1892: 179.

Gastroclonium obovatum (Sonder)Kützing 1849: 865; 1865: 35, pl. 99a–f.

Botryocladia obovata (Sonder)Kylin 1931: 18. G. Feldmann 1945: 57, fig. 1. Guiler 1952: 93. Huisman & Walker 1990: 415. May 1965: 360. Womersley 1950: 174; 1953: 38; 1966: 150.

Halymenia botryoides Richard 1834: 145. J. Agardh 1851: 214.

FIG. 15

Thallus (Fig. 15A) dark red-brown, 10–30 cm high, rigid and cartilaginous, with sparsely and irregularly branched, solid, terete, main branches 1–1.5 mm in diameter, bearing radially ovoid to obovoid, hollow, membranous, vesicular laterals 5–20 (-25) mm long and 3–10 (-14) mm in diameter, usually closely adjacent and each with a short, narrow, stipe, lost from lower axes with the stipe remnant remaining. Holdfast discoid, 2–10 mm across; epilithic. *Structure* multiaxial, branches solid with a small-celled cortex 3–6 cells thick, outer cells ovoid, 4–8 µm in diameter, grading to a larger-celled medulla, cells 40–80 µm in diameter and L/D 1–3 in longitudinal section, with frequent secondary pit-connections. Vesicular laterals with a continuous cortex 2–3 cells thick, outer cells ovoid, 4–10 µm in diameter, grading rapidly to a medulla 2–3 cells thick, the inner cells rounded, 40–65 µm across, lengthwise L/D 1–3, these larger cells cutting off smaller inner cells over their joint walls forming rosettes which become 3–5 cells broad. Secretory cells (Fig. 15B)

* This name, to replace the misapplied name *B. obovata* (Sonder)Kylin, is being proposed by Dr P.C. Silva in his "Indian Ocean Catalogue", scheduled for publication in 1996.

scattered, sparse, on inner larger medullary cells, single or in groups of 2–4 (-9), subspherical, 30–40 µm in diameter, with a thick gelatinous wall. Rhodoplasts discoid.

Reproduction. Gametangial thalli probably dioecious. Carpogonial branches and auxiliary cell branches unknown. Carposporophyte (Fig. 15C) with an erect, basal, fusion cell producing dense, compact, lobes of carposporangia 8–12 µm in diameter. Basal nutritive tissue broad and shallowly concave, erect filaments (which disintegrate) continuing to anticlinal pericarpic filaments. Cystocarps 0.8–1.3 mm across, protruding both outwardly and into the vesicle, with an outer pericarp 150–250 µm and 10–12 cells thick, ostiolate. Spermatangia unknown.

Tetrasporangia in shallow nemathecia (Fig. 15D) over the vesicles, the sporangia (Fig. 15E) lying among elongate outer cortical cells (L/D 2–6), basally pit-connected to inner cortical cells and with slight pit-connections to the outer cells, ovoid, 25–45 µm long and 15–25 µm in diameter, decussately or cruciately divided.

Type from W. Aust. (*Preiss*); holotype in MEL, 504344.

Distribution: Port Denison, W. Aust., to N Waratah Bay, Vic., and the N coast of Tasmania.

Selected specimens: Port Denison, W. Aust., 1–5 m deep on jetty (*Kraft*, 14.xii.1971; AD, A41169). Cowaramup Bay, W. Aust., 2–3 m deep (*Clarke & Engler*, 1.ix.1979; AD, A50652). Emu Beach, King George Sound, W. Aust., drift (*Mitchell*, 27.ix.1966; AD, A30818). Point Sinclair, S. Aust., drift (*Womersley*, 25.i.1951; AD, A13872). Waldegrave I., S. Aust., 22 m deep (*Shepherd*, 23.x.1970; AD, A37394). N Spencer Gulf, S. Aust., 6 m deep (*Shepherd*, 5.ix.1973; AD, A44179). Tiparra reef, S. Aust., 6 m deep (*Shepherd*, 24.v.1969; AD, A34914). Port Moorowie, Yorke Pen., S. Aust., 2–3 m deep (*Cannon*, 7.i.1989; AD, A59848). Somerton Beach, S. Aust., drift (*Womersley*, 4.iii.1944; AD, A1635). Aldinga, S. Aust., drift (*Womersley*, 28.v.1994; AD, A63569). Bay of Shoals, Kangaroo I., S. Aust., 3 m deep (*Womersley*, 5.i.1990; AD, A60124). American R. inlet, Kangaroo I., S. Aust., drift (*Womersley*, 5.ix.1946; AD, A4005). Vivonne Bay, Kangaroo I., S. Aust., just below low tide level (*Womersley*, 15.i.1947; AD, A4252). Robe, S. Aust., drift (*Womersley*, 25.v.1963; AD, A26515). Dutton Bay, Portland, Vic., drift (*Womersley*, 13.iv.1959; AD, A22671). Corio Bay, Vic., 12 m deep (*Macpherson*, 17.v.1963; AD, A28809). Point Lonsdale, Vic., upper sublittoral (*Womersley*, 21.i.1967; AD, A31718). San Remo, Vic., drift (*Sinkora* A846, 6.ix.1970; AD, A62598). N Waratah Bay, Vic., drift (*Sinkora* A2561, 15.iii.1979; AD, A60979). Georgetown, Tas., upper sublittoral (*Womersley*, 29.i.1949; AD, A10257).

In describing *Chrysymenia obovata* as a new species, Sonder cited also *Gigartina ovata* Lamouroux (1813, p. 136, pl. 4 fig. 7) and *Chondria ovalis* var. ß *obovata* C. Agardh (1822, p. 349). Lamouroux's type is *Claviclonium ovatum* (Lamouroux)Kraft & Min-Thein (1983, p. 172). Silva is discussing and renaming the well known *B. obovata* (Sonder)Kylin as *B. sonderi*. *Halymenia botryoides* Richard is almost certainly the same as *B. australis*, but the epithet cannot be transferred to *Botryocladia* since *Botryocladia botryoides* (Wulfen) J. Feldmann (1941, p. 90) is recognised as a separate species from the Mediterranean.

B. sonderi is a common species on most southern Australian coasts, from rough-water situations to calm areas with a strong current flow, and from low tide level to 24 m deep. Plants are often denuded of ramuli except near the apices, and commonly are heavily overgrown with encrusting coralline and other algae.

Genus CORDYLECLADIA J. Agardh 1852: 702

Thallus erect, cartilaginous, with numerous terete to slightly compressed fronds from a crustose base, irregularly and sparsely branched, with swollen or short, ovoid, laterals. *Structure* multiaxial, solid, with a small-celled cortex 2–5 cells thick and a medulla of larger, pseudoparenchymatous, closely packed cells.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Fertile structures in swollen branch ends or ovoid, lateral ramuli near branch apices. Gametangial thalli dioecious. Carpogonial branches 3- or 4-celled, borne on inner cortical (supporting) cells together with a 2- or 3-celled auxiliary cell branch. Carposporophyte with a basal, usually branched, fusion cell and lobes of carposporangia

developed from all cells. Basal nutritive tissue present, erect filaments weakly developed or absent. Cystocarps largely external, with a thick, ostiolate, pericarp. Spermatangia in sori on swollen apices or ovoid laterals, cut off via elongate initials from outer cortical cells.

Tetrasporangia terminal or intercalary, formed in sori in swollen apices or the ovoid ramuli, cruciately or decussately divided.

Lectotype species: *C. erecta* (Greville)J. Agardh.

A genus of 3 species, the type from Europe, *C. furcellata* from southern Australia, and *C. guiryi* Gargiulo, Furnari & Cormaci (1990, p. 632) from Sicily.

The type has been investigated in detail by Brodie & Guiry (1988b).

Cordylecladia furcellata J. Agardh 1872: 19; 1876: 327; 1896: 94. De Toni 1900b: 508. G. Feldmann 1967: 372.? May 1965: 392. Sonder 1881: 18. Tisdall 1898: 506. Wilson 1892: 179.
Gymnogongrus furcellatus sensu Harvey 1860a: 322.

PLATE 1 fig. 2; FIGS 16, 30A

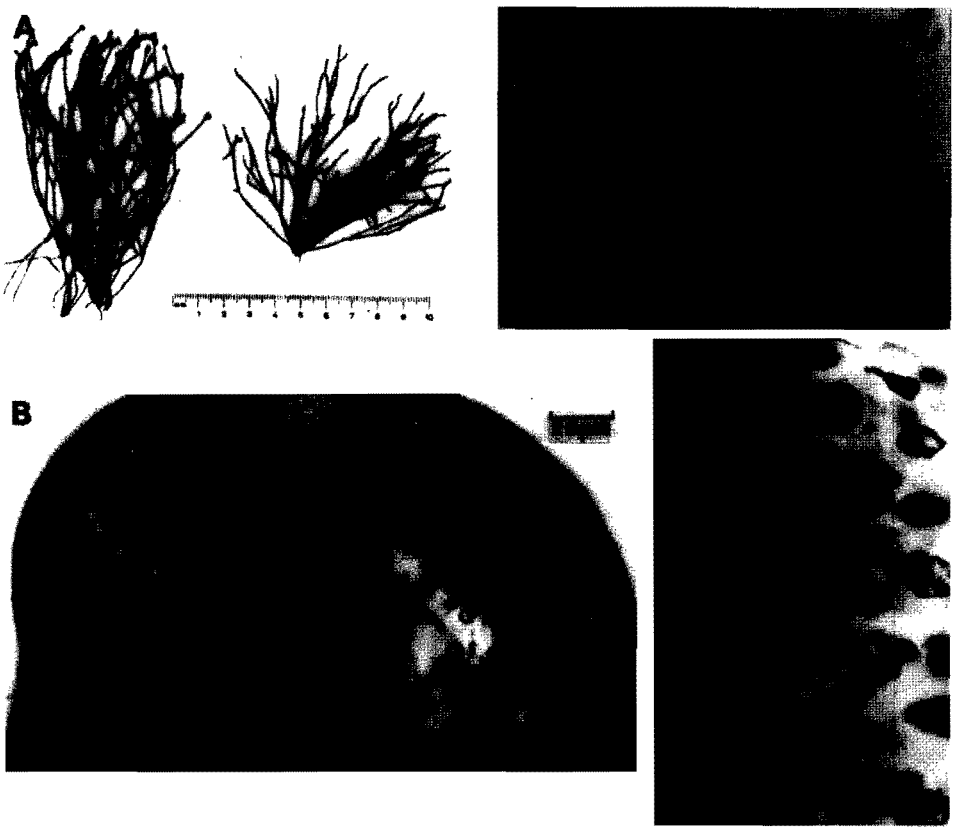


Fig. 16. *Cordylecladia furcellata* (**A, C,** AD, A58702; **B,** AD, A53174; **D,** AD, A26474). **A.** Habit. **B.** Section of a cystocarp with basal tissue below carposporophyte and thick pericarp (not through ostiole). **C.** Section of spermatangial thallus. **D.** Transverse section of bladder with sorus of tetrasporangia.

Thallus (Fig. 16A) dark red-brown, cartilaginous, 10–25 cm high, with numerous erect, linear, terete to slightly compressed, branches from a basal crust. Branches sparsely and irregularly branched (often subdichotomous) at intervals of (1-) 2–6 cm, solid, 0.7–1 mm in diameter or broad from base to apices, with swollen or ovoid fertile laterals 1.2–2.5 mm long and 0.9–1.5 mm in diameter near the branch apices. Holdfast crustose, 2–10 mm across; epilithic. *Structure* multiaxial, developing a cortex 3–5 cells broad, outer cells ovoid and 2–4 (-5) µm in diameter, grading fairly abruptly to a medulla of compact angular cells becoming 80–120 µm across, walls 4–8 µm thick, with no or very slight intercellular spaces and with few secondary pit-connections. Rhodoplasts discoid to elongate, ribbon like in inner cells.

Reproduction. Fertile structures formed in swollen apices or the ovoid lateral ramuli, these being shed after maturity and often becoming hollow by breakdown of the central medullary cells. Gametangial thalli dioecious. Carpogonial branches (Fig. 30A) 3-celled, borne on inner cortical cells together with a 2-celled auxiliary cell branch. Carposporophyte dendroid, with a basal fusion cell, branched above, and several lobes of ovoid to angular carposporangia 8–12 µm in diameter. Basal nutritive tissue prominent, with the erect filaments largely disintegrating, with cells adjacent to the pericarp remaining stellate. Cystocarps (Fig. 16B) single or crowded, sessile and largely protuberant, 1–2 mm across, pericarp 200–300 µm thick, with a narrow ostiole. Spermatangia (Fig. 16C) cut off from outer cortical cells via elongate initials, ovoid, 2–3 µm in diameter.

Tetrasporangia (Fig. 16D) scattered or in slight sori in the outer cortex, with elongate cortical cells, basally pit-connected, elongate-ovoid, 30–45 µm long and 12–20 µm in diameter, cruciately or (usually) decussately divided.

Type from Port Phillip Heads, Vic. (*Harvey*, Alg. Aust. Exsicc. 395E); holotype in Herb. Agardh, LD, 26690.

Distribution: West I., S. Aust., to Flinders, Vic., and the E coast of Tasmania.

Selected specimens: "The Amphitheatre", West I., S. Aust., 10–20 m deep (*Edyvane*, 24.v.1982; AD, A53174). Robe, S. Aust., 13 m deep (*Mitchell*, 25.v.1963; AD, A26474); 0–2 m deep near jetty (*Womersley*, 26.ix.1992; AD, A62818) and 1 m deep in shaded pool, outer coast (*Guiry*, 4.vii.1988; AD, A58702). Nora Creina, S. Aust., 3–8 m deep (*Owen*, 3.ix.1971; AD, A39609) and 5–6 m deep (*R. Lewis & Kraft*, 13.v.1972; AD, A42220). Port MacDonnell, S. Aust., drift (*Womersley*, 2.xii.1989; AD, A60030). Point Lonsdale, Vic., 14 m deep (*Macpherson*, 15.v.1963; AD, A28925). Portsea, Vic., 3–5 m deep near jetty (*Kraft* 8978 *& Saunders*, 24.iii.1992; MELU). Flinders, Vic., 20 m deep (*Millar*, 20.iii.1988; MELU; AD, A63404). Swan I., NE Tas., 5–8 m deep (*Edgar*, 15.iv.1995; AD, A64395). Lady Bay, Southport, Tas., 7 m deep (*Brown & Kenchington*, 14.x.1986; AD, A57692).

This taxon was first recognised by Harvey (1860a, p. 322) who referred to it doubtfully as *Gymnogongrus furcellatus* (C. Agardh)J. Agardh (1851, p. 318). J. Agardh (1872, p. 20) realised this was incorrect, and described it as a new species of *Cordylecladia*, based on Harvey Alg. Aust. Exsicc. 395 (not 295) from Port Phillip Heads, Vic.

G. Feldmann (1967, p. 372) commented on a specimen from Champion Bay, W. Aust., which was sterile and probably not this species.

Cordylecladia ?australis Harvey is a nomen nudum used by Harvey for his Alg. Aust. Exsicc. 375H from Phillip I., Vic.; it appears to be *C. furcellata*, based on MEL, 675972.

Cordylecladia furcellata doubtfully belongs to *Cordylecladia* since the fertile, caducous, bladders are distinct from the swollen upper fertile branches in the type species, the cystocarps have weakly-developed erect filaments from the basal nutritive tissue and the tetrasporangia are basally pit-connected to inner cortical cells and not transformed from intercalary cortical cells as in the type species, *C. erecta* (Brodie & Guiry 1988b).

Genus GLOIOSACCION Harvey 1859a, pl. 83

Thallus simple or rarely branched, ovoid to clavate or fusiform, saccate with abundant mucilage, single or clustered from a discoid holdfast. *Structure* multiaxial, developing a cortex of outer small-celled anticlinal filaments and inner ovoid cells, and a medulla 1–3 cells thick, the inner cells large and bearing secretory cells on their inner sides directly or on derivative cells or their arms.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

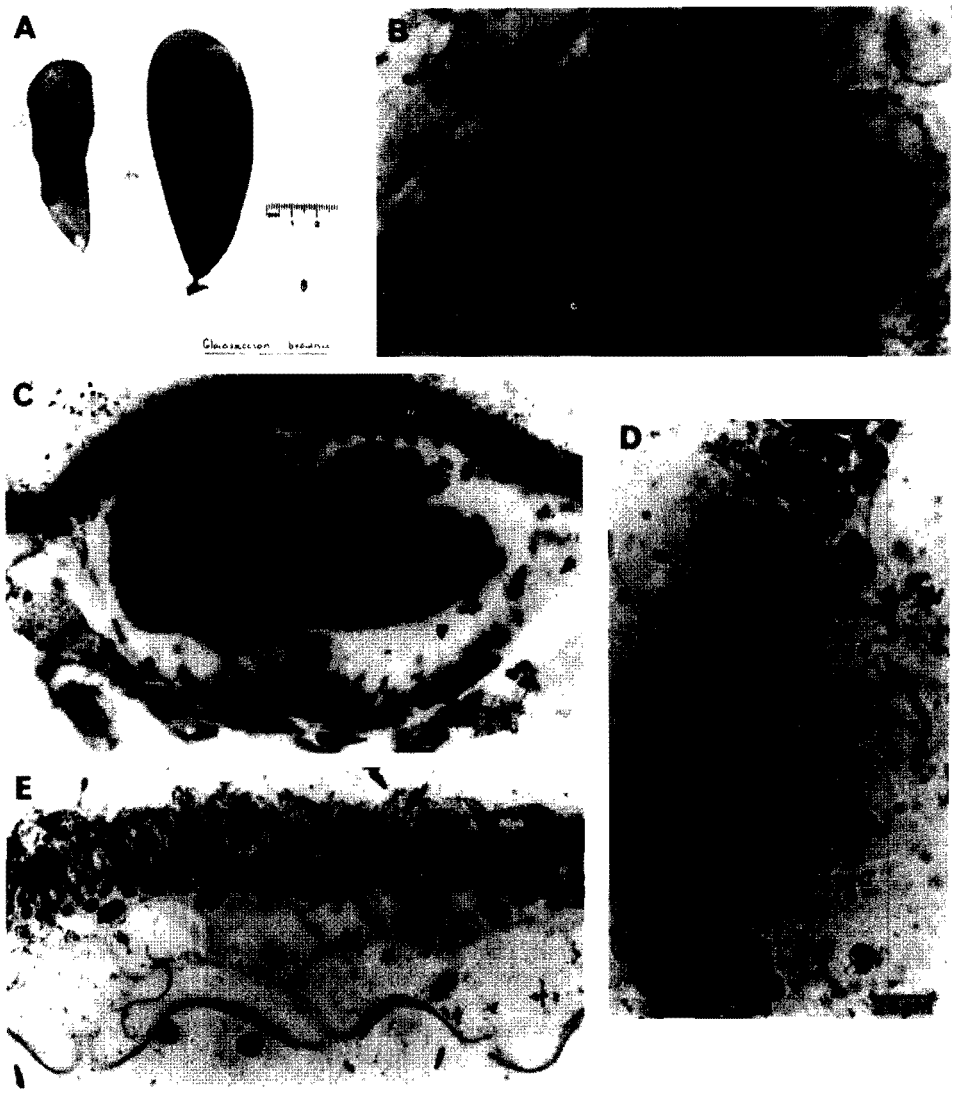


Fig. 17. *Gloiosaccion brownii* (**A, D,** AD, A52848; **B,** AD, A57448; **C,** AD, A60172; **E,** AD, A22372). **A.** Habit. **B.** Secretory cells on inside of inner medullary cells. **C.** Cross section of a cystocarp. **D.** Transverse section of spermatangial thallus. **E.** Cross section of tetrasporangial thallus; two secretory cells on inner medullary cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 4-celled, borne on inner cortical (supporting) cells along with a 2-celled auxiliary cell branch. Carposporophytes directed outwards, with a basal, erect, usually branched fusion-cell and dense, compact, lobes of carposporangia, formed from all cells. Basal nutritive tissue present, with erect filaments of elongate cells not persistent, and short-celled filaments around the ostiole. Cystocarps scattered, only slightly protruding on the thallus surface, more so inwardly, with a thick pericarp, ostiolate. Spermatangia cut off from surface cortical cells via initials.

Tetrasporangia scattered in the slightly thickened cortex, intercalary and transformed from mid cortical cells, with slender pit-connections to outer cortical cells, or decussately divided.

Type species: *G. brownii* Harvey 1859a: pl. 83.

A monospecific genus from southern Australia but also known from New Zealand.

G. Feldmann & Bodard (1965, p. 9) considered that *Gloiosaccion* could not be separated from *Botryocladia*, and proposed (see also Silva 1980a, p. 124) that *Botryocladia* be conserved. However, the two genera differ in habit, in cortical construction, in cystocarp protrusion (see key above) and in how the tetrasporangia are borne, and these features are considered adequate to separate the two genera.

Gloiosaccion brownii Harvey 1859a: pl. 83; 1859b: 322; 1863, synop.: xliv. J. Agardh 1876: 317; 1892: 86. Guiler 1952: 94. Huisman & Walker 1990: 416. Kylin 1931: 19. Lucas & Perrin 1947: 202, fig. 66. May 1965: 360. Reinbold 1897: 52. Sonder 1881: 18. Tisdall 1898: 506. Wilson 1892: 179. Womersley 1950: 175; 1966: 150.
Halosaccion hydrophora sensu Harvey 1855a: 556 (NON Postels & Ruprecht 1840: 19, pl. 35C).
Halosaccion firmum sensu Harvey 1855a: 556 (NON Postels & Ruprecht 1840: 19, pl. 35B).
Gloiosaccion hydrophora J. Agardh 1892: 85. Tisdall 1898: 506. Wilson 1892: 179.
Chrysymenia brownii (Harvey)De Toni 1900b: 545. Lucas 1929a: 19; 1929b: 50.
Gloiosaccion pumilum J. Agardh 1892: 85.
Botryocladia brownii (Harvey)Silva *ex* Nelson & Adams 1984: 21.

FIG. 17

Thallus (Fig. 17A) dark red-brown, fading to grey-red, with one to a few simple, saccate, bladders from the holdfast, bladders clavate to tapering above, rarely furcate, 4–16 (-20) cm long and (1-) 2–5 (-6) cm in diameter, apex usually broad and rounded with a short, slender stipe; contents highly mucilaginous. Holdfast discoid, 1–5 mm across; usually epilithic, occasionally epiphytic (e.g. on *Amphibolis* or *Osmundaria*). *Structure* multiaxial, developing a cortex increasing from 35–45 µm thick in calm-water plants to 110–140 µm thick in rough-water plants, with an outer cortex (30-) 40–50 µm thick in calm-water plants to 60–100 µm thick in rough-water plants, consisting of simple or basally branched anticlinal filaments (3–4 cells long, becoming 6–8 cells long), outer cells ovoid, 2–3 µm in diameter, arising from periclinally ovoid inner cortical cells 10–20 µm in diameter. Medulla 1–3 cells thick, inner cells irregular in size, more or less ovoid, 120–180 (-320) µm in diameter, with numerous secondary pit-connections. Secretory cells (Fig. 17B, E) formed directly on some inner medullary cells, 1–12 per cell, ovoid, (15-) 25–55 µm in diameter; in some larger plants, clusters of laxly branched filaments also occur on inner medullary cells, occasionally also with secretory cells. Rhodoplasts discoid to elongate in cortical cells, becoming ribbon shaped and branched in medullary cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 4-celled, borne on inner cortical (supporting) cells together with a 2-celled auxiliary cell branch, the auxiliary cell with a spherical proteinaceous inclusion. Carposporophytes (Fig. 17C) with a basal fusion cell, branched above and bearing lobes with all cells forming ovoid carposporangia 10–18 µm in diameter. Basal nutritive tissue small-celled, with non-persistent erect filaments, and small-celled erect filaments forming the pericarp. Cystocarps scattered, 0.5–1

mm across, very slightly protruding on the surface but more so inwardly, with a thick pericarp similar to the cortex but becoming 130–150 µm thick, ostiolate. Spermatangia (Fig. 17D) in scattered sori, cut off from outer cortical cells, ovoid, 1.5–2 µm in diameter.

Tetrasporangia (Fig. 17E) in extensive nemathecia with or without defined margins, scattered in the outer, thickened, cortex, transformed from intercalary cells and basally pit-connected to mid cortical cells with other very slender pit-connections (Fig. 17F) to outer cortical cells, lying in the outer cortex, ovoid, 40–55 µm long and 10–22 µm in diameter, decussately divided.

Type from Georgetown, Tas. (*Harvey*, Alg. Aust. Exsicc. 419); lectotype (designated by Womersley in 1952) in Herb. Harvey, TCD.

Distribution: Geraldton, W. Aust., to Jervis Bay, N.S.W., and around Tasmania.
Also recorded from the Kermadec Islands by Nelson & Adams (1984, p. 21).

Selected specimens: Geraldton, W. Aust. (MEL, 608502). Cottesloe, W. Aust., drift (*Royce* 1065, 12.vi.1951; AD, A16243). Twilight Cove, Eyre, W. Aust., drift (*Cambridge*, 16.xii.1981; AD, A56706). Twin Rocks, Head of Great Australian Bight, S. Aust., 20–22 m deep (*Branden*, 19.i.1991; AD, A61128). Pearson I., S. Aust., 10–15 m deep (*Shepherd*, 28.iii.1982; AD, A53025). Wanna, S. Aust., drift (*Womersley*, 19.ii.1959; AD, A22372). Tiparra Reef, S. Aust., 9–12 m deep on *Osmundaria* (*Shepherd*, 13.v.1982; AD, A53333). Troubridge I., S. Aust., 23 m deep (*Shepherd*, 4.ii.1969; AD, A33813). Port Noarlunga, S. Aust., 19 m deep (*Branden*, 26.iii.1987; AD, A57448). Victor Harbor, S. Aust., 6 m deep (*Clarke*, 30.xii.1981; AD, A52848 —"Marine Algae of southern Australia" No. 94a). Kingscote, Kangaroo I., S. Aust., 1–2 m deep on jetty piles (*Latz*, 29.xi.1968; AD, A33000). Muston, American R. inlet, Kangaroo I., S. Aust., 4–5 m deep (*Shepherd*, 29.xii.1977; AD, A48961). Vivonne Bay, Kangaroo I., S. Aust., 3–4 m deep on jetty piles (*Latz*, 22.xi.1968; AD, A33024). Nora Creina, S. Aust., drift (*Womersley*, 17.i.1971; AD, A37830 —"Marine Algae of southern Australia" No. 94). The Fort, Port Phillip Bay, Vic., 7.5 m deep on old logs (*Berthold*, 6.ii.1990; AD, A60172). Shoreham, Westernport Bay, Vic., drift on *Amphibolis antarctica* (*Sinkora* A1260, 29.x.1971; AD, A54209). Crawfish Rock, Westernport Bay, Vic., 3–5 m deep (*Watson*, 29.viii.1971; AD, A39366). Walkerville, Vic., drift on *Amphibolis* (*Sinkora* A1640, 23.ii.1972; AD, A43162). Ulverstone, Tas., drift (*Gordon*, 18.i.1966; AD, A29981). Port Arthur, Tas., 18 m deep (AIMS-NCI, Q66C 3885-K, 1.iii.1990; AD, A60340). Satellite I., D'Entrecasteaux Ch., Tas., 15 m deep (*Shepherd*, 17.ii.1972; AD, A41624). Green I., Jervis Bay, N.S.W., 8 m deep (*Millar & Richards*, 31.i.1991; NSW, 10309; AD, A63402).

The earliest manuscript name applied to this species is *Fucus allantoides*, by Brown, mentioned in the Latin (but not the English) description of *Fucus saccatus* by Turner (1819, p. 105, pl. 241). This brief mention, though it almost certainly applies to *G. brownii* (as Harvey considered) is considered not to be a valid description (Art. 34), and Turner's comparisons with *F. radula* (*Sarcothalia*) and *Asperococcus bullosus* are both erroneous.

G. brownii varies considerably in thickness of the cortex; young plants and those from calm-water situations have relatively thin cortices, but are consistent in having sessile gland cells on some of the large inner cortical cells.

Harvey (1859a, pl. 83) described two varieties, α *membranaceum* and β *firmum*; these probably correspond to young and older plants and are not worth recognising. These varieties were distributed in Alg. Aust. Exsicc. nos 419 and 420 respectively. Harvey (1860a, p. 322) apparently changed *firmum* to *coriacea*, referring to No. 420 also, and in 1863 (synop.: xliv) described var. *furcatum*, based on a plant which had become furcate.

G. pumilum J. Agardh appears to be a slender and young plant of *G. brownii*, based on the type from Port Phillip Heads, Vic. (holotype in Herb. Agardh, LD, 26407). A few specimens in MEL originally named *pumilum* were collected after 1892.

Genus COELARTHRUM Børgesen 1910: 192

Thallus erect or decumbent, irregularly or regularly and synchronously branched, with or without percurrent axes, constricted with ovoid to elongate, hollow, mucilage-filled segments. *Structure* multiaxial, segments with a thin cortex with usually a single layer of outer cells, and a large-celled medulla 1–2 cells broad, bearing secretory cells on smaller inner cells or filaments; partitions one or many cells thick.

Life history triphasic, with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 4-celled, borne on mid cortical supporting cells, auxiliary cells borne on an intercalary cortical cell on the supporting cell. Carposporophytes erect with a basal fusion cell and gonimoblast cells all becoming carposporangia. Basal nutritive tissue present, with erect filaments disintegrating early. Cystocarps protruding, with a thick pericarp, ostiolate. Spermatangia in sori, cut off from outer cortical cells.

Tetrasporangia scattered, transformed from inner cortical intercalary cells, decussately divided.

Type species: *C. albertisii* (Piccone) Børgesen 1910: 192, figs 11, 12.

A genus of about six species, characterised by the hollow segments, external cystocarps without persistent erect filaments around the carposporophyte, and scattered tetrasporangia transformed from inner cortical cells. The Australian species have been monographed by Huisman (1996).

KEY TO SPECIES OF *COELARTHRUM*

1. Thallus even-topped, with segments branched apically, growth largely synchronous; constrictions 0.5–1 mm long, with pseudoparenchymatous, relatively thick, partitions ..... 1. *C. opuntia*
1. Thallus irregularly branched with percurrent main axes and branches, new branches arising from any part of the upper half of segments; constrictions very short, partitions monostromatic ..... 2. *C. cliftonii*

1. **Coelarthrum opuntia** (Endlicher)Børgesen 1937: 333, figs 9, 10. Huisman 1996: 100, figs 16–25.
Chondria opuntia J. Agardh 1841: 21 (*nom. illegit.* – see Huisman 1996: 103).
Chrysymenia opuntia Endlicher 1843: 42.
Lomentaria opuntia (J. Agardh)J. Agardh 1852: 737. Kylin 1931: 33, pl. 20 fig. 48.
Lomentaria muelleri Sonder 1853: 693.
Chylocladia muelleri (Sonder)Harvey 1860: pl. 138. J. Agardh 1876: 302. Sonder 1881: 17. Tisdall 1898: 506. Wilson 1892: 180.
Erythrocolon muelleri (Sonder)J. Agardh 1896: 91. Biswas 1945: 529, pl. II fig. 6. De Toni 1900b: 585. Lucas & Perrin 1947: 208, fig. 73.
Coelarthrum muelleri (Sonder) Børgesen 1931: 9, figs 6, 7. Huisman 1993: 16. Kylin 1931: 15. May 1965: 361. Womersley 1950: 175.
Lomentaria valida Kützing 1865: 30, pl. 85a, b.
Chylocladia ?valida (Kützing)J. Agardh 1890: 24. Reinbold 1897: 53.

PLATE 1 fig. 3; FIG. 18

Thallus (Fig. 18A) medium red to dark red-brown, (5-) 10–30 cm high, much branched with even-topped branches of similar height (growth usually synchronous), branches segmented with slender constrictions mostly 0.5–1 mm long and ovoid to elongate, hollow, segments bearing (1-) 2–4 branches from the apex of most segments; mature segments increasing in length below, 0.5–3 (-4) cm long and 2–7 mm in diameter, lowest segments (stipe) terete, 1–2 mm in diameter. Holdfast crustose and thick, 2–10 mm across, bearing one to several fronds; epilithic. *Structure* multiaxial, with a cortex 30–50 µm and 2–3 cells thick, outer cells laxly arranged, often in slight rosettes, ovoid and 5–8 (-10) µm in diameter, and a large-celled medulla 1–2 cells thick bordering the central weakly mucilaginous cavity, with the inner cells ovoid and 50–100 (-220) µm in diameter, walls 4–10 µm thick, with

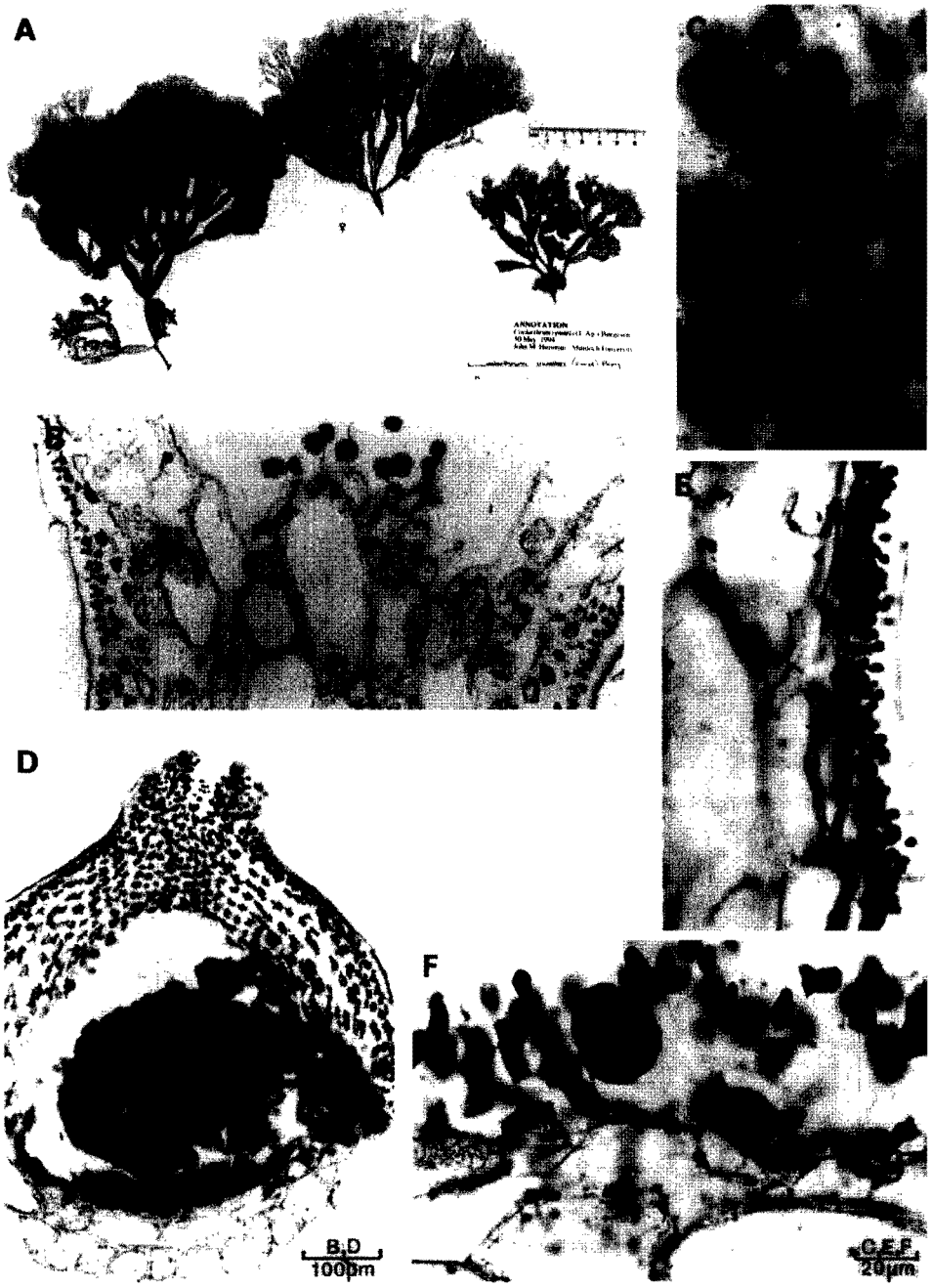


Fig. 18. *Coelarthrum opuntia* (**A–C, E, F,** AD, A46643; **D,** AD, A52095). **A.** Habit. **B.** Longitudinal section of a diaphragm with cluster of secretory cells on upper side. **C.** Filaments with secretory cells on inside of medullary cells. **D.** Section of cystocarp. **E.** Longitudinal section of spermatangial thallus. **F.** Section of tetrasporangial thallus.

frequent secondary pit-connections and bearing 1–3 ovoid or pyriform secretory cells (Fig. 18C) 20–30 µm in diameter, on cells on the inner medullary cells; long surface hairs frequent. Constrictions with pseudoparenchymatous partitions 6–12 cells thick, of large and small cells intermixed with a cluster of secretory cells borne on the upper side of the partition (Fig. 18B). Rhodoplasts discoid to elongate, in chains or ribbon like in inner cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 4-celled, borne on mid cortical cells; auxiliary cell branches 2-celled, auxiliary cell with a large, globular inclusion. Carposporophyte (Fig. 18D) with a basal fusion cell and all gonimoblast cells becoming ovoid to angular carposporangia 20–30 µm in diameter. Basal nutritive tissue moderate, erect filaments disintegrating but walls of lower cells remaining. Cystocarps scattered, external, 1–1.5 mm in basal diameter, conical to hemispherical and often beaked around the ostiole; pericarp 130–220 µm and 6–12 cells thick, cells laxly arranged, ostiolate. Spermatangia (Fig. 18E) in sori, cut off from outer cortical cells, ovoid, 3–4 µm in diameter.

Tetrasporangia (Fig. 18F) scattered, transformed from inner cortical intercalary cells, subspherical to ovoid and 25–50 (-55) µm in diameter, decussately divided.

Type from the Indian Ocean; lectotype in Herb. Agardh, LD, 36065.

Distribution: North Indian Ocean (see Huisman 1996).

Darwin, N.T., around western and southern Australia to Walkerville, Vic., and the N coast of Tasmania.

Selected specimens: Port Denison, W. Aust., drift (*Kraft* 4127, 14.xii.1971; AD, A41792). Esperance, W. Aust., drift (*Firman*, Dec. 1952; AD, A18947). Egg I., Isles of St Francis, S. Aust., 35 m deep (*Shepherd*, 7.i.1971; AD, A38098). N Spencer Gulf, S. Aust., 9 m deep (*Shepherd*, 13.ix.1973; AD, A44182). Wallaroo, S. Aust., 0.5–2.5 m deep (*Gill*, 9.xi.1980; AD, A51898). Stenhouse Bay, S. Aust., 7 m deep (*Gilbert*, 15.x.1988; AD, A59188). Edithburg, S. Aust., 3–4 m deep (*Gowlett-Holmes*, 9.ix.1995; AD, A64473). Investigator Strait, S. Aust., 26 m deep (*Watson*, 28.i.1971; AD, A38526). Marino, S. Aust., drift (*Womersley*, 26.x.1975; AD, A46643). Port Noarlunga, S. Aust., 24 m deep offshore (*Ottaway*, 3.ii.1981; AD, A52095). Kingscote, Kangaroo I., S. Aust., 1–2 m deep (*Latz*, 29.xi.1968; AD, A33001). Vivonne Bay, Kangaroo I., S. Aust., 3–4 m deep (*Latz*, 22.xi.1968; AD, A33018). Nora Creina, S. Aust., drift (*Womersley*, 4.x.1970; AD, A37342). Walkerville, Vic., drift (*Sinkora* A2550, 10.iii.1979; AD, A60969). Currie R., Tas. (*Perrin*, April 1935; AD, A49704).

C. muelleri has been shown by Huisman (1996) to be not specifically distinct from *C. opuntia* (Endlicher)Børgesen.

Lomentaria valida Kützing was described from Tasmania. However, what appears to be the type in L, 941, 149 ... 246 is from Lefevre Pen., S. Aust., Dec. 16, 1947 (probably a *Mueller* collection).

2. **Coelarthrum cliftonii** (Harvey)Kylin 1931: 15. Huisman 1996: 96, figs 1–15. Huisman & Walker 1990: 415. May 1965: 361. Norris 1986: 537, figs 1–5(?).
Chylocladia cliftoni Harvey 1855a: 556; 1858: pl. 57. Sonder 1881: 17.
Erythrocolon cliftoni (Harvey)J. Agardh 1876: 302; 1896: 91. De Toni 1900b: 584.
Chylocladia tenera J. Agardh 1896: 87, *nom. nudum.*

FIG. 19

Thallus (Fig. 19A) medium red to red-brown, fading to yellow-red, 5–20 cm high, much branched radially to 3 or 4 orders, with percurrent main axes or branches, laterals and lesser branches progressively shorter. All branches segmented, branches arising irregularly from the upper half of each segment, with occasional anastomoses, segments hollow, elongate ovoid, increasing in size from the branch apices, 1–3 (-4) cm long and 3–6 mm in diameter near the thallus base; constrictions very short in length and 0.5–1.5 mm broad. Holdfast discoid, epilithic or on solid substrata. *Structure* multiaxial, with a cortex 20–30 µm and 1–2 cells thick, outer cells laxly arranged, often in slight rosettes, ovoid and 4–6 µm in diameter, changing abruptly to a large-celled medulla 1–2 cells thick bordering the central weakly mucilaginous cavity, with the inner cells ovoid and 90–250 µm in diameter, walls 3–8 µm thick with some secondary pit-connections and bearing branched filaments (Fig. 19B) from initials on the inner medullary cells which cut off ovoid secretory cells 7–14 µm in diameter. Rhodoplasts discoid, in chains in inner cells. Constrictions with partitions (Fig. 19C) one

cell thick, with occasional smaller cells between the larger ones and with slender branched filaments bearing secretory cells on both sides.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 4-celled, arising on mid cortical supporting cells with an attached cortical cell producing the auxiliary cell. Carposporophytes with a basal fusion cell and a subspherical mass of carposporangia each 15–20 μm in diameter. Basal nutritive tissue slight, with non-persistent erect filaments. Cystocarps scattered, 700–800 μm across, protruding mainly inwardly, with a thickened pericarp, ostiolate. Spermatangia cut off from laterally proliferating surface cortical cells, ovoid, 2–3 μm in diameter (Huisman 1996, p. 98).

Tetrasporangia (Fig. 19D) scattered, transformed from inner cortical intercalary cells, ovoid, 18–30 μm in diameter, decussately divided.

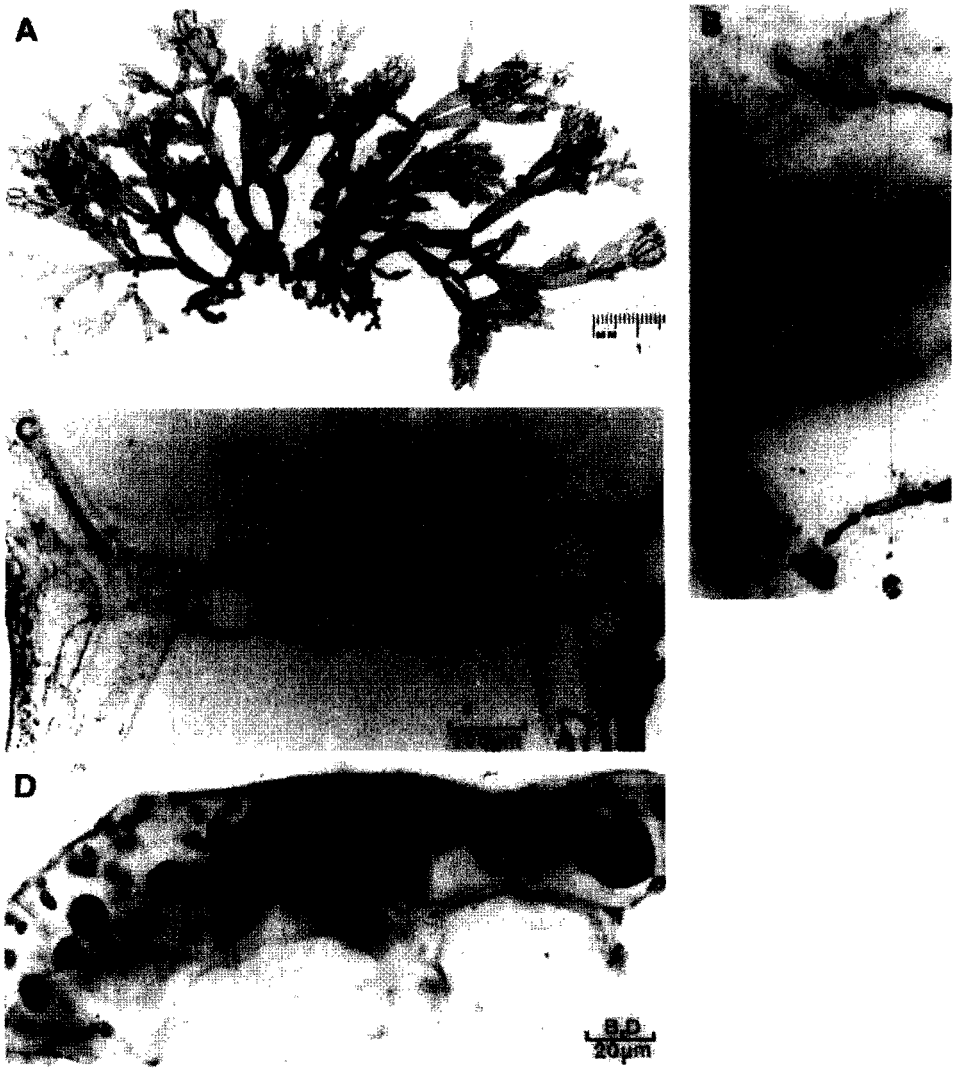


Fig. 19. *Coelarthrum cliftonii* (**A**, AD, A18250 (isotype); **B–D**, AD, A38099). **A.** Habit. **B.** Filaments bearing secretory cells, on inside of medullary cells. **C.** Longitudinal section of diaphragm. **D.** Transverse section of thallus with tetrasporangia.

Type from Fremantle, W. Aust. (*Clifton*); lectotype (Trav. Set 265) in Herb. Harvey, TCD. Isolectotypes in MEL, 502097 and AD, A18250.

Distribution: Montebello Is, W. Aust., to Troubridge I., S. Aust., and Vivonne Bay, Kangaroo I., S. Aust.

Canary Is; Natal, Mauritius; West Indies; Indonesia (see Huisman 1996, p. 96).

Selected specimens: Egg I., Isles of St Francis, S. Aust., 35 m deep (*Shepherd*, 7.i.1971; AD, A38099). Pearson I., S. Aust., 30–32 m deep (*Shepherd*, 7.i.1969; AD, A33692). Off Troubridge I., S. Aust., 23 m deep (*Shepherd*, 4.ii.1969; AD, A33812). Vivonne Bay, Kangaroo I., S. Aust., 0–3 m deep (*Kraft & Min-Thein*, 4.xii.1971; AD, A41412).

C. cliftonii was based on Harvey's Trav. Set 265 which was not located in TCD in 1952. A Clifton specimen in TCD (Alg. Aust. Exsicc. 425a) is chosen as lectotype.

Chylocladia tenera J. Agardh is based on a single specimen of Harvey (or Clifton), named *C. cliftoni* by Harvey, in Herb. Agardh, LD, 25822.

Norris (1986, fig. 1), followed by Huisman (1996, p. 96) recorded *C. cliftonii* from South Africa, but his description differs from *C. cliftonii* in the description of tetrasporangia ("borne on inner cortical cells") and in the apparent presence (Norris fig. 5) of rows of small cells lying in the angles of the large medullary cells.

Genus **WEBERVANBOSSEA** J. De Toni 1936: 5

Thallus erect, irregularly radially branched, segmented with narrow constrictions, segments hollow but mucilage filled. *Structure* multiaxial, segments with a thin cortex, outer cells in very short anticlinal chains, and a medulla 1–2 cells thick with inner filaments bearing secretory cells.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 3-celled, borne on inner cortical supporting cells together with auxiliary cell branches. Carposporophytes developing outwards, with erect fusion cells and a dense mass of carposporangia from all gonimoblast cells, often with later lobes developing. Basal nutritive tissue present, with the erect filaments persistent or not. Cystocarps immersed in the segments, relatively flat-topped, with an underlying layer of large medullary cells, pericarp moderately thick, ostiolate. Spermatangia in surface sori, cut off from outer cortical cells.

Tetrasporangia in scattered nemathecia, among paraphyses 4–8 cells long, pit-connected basally to outer cortical or lower paraphysal cells, decussately or cruciately divided.

Type species: *W. splachnoides* (Harvey)J. De Toni 1936: 6.

A genus of three southern Australian species, probably most closely related to *Coelarthrum* but differing in having a cortex of short anticlinal filaments, immersed cystocarps and tetrasporangia in nemathecia and borne laterally on inner cells.

KEY TO SPECIES OF *WEBERVANBOSSEA*

1. Thallus simple, saccate, cylindrical to inflated, not constricted ..... 3. *W. tasmanensis*
1. Thallus much branched, constricted at branch bases or along the branches 2

2. Thallus with constrictions only at the base of lateral branches; partitions of constrictions thick, pseudoparenchymatous; cystocarps with erect filaments from nutritive tissue not persistent ..... 1. *W. splachnoides*
2. Thallus with constrictions at the base of lateral branches and also along the branch; partitions of constrictions essentially monostromatic; cystocarps with erect filaments from nutritive tissue persistent (a "tela arachnoidea") ..... 2. *W. kaliformis*

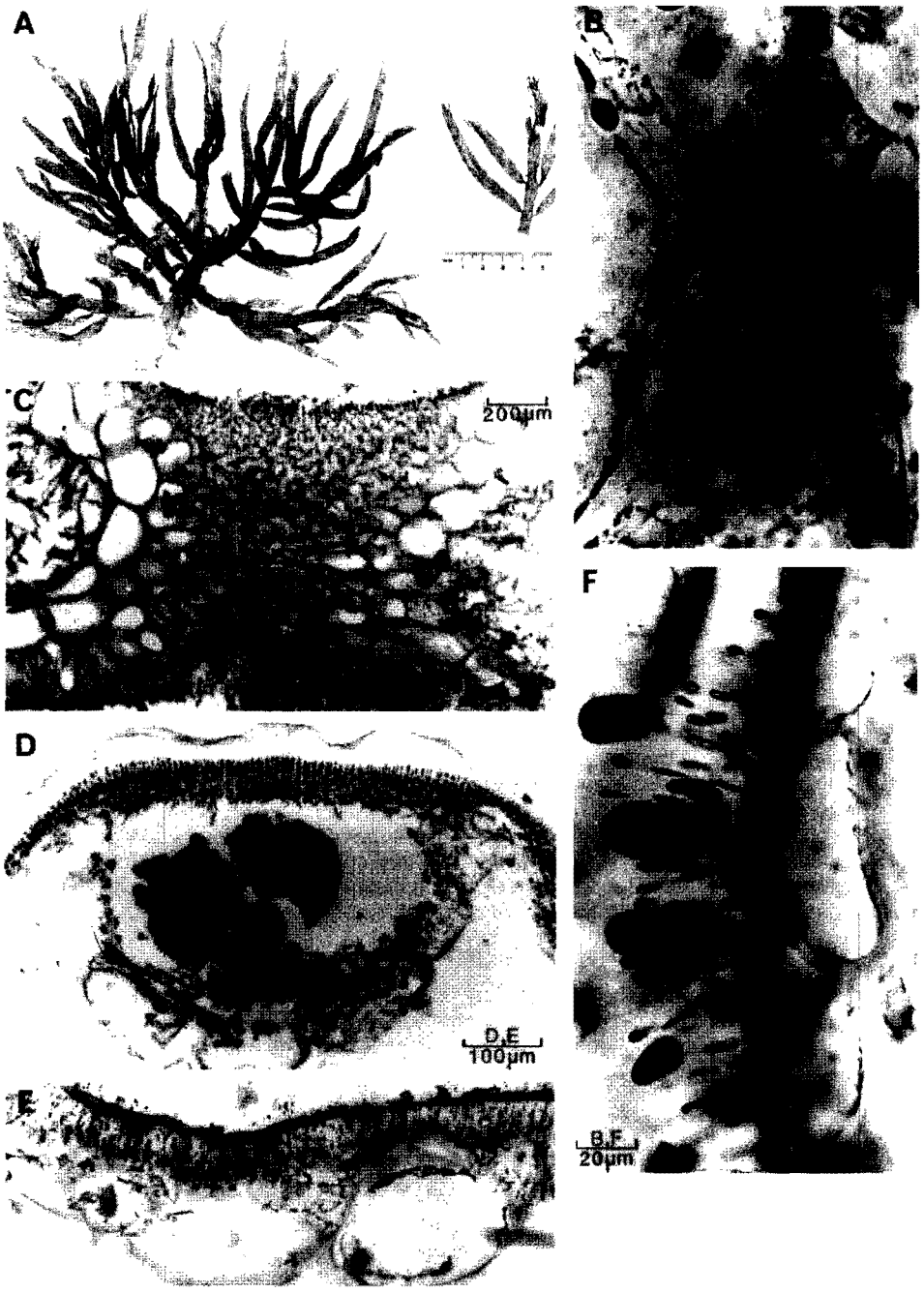


Fig. 20. *Webervanbossea splachnoides* (**A**, AD, A61671; **B, E,** AD, A34766; **C**, AD, A38108; **D, F,** AD, A37410). **A.** Habit. **B.** Filaments on the inside of the medulla, bearing secretory cells. **C.** Longitudinal section of a branch through a constriction. **D.** Section through a cystocarp. **E.** Transverse section of a spermatangial sorus. **F.** Transverse section of a tetrasporangial nemathecium.

1. **Webervanbossea splachnoides** (Harvey)J. De Toni 1936: 6. Huisman 1995: 368. May 1965: 361.
Bindera splachnoides Harvey 1859a, pl. 111, figs 1, 2 (*non* figs 5 & 6). J. Agardh 1876: 536; 1885: 46. De Toni 1900b: 548. Guiler 1952: 93. Kylin 1931: 5, fig. 1A–C; 1956: 329, fig. 255A, B. Lucas 1929b: 50. Lucas & Perrin 1947: 204, fig. 68a–d. Reinbold 1899: 45. Sonder 1881: 25. Wilson 1892: 172.
Chondrosiphon splachnoides (Harvey)Kützing 1869: 7, pl. 19.
Halymenia saccata Harvey 1860a: 327; 1860b: pl. 133. J. Agardh 1876: 141.
Bindera saccata (Harvey)J. Agardh 1885: 46. De Toni 1900b: 549. Lucas 1929a: 19.

FIG. 20

Thallus (Fig. 20A) medium red to red-brown, (5-) 10–30 cm high, much branched with hollow (mucilage filled), percurrent, terete axes and main branches bearing radially elongate-ovoid to terete and tapering laterals for 3–4 orders, all with a slender basal constriction, apices rounded to pointed. Axes 3–10 mm in diameter, laterals 2–8 (-12) mm in diameter, ultimate branchlets 0.5–3 (-6) cm long and 2–4 mm in diameter. Holdfast discoid, epiphytic or epilithic. *Structure* multiaxial, with a cortex 80–120 µm and 2–3 (-4) cells thick, outer cells in short anticlinal chains of 2 (-3) cells, arranged in rosettes around inner cortical cells, outer cells ovoid and 2–3 µm in diameter, and a large celled medulla 1 (-2) cells thick, inner cells ovoid, 45–75 (-130) µm in diameter with walls 3–15 (-40) µm thick bordering the mucilage filled cavity. Long, branched, slender filaments extend over the inner medullary cells from stellate initials, often interconnecting, and bear few to numerous intercalary or lateral, ovoid, secretory cells (Fig. 20B) 8–15 (-25) µm in diameter; lax, often tufted, slender filaments (not bearing secretory cells) are common in older segments, particularly on or near the partitions (Fig. 20C). Constrictions 1–1.5 mm, thick, pseudoparenchymatous (Fig. 20C). Rhodoplasts discoid to elongate, in chains in inner cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 3-celled, borne on inner cortical (supporting) cells which also bear the auxiliary initial and auxiliary cell (Huisman 1995). Carposporophytes (Fig. 20D) globular, 300–400 µm across with a basal, erect, fusion cell and (1-) 2–3 compact lobes of ovoid to angular carposporangia 16–30 µm in diameter. Basal nutritive tissue relatively slight, erect filaments present when young but soon disintegrating leaving stellate cells with long arms; inner medullary cells remaining as a distinct, depressed layer under the carposporophyte. Cystocarps (Fig. 20D) internal, 500–800 µm in diameter, not or only slightly bulging the thallus; pericarp flat topped, 70–120 µm and 6–10 (-15) cells thick, cells in anticlinal chains, ovoid, innermost stellate, ostiolate. Spermatangia (Fig. 20E) in surface sori, cut off from outer cortical cells, ovoid, 1–2 µm in diameter.

Tetrasporangia (Fig. 20F) in discrete, scattered, ovate to elongate, nemathecia 0.5–1 mm across and 60–85 µm thick. Paraphyses (2-) 4–6 cells long, branched, cells elongate; tetrasporangia lateral, pit-connected to inner cortical cells, ovoid, 25–35 µm in diameter, decussately or cruciately divided.

Type from Garden I., W. Aust.; lectotype in Herb. Harvey, TCD.

Distribution: Houtman Abrolhos, W. Aust. (Huisman 1995) to Port Phillip Heads, Vic., and the N coast of Tasmania.

Selected specimens: Hopetoun, W. Aust., drift (*Gordon*, 20.xi.1968; AD, A34170). Egg I., Isles of St Francis, S. Aust., 32–38 m deep (*Shepherd*, 11.i.1971; AD, A38108). Topgallant I., S. Aust., 10 m deep (*O'Leary*, 20.i.1992; AD, A61671). Waldegrave I., S. Aust., 22 m deep (*Shepherd*, 23.x.1970; AD, A37410). Pearson I., S. Aust., 13–23 m deep (*Shepherd*, 8.i.1969; AD, A34099). West Point, Eyre Pen., S. Aust. 15–25 m deep (*Shepherd*, 25.x.1969; AD, A34766). Avoid Bay, S. Aust., drift (*Womersley*, 30.xi.1975; AD, A46848). Wedge I., S. Aust., 11 m deep (*Baldock*, 28.xii.1963; AD, A27247). Tiparra Reef, S. Aust., 11 m deep (*Shepherd*, 31.x.1970; AD, A37651). Stenhouse Bay, S. Aust., 3–7 m deep (*Kraft*, 18.ix.1973; AD, A44566). Vivonne Bay, Kangaroo I., S. Aust., 0–5 m deep (*Kraft & Min-Thein*, 4.xii.1971; AD, A41411). Pennington Bay, Kangaroo I., S. Aust., drift (*Womersley*, 22.viii.1954; AD, A19750). Port Phillip Hds, Vic. (*Wilson*, 28.i.1886; AD, A886). Musselroe Bay, Tas. (*Perrin*, 7.ii.1948; AD, A49705).

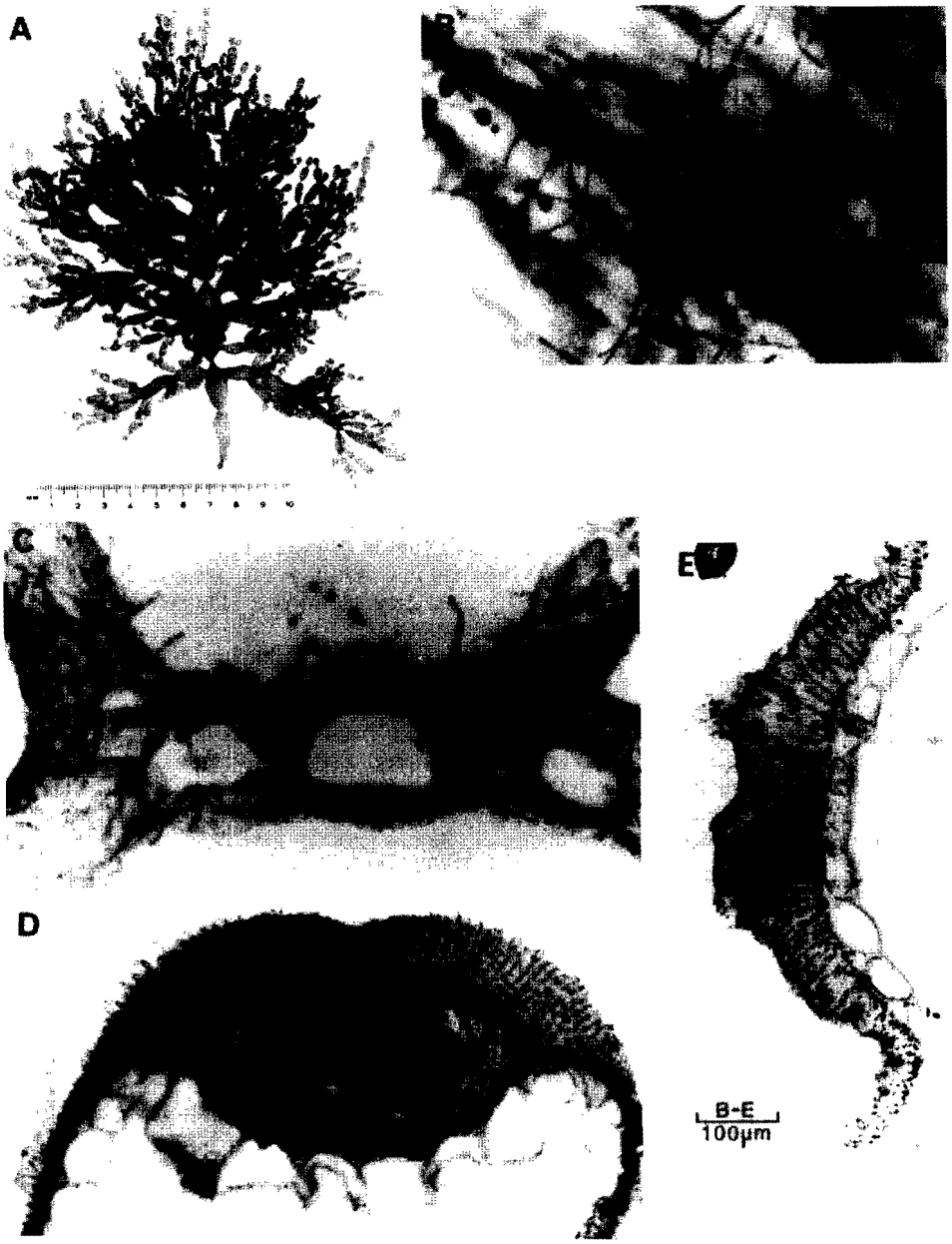


Fig. 21. *Webervanbossea kaliformis* (**A,** AD, A10650; **B, C,** AD, A38107; **D, E,** AD, A6927). **A.** Habit. **B.** Filaments with secretory cells, on the inside of the medulla. **C.** Longitudinal section of a branch through a constriction. **D.** Section through a cystocarp. **E.** Transverse section of a tetrasporangial nemathecium.

In TCD there are (1952) four specimens of *Bindera splachnoides* Harvey. Three are tetrasporangial and are *W. splachnoides*, while the fourth is cystocarpic *Binderella neglecta* Schmitz (=*Amphiplexia hymenocladioides* J. Agardh).

W. splachnoides is essentially a deep-water alga on moderate to rough-water coasts.

2. **Webervanbossea kaliformis** (J. Agardh)J. De Toni 1936: 6. Huisman & Walker 1990: 416. May 1965: 361.
Bindera kaliformis J. Agardh 1896: 75. De Toni 1900b: 549. Kylin 1931: 7, fig. 1D, pl. 1 fig. 1. Lucas & Perrin 1947: 204. Womersley 1950: 174.

FIG. 21

Thallus (Fig. 21A) medium to dark red-brown, mucilaginous, 10–25 cm high, with percurrent axes bearing hollow, segmented laterals irregularly radially for 2–4 orders, arising from any position on parent segments but mainly apically on lesser branches with some segments without laterals; segments with a slender constriction; lower segments elongate-ovoid, 2–4 cm long and 5–10 mm in diameter, decreasing in size to upper segments mostly 0.5–2 cm long and 2–4 mm in diameter. Holdfast discoid, 1–3 mm across; epilithic. *Structure* multiaxial, with a cortex 20–45 µm and 3–4 cells thick, outer cells in short anticlinal chains of 2–3 cells, arising from a layer of ovoid cells 6–10 µm in diameter over the medullary cells, surface rosettes not apparent, outer cortical cells ovoid and 3–4 µm in diameter; medulla as a distinct layer one cell thick, cells ovoid and 40–100 µm in diameter with walls (6-) 10–25 µm thick, with smaller cells lying between the larger cells over their joins and under the cortex. Long, branched, slender filaments (Fig. 21B) extend from stellate cells on some inner medullary cells and bear lateral, ovoid, secretory cells 6–10 µm in diameter, and in older segments lax, branched, slender filaments are common within the mucilage-filled cavity. Constrictions (Fig. 21C) are partitioned by essentially monostromatic layers of large cells, with small irregular cells and filaments forming a thin layer on each side. Rhodoplasts discoid, in chains in inner cells.

Reproduction. Gametangial thalli probably dioecious. Carpogonial and auxiliary cell branches not observed. Carposporophytes (Fig. 21D) 350–450 µm across, with a basal, erect, fusion cell and a dense mass of ovoid carposporangia each 15–30 µm in diameter, with younger lobes developing. Basal nutritive tissue relatively slight, erect filaments persistent, of stellate filaments with long arms. Cystocarps (Fig. 21D) slightly protruding but largely immersed, 500–900 µm across, with a distinct layer of large medullary cells at their base; pericarp 100–200 µm and 10–15 cells thick, ostiolate. Spermatangia unknown.

Tetrasporangia (Fig. 21E) in scattered nemathecia 0.5–1 mm across and 120–180 µm thick. Paraphyses 6–8 cells long, lower cells elongate, upper ovoid and often branched, tetrasporangia lateral, pit-connected to a lower cell of the paraphyses, ovoid, (16-) 20–40 µm in diameter, decussately divided.

Type from Waterloo Bay, S. Aust. (*O'Halloran*); holotype in Herb. Agardh, LD, 25731.

Distribution: Isles of St Francis, S. Aust., to Walkerville, Vic.

Selected specimens: Egg I., Isles of St Francis, S. Aust., 32–38 m deep (*Shepherd*, 11.i.1971; AD, A38107). Elliston, S. Aust., drift (*Womersley*, 27.ii.1959; AD, A22179). Wanna, S. Aust., drift (*Womersley*, 19.ii.1959; AD, A22369). Hopkins I., S. Aust., 33 m deep (*Branden*, 8.i.1989; AD, A60007). Investigator Strait, S. Aust., 33 m deep (*Watson*, 24.i.1971; AD, A41073). Western R., Kangaroo I., S. Aust., drift (*Womersley*, 7.i.1946; AD, A2964 and 2.i.1949; AD, A10650). Vivonne Bay, Kangaroo I., S. Aust., drift (*Womersley*, 14.i.1948; AD, A6927). Walkerville, Vic., drift (*Sinkora* A1639, 23.ii.1972; AD, A43164).

The type locality is probably Waterloo Bay on the south coast of Yorke Peninsula (not Waterloo Bay on Eyre Peninsula) and the collector is O'Halloran (not 'Halloran' as given with the type description).

W. kaliformis differs from *W. splachnoides* in habit, having constrictions along the length of the branches, and also in having more persistent erect filaments from the nutritive tissue. It is essentially a deep-water species of the central and eastern region of southern Australia.

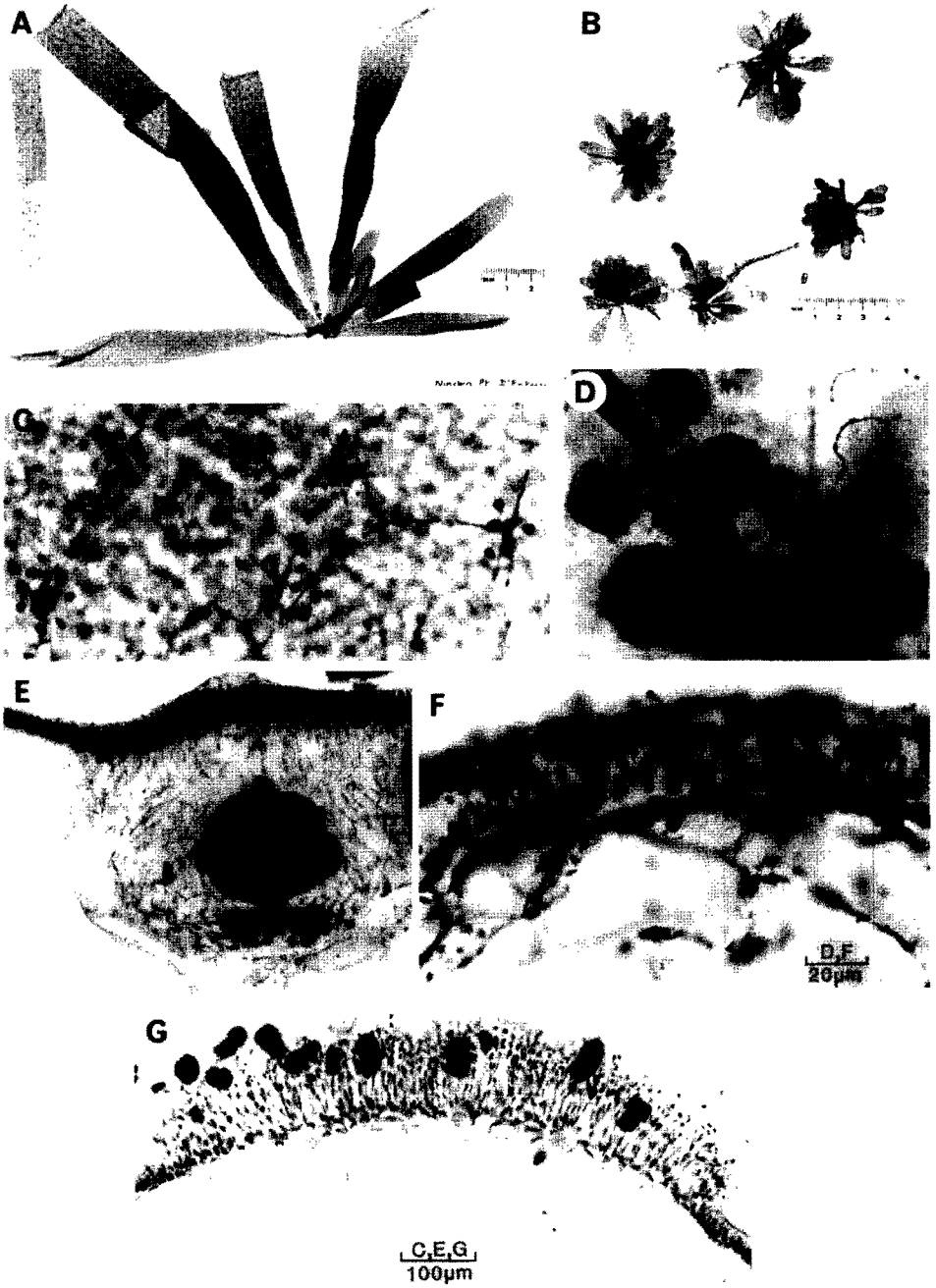


Fig. 22. *Webervanbossea tasmanensis* (**A, D, E, G,** AD, A56484; **B,** AD, A52847; **C, F,** AD, A54748). **A.** Habit of holotype specimen. **B.** Habit of small Victor Harbor specimens. **C.** Secretory cell filaments on inner medullary cells. **D.** Secretory cell filaments on inner medullary cells. **E.** Cross section of a cystocarp. **F.** Transverse section of a spermatangial thallus. **G.** Transverse section of a tetrasporangial nemathecium.

3. **Webervanbossea tasmanensis** Womersley, *sp. nov.*

Bindera levringii Lindauer, *ined.*

Halosaccion levringii Chapman & Dromgoole 1970: 126, fig. 42, pl. 41, left (*nom. nud.*).

FIG. 22

Thallus (Fig. 22A, B) medium red-brown, fading to grey-red, with one to several elongate-ovoid to clavate or fusiform, terete to compressed, mostly simple (some with small ovoid proliferations) bladders from the holdfast, (0.5-) 4–10 (-30) cm long and (2-) 3–6 (-35) mm in diameter, with rounded apices and tapering below gradually or abruptly to a short, slender, stipe; contents mucilaginous. Holdfast discoid, 1–3 mm across; epiphytic on larger algae and seagrasses, or epilithic. *Structure* multiaxial, developing a cortex with short, simple or branched anticlinal filaments (1-) 2–3 cells and 15–30 (-40) µm long, outer cells ovoid and 3–5 µm in diameter, borne on inner, periclinally ovoid, cells 6–10 µm in diameter, with a medulla 1 (-2) cells thick, cells fairly regularly placed in a single row, the larger inner cells ovoid, 90–200 (-300) µm in diameter, with numerous secondary pit-connections. Outer cortical cells sometimes forming rosettes in surface view, soon forming a continuous layer. Secretory cells (Fig. 22C, D) borne on cells cut off inwards from the large medullary cells, with long, slender arms which often link with arms of adjacent cells forming a lax reticulum; secretory cells on both the cells and their arms, ovoid, 12–22 (-30) µm in diameter. Hairs common. Rhodoplasts discoid to elongate, becoming ribbon like in medullary cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches unknown. Carposporophytes (Fig. 22E) ovoid, compact, (200-) 300–700 µm broad, with a basal, often branched, fusion cell bearing one to a few closely adjacent lobes of ovoid carposporangia 15–30 µm in diameter. Basal nutritive tissue with erect, slender, and relatively persistent filaments around the carposporophyte, and small-celled filaments around the ostiole. Cystocarps (Fig. 22E) scattered, 500–800 µm across, slightly swelling the surface but more so inwardly, pericarp 60–100 µm thick, ostiolate. Spermatangia (Fig. 22F) cut off from surface cortical cells via initials, ovoid, 1.5–2.5 µm in diameter.

Tetrasporangia (Fig. 22G) in discrete, scattered, ovate nemathecia 1–1.5 mm across, with extended cortical filaments 6–9 cells and 130–270 µm long, branched from most cells, mid cells 4–6 µm in diameter and L/D 4–6, outermost cells 3–5 µm in diameter and L/D 1–2. Tetrasporangia pit-connected basally to mid cells, ovoid, 30–85 µm long and 22–50 µm in diameter, decussately or cruciately divided.

Thallus uno vel aliquot vesicis elongatis ovoideis vel clavatis compressive, plerumque simplicibus (0.5-) 4–10 (-30) cm longis et (2-) 3–6 (-35) cm diametro, decrescens ad stipitem brevem. Hapteron discoideum, 1–3 mm latum; epiphyticum aut epilithicum. Structura corticis filamentorum brevium verticalium, (1-) 2–3 cellulas et 15–30 (-40) µm longorum, in cellulis internis ovoideis 6–10 µm in diametro, cum medulla 1 (-2) cellulas crassa, internis cellulis ovoideis, 90–200 (-300) µm in diametro. Cellulae secretoriae in brachiis longis cellularum ex cellulis magnis medullosis abscissarum.

Reproductio. Dioecia. Carposporophyta ovoidea (200-) 300–700 µm lata, cellula basali coalescenti. Textura basali nutritiva filamentis erectis, gracilibus perdurantibus. Cystocarpa dispersa, 500–800 µm lata, paulatim tumida extrinsecus, plus intro, ostiolata. Spermatangia ex cellulis superficialibus corticalibus abscissa. Tetrasporangia in nemathecis discretis dispersis, filamentis ramosis corticalibus 6–9 cellulis et 130–270 µm longis, basaliter lacunis iunctis cum cellulis mediis, 30–85 µm longis et 22–50 µm in diametro, decussate vel cruciatim divisis.

Type from Ninepin Point, D'Entrecasteaux Ch., Tas., 1–2 m deep (*Thomas & Womersley*, 1.xi.1982); holotype in AD, A56484 — isotypes in "Marine Algae of southern Australia" No. 381.

Distribution: Redcliff Point and Tiparra Reef to Port MacDonnell, S. Aust., and N and SE Tasmania.

New Zealand (southern S. Island, Stewart I.).

Selected specimens: 4 km S of Redcliff Point, Spencer Gulf, S. Aust., on *Posidonia sinuosa*, 10 m deep (*Johnson*, 27.vi.1978; AD, A50514); Tiparra Reef, S. Aust., on *Amphibolis antarctica*, 5 m deep (*Shepherd*, 13.vii.1971; AD, A39250); Young Rocks, S of Kangaroo I., S. Aust., 16–30 m deep, on stalked sponge (*Branden*, 18.vi.1991; AD, A61454). Victor Harbor, S. Aust., on *Amphibolis antarctica*, 6 m deep (*Clarke*, 30.xii.1981; AD, A52847). Port MacDonnell, S. Aust., on *Caulerpa papillosa*, drift (*Kraft* 7769 & *Herrington*, 31.x.1988; MELU). Stanley, N Tas., drift on *Heterozostera* (*Womersley*, 17.x.1982; AD, A56228). Bluestone Bay, Freycinet Pen., Tas., 6–13 m deep on *Galaxaura marginata* (Ellis & Solander)Lamouroux (*Brown, McGeary & Womersley*, 6.xi.1982; AD, A54748). Lady Bay, Southport, Tas., 5 m deep (*Brown & Womersley*, 28.x.1982; AD, A56540). Ninepin Point., Tas., 8–11 m deep, on rock (*Kraft* 9157 & *Sanderson*, 22.xii.1992; MELU).

New Zealand: Ringa Ringa, Stewart I., drift (*Womersley*, 4.i.1966; AD, A29837). Halfmoon Bay, Stewart I., 4 m deep (*Hay*, 26.i.1983; AD, A54341).

This species has been known in New Zealand as *Bindera levringii* Lindauer (Alg. Nova-Zel. Exsicc. 265) and *Halosaccion levringii* Chapman & Dromgoole; the first name had no description and the latter is invalid since there was no latin description. Since the species occurs on both sides of the Tasman Sea, it is here named *Webervanbossea tasmanensis*.

W. tasmanensis varies greatly in size, with the largest plants from the cooler waters of SE Tasmania and Stewart I. It becomes fertile when very small (about 5 mm long, as in AD, A61454) but the small and large plants appear identical in structure and reproduction.

W. tasmanensis is similar in structure to the previous two species of the genus, but has a simple, unconstricted, saccate thallus. In this respect it is similar in form to *Gloiosaccion brownii*, but the tetrasporangia are borne laterally rather than transformed from intercalary cortical cells, and the gland cells on branched cells internal to the medulla are similar to those of the other species of *Webervanbossea*.

Genus **ERYTHRYMENIA** Schmitz *ex* Mazza 1921: 107

Thallus erect, ovate to foliose, solid and relatively thick, margin smooth or spinous, branched only from the short stipe or discoid holdfast. *Structure* multiaxial, developing a small-celled cortex of anticlinal chains of 2–5 cells and medulla several cells broad, of large cells with intermixed smaller cells.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious. Carpogonial and auxiliary cell branches unknown. Carposporophyte erect, with a basal fusion cell and lobes with all cells forming carposporangia; basal nutritive tissue present, erect filaments disintegrating early. Cystocarps scattered or marginal, smooth, protruding outwards, ostiolate. Spermatangia in sori, cut off via initials from the surface cortical cells.

Tetrasporangia in scattered sori with the cortex slightly thickened, transformed from intercalary cortical cells, irregularly cruciately divided.

Type species: *E. obovata* Schmitz *ex* Mazza 1921: 107.

The type species was described by Sparling (1957, p. 363, fig. 13a–c, pl. 57), following the brief descriptions in Mazza (1921) and Kylin (1931, p. 13), and commented on by Irvine & Guiry (1986, p. 298). Sparling was unable to clarify the origin of the tetrasporangia in the type, but AD, A62891 (The Kowie, South Africa, *Becker*) clearly shows their intercalary origin.

A genus of two species, the type from South Africa and one from southern Australia. *Erythrymenia* differs from *Rhodymenia* in its thicker thallus with a cortex of anticlinal filaments and medulla several cells thick, of varying cell sizes, and in having tetrasporangial sori scattered over the blade surface with the tetrasporangia always transformed from intercalary cells.

Erythrymenia minuta Kylin 1931: 13, pl. 4 fig.10. Womersley 1950: 175; 1966: 150.

FIGS 23, 30B

Thallus (Fig. 23A) erect, medium to dark red with a mottled surface when fresh, flat and more or less ovate, (2-) 4–10 (-14) cm high and 1–6 (-12) cm broad, solid, 500–1000 (-1250) µm thick, margin and surface smooth. Holdfast crustose, 2–5 mm across, with one to several fronds, often with branches only from the short stipe; epilithic, rarely epiphytic (on *Perithalia*). *Structure* (Fig. 23B) multiaxial, developing a cortex 3–6 cells and 20–50 µm thick, outer cells ovoid, 2–4 µm in diameter, grading to the compact pseudoparenchymatous medulla of large, ovoid, thick-walled (6–10 µm) cells 60–100 µm in diameter, with frequent secondary pit-connections, with abundant intermixed smaller cells 15–30 µm in diameter. Hair clusters present. Rhodoplasts discoid to elongate, in chains in medullary cells.

Reproduction. Gametangial thalli probably dioecious. Carpogonial and auxiliary cell branches unknown. Carposporophytes (Fig. 23C) erect, 400–650 µm across, with a basal fusion cell extensively branched above, the branches bearing dense chains of ovoid carposporangia 16–25 µm in diameter, all upper cells forming carposporangia. Basal nutritive tissue thick, with horizontal radiating filaments producing erect filaments connected to inner pericarp cells, but disintegrating early. Cystocarps (Fig. 23C) 1–1.5 mm across, scattered, hemispherical and protruding, with a pericarp 270–360 µm thick, narrower near the central, depressed, ostiole. Spermatangia uncertain, probably cut off from surface cortical cells.

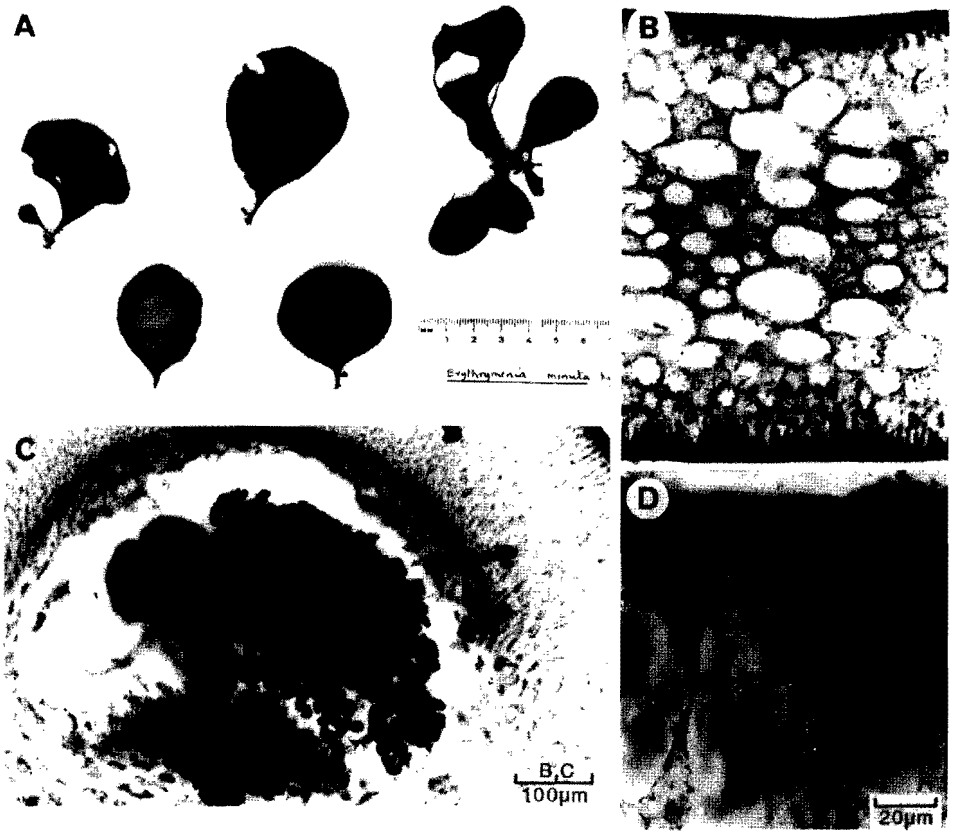


Fig. 23. *Erythrymenia minuta* (**A, C,** AD, A27303; **B,** AD, A22254; **D,** AD, A53673). **A.** Habit. **B.** Transverse section of thallus. **C.** Section of cystocarp. **D.** Transverse section of tetrasporangial thallus.

Tetrasporangia (Fig. 23D) in scattered cortical sori, not elevated but with longer mid cortical cells (L/D 4–6), transformed from intercalary cortical cells (Fig. 30B) and often with lateral secondary pit-connections as well as connections to outer cortical cells, elongate-ovoid, 50–85 μm long and 30–45 μm in diameter, decussately divided.

Type from Port Phillip Heads, Vic. (*Wilson*, 31.i.1890); lectotype (Kylin) in Herb. Agardh, LD, 26337.

Distribution: Sorrento , W. Aust., to Portsea, Vic., and the east coast of Tasmania.

Selected specimens: Ocean Reef Marina, Sorrento, W. Aust., 6 m deep (*Millar & O'Brien*, 9.xii.1980; MELU, Kraft 7326). Walker Rock, Anxious Bay, S. Aust., 8–10 m deep (*Edyvane*, 1.x.1982; AD, A53673). Elliston, S. Aust., 6 m deep, shaded, near entrance (*Shepherd*, 24.x.1969; AD, A34781). South West R., Kangaroo I., S. Aust., reef edges (*Womersley*, 17.i.1965; AD, A28902). Pennington Bay, Kangaroo I., S. Aust., drift (*Womersley*, 25.i.1946; AD, A3102) and upper sublittoral (*Kraft & Min-Thein*, 1.xii.1971; AD, A41376). Margaret Brock Reef, Cape Jaffa, S. Aust., 10 m deep (*R. Lewis*, 15.ii.1974; AD, A45034). Robe, S. Aust., upper sublittoral (*Womersley*, 28.iii.1959; AD, A22254 and 29.i.1964; AD, A27303). 1.3 km off Cape Northumberland, S. Aust., 15 m deep (*Shepherd*, 13.ii.1976; AD, A55102). Lawrence Rock, Portland, Vic., in low pool (*Beauglehole*, 15.i.1960; AD, A24014). Warrnambool, Vic., drift on *Perithalia* (*Kraft* 7586, 10.viii.1984; MELU). Portsea, Vic., outer coast, 20 m deep (*Macpherson*, 15.v.1963; AD, A28814). Satellite I., D'Entrecasteaux Ch., Tas., 2–7 m deep (*Shepherd*, 17.ii.1972; AD, A41748). Fluted Cape, Bruny I., Tas., 0–6 m deep (*Shepherd*, 12.ii.1972; AD, A41870).

E. minuta is found on rough-water coasts at and just below low tide level, extending to 15 m deep. The ovate form, relatively thick blades, and mottled surface appearance are distinctive.

Kylin's photo of the lectotype includes also one specimen from LD, 26338.

Harvey (1862, pl. 237) illustrated *E. minuta* as young plants of his *Calliblepharis* (=*Hymenocladia*) *conspersa*, but the two appear quite distinct and there is nothing in Herb. Harvey, TCD, to associate the two taxa. Harvey's plants of *E. minuta* may have been from his Port Fairy, Vic., record rather than from Garden I., W. Aust. *H. conspersa* as recorded from Hogan I., Bass Strait, by Saenger (1974, p. 80) is probably *E. minuta*.

Genus **RHODYMENIA** Greville 1830: xlviii, 84, *nom. cons.*

Thallus usually erect, occasionally prostrate, cartilaginous, foliose (some perforate) and simple or divided, or with flat, subdichotomous to lateral, complanate branches 2–20 mm broad, with or without surface or marginal proliferations (often proliferous from damaged ends of branches), stipes usually present; holdfast crustose or stoloniferous. *Structure* multiaxial, with a small-celled cortex 2–5 cells thick and a pseudoparenchymatous medulla of larger ovoid cells, elongate lengthwise to the branch, in older or robust thalli often with smaller intermixed cells and in some species with a secondary cortex in the stipe.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 3- or 4-celled, borne on inner cortical (supporting) cells together with a 2- or 3-celled auxiliary cell branch. Carposporophyte developing outwards, usually with several branched basal fusion cells and a dense mass of ovoid to angular carposporangia. Basal nutritive tissue present, erect filaments absent or disintegrating apart from inner stellate cells to the pericarp. Cystocarps scattered (often clustered) on the blades or proliferations, protruding, usually basally constricted, pericarp thick, usually smooth (verrucose in one species). Spermatangia in sori, subapical on the branches or scattered on foliose thalli, cut off from elongate outer cortical initials.

Tetrasporangia in subapical sori or nemathecia, or scattered, terminal on cortical cells or transformed from mid cortical cells, decussately or cruciately divided, with adjacent cortical cells in most species becoming elongate and often dividing.

Lectotype species: *R. palmetta* (Lamouroux)Greville [= *R. pseudopalmata* (Lamouroux)Silva 1952: 265].

Rhodymenia is a common world-wide genus of 50–60 described species, but the limits of many species are uncertain. The most recent attempt to survey the genus is by Dawson (1941), and critical studies of the genus are needed in most countries.

Rhodymenia is here considered to include *Epymenia* Kützing (1849, p. 787), a southern hemisphere genus with the lectotype species *E. obtusa* (Greville)Kützing. *Epymenia* has been distinguished by the presence of small proliferations on the thallus surface, these bearing the reproductive sori or cystocarps. However, as others (e.g. Sparling 1957, p. 356) have noted, this is not a clear-cut distinction since several species form a few surface proliferations, many species form marginal or apical proliferations (especially following damage) and while such proliferations often bear reproductive structures, some species (e.g. *R. prolificans, R. obtusa, R. australis*) also have cystocarps and tetrasporangial sori on the branch surfaces. In *R. halymenioides* tetrasporangia occur on small leaflets but cystocarps occur on the thallus surface.

The origin of the tetrasporangia in the cortex is not easy to establish. The genus is sometimes said to have intercalary tetrasporangia (Irvine & Guiry 1983, p. 93) but the illustrations of Guiry (1974, fig. 1) appear to show them as terminal in the type species. Hawkes & Scagel (1986, p. 1570) refer to them as terminal for the genus while Lee (1978, p. 84) for *R. pertusa*, states initials intercalary to terminal. Few authors have clearly illustrated pit-connections on the tetrasporangia. Such pit-connections are usually slender and faint, and are usually visible only with juvenile, undivided, tetrasporangia. As the sporangium matures and enlarges greatly, it extends both towards and away from the thallus surface so that the basal pit-connection, as well as ones to small outer cortical cells if present, are often moved to lateral positions on the inner half of the sporangium. In southern Australian species, even within a species, it appears that tetrasporangia may be either terminal on cortical cells or transformed from intercalary mid cortical cells. This needs further study since other genera of the Rhodymeniaceae are separated on whether the tetrasporangia are terminal or intercalary.

While a few species are distinctive in habit, others appear to be very variable depending on their habitat, probably influenced by depth, shading, and water motion in particular. One such species, *R. australis*, on southern Australian coasts, is interpreted broadly, and several other specimens in AD are not currently placed within a species. Further detailed studies, based on *in-situ* populations and from ecological and seasonal bases, are needed to clarify most species.

The following key and descriptions do not include all species on southern Australian coasts. One species occurs as loose lying plants in bays (e.g. Marion Bay) on SE Tasmanian coasts, being 20–40 cm long with distant branches 6–10 mm broad, often proliferous from damaged ends. No reproductive structures are known.

KEY TO SPECIES OF *RHODYMENIA*

1. Thallus moderately to much branched, essentially complanately, subdichotomous to irregularly lateral or proliferous, branches 2–20 mm broad 2
1. Thallus foliose, simple or divided below into cuneate lobes 1–8 cm across, surface smooth or with small proliferations 7

2. Thallus with tetrasporangial sori or nemathecia and cystocarps on the branches, proliferous only from damaged branch ends 3
2. Thallus with numerous surface or marginal proliferations bearing the tetrasporangia or cystocarps 6

3. Thallus with erect, clumped, linear fronds from a crustose base, branched near the apices ..... 1. *R. stenoglossa*
3. Thallus with one to a few spreading, subdichotomous fronds from a small crustose base, with or without stolons 4

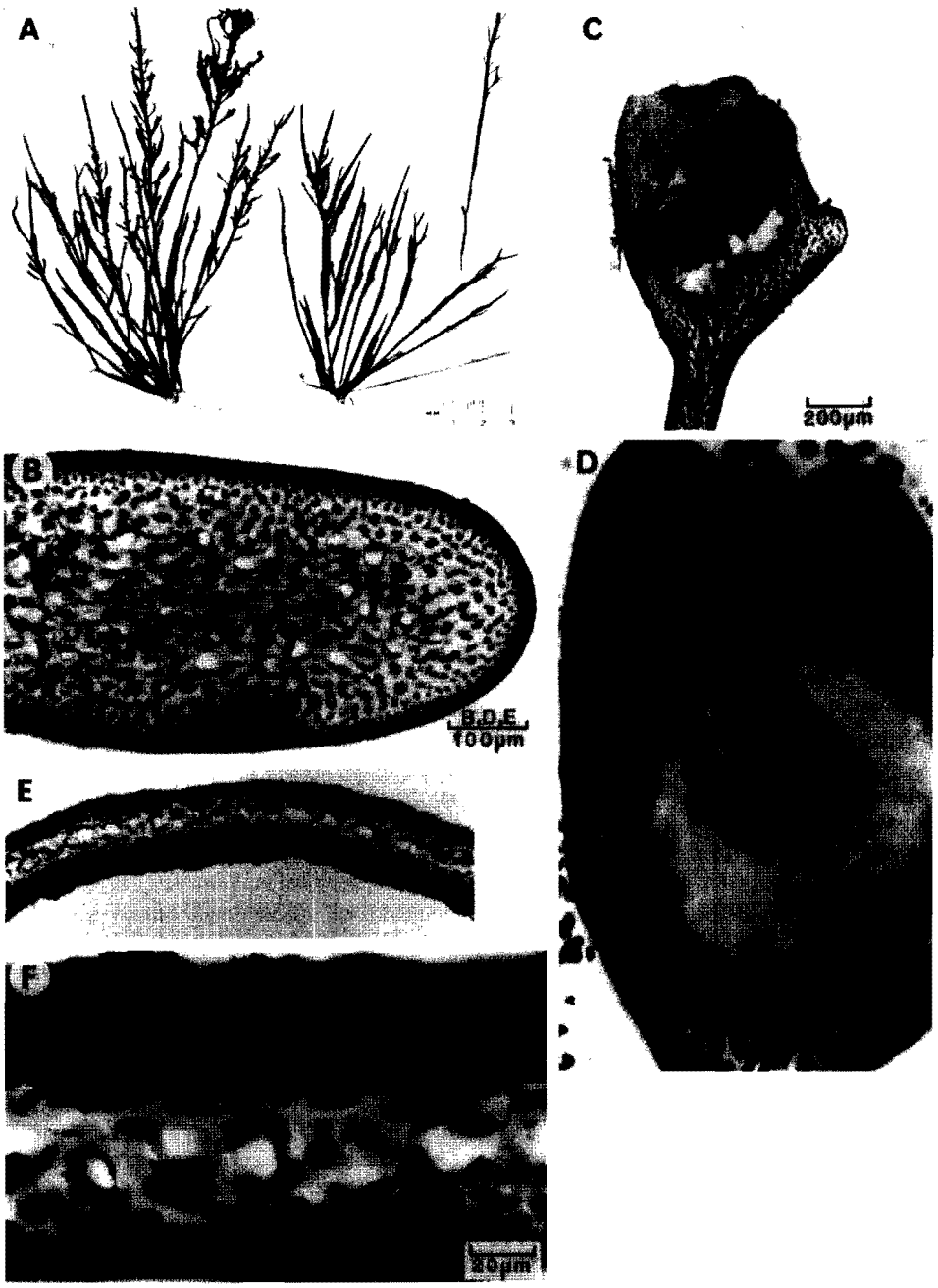


Fig. 24. *Rhodymenia stenoglossa* (**A**, AD, A64515; **B, E, F,** MELU, 38414; **C, D,** MELU, 38415). **A.** Habit. **B.** Transverse section of older branch. **C.** Section of cystocarp with partly displaced carposporophyte. **D.** Section of cystocarp with carposporophyte, erect fusion cell and slight basal nutritive tissue. **E.** Transverse section of branch with tetrasporangial sorus. **F.** Transverse section of branch with tetrasporangia.

4. Basal stolons and stipes slender, prominent, 300–600 µm in diameter, erect fronds little to much branched ..... 2. *R. leptophylla*
4. Basal stolons (if present) and stipes relatively robust, usually 1–1.4 mm in diameter, fronds subdichotomously branched 5

5. Cystocarp pericarp smooth, tetrasporangial sori with an irregular and not sharply defined margin ..... 3. *R. australis*
5. Cystocarp pericarp verrucose, tetrasporangial nemathecia with a sharply defined margin ..... 4. *R. verrucosa*

6. Thallus with frequent fertile surface proliferations, branches 0.5–1.5 cm broad, often with a midrib near the base ..... 5. *R. obtusa*
6. Thallus with numerous marginal proliferations and occasional surface ones, branches 2–6 (-8) mm broad, without a midrib ..... 6. *R. prolificans*

7. Thallus simple or irregularly lacerate, often perforate, surface smooth if cystocarpic or covered with numerous ovate, tetrasporangial, proliferations 2–5 (-8) mm long ..... 7. *R. halymenioides*
7. Thallus with several cuneate lobes 1–8 cm broad, surface without proliferations ..... 8. *R. cuneata*

1. **Rhodymenia stenoglossa** J. Agardh 1885: 50. Dawson 1941: 138. De Toni 1900b: 520. Kylin 1931: 21, pl. 7 fig. 18. May 1965: 407. Tisdall 1898: 506. Wilson 1892: 178.

FIG. 24

Thallus (Fig. 24A) medium to dark red-brown, 10–25 cm high, with numerous erect, cartilaginous fronds from a clumped base, fronds flat, simple to distantly furcately branched at intervals of 2–5 cm, or with short, often spathulate upper laterals; branches more or less linear, 1–3 mm broad and 90–280 µm thick, apices rounded; stipes short, compressed. Holdfast crustose, 5–15 mm across, bearing numerous fronds; epilithic. *Structure* multiaxial, developing a cortex 3–4 cells broad (Fig. 24C, E), outer cells ovoid and 3–4 µm in diameter, grading over 2–4 cells to the medulla 2–5 cells broad in young parts, 8–15 cells thick in older parts (Fig. 24B), cells ovoid and 20–45 µm in diameter, thick walled when older. Rhodoplasts discoid to elongate, in chains in inner cells.

Reproduction. Gametangial thalli probably dioecious. Carpogonial branches not observed. Carposporophytes (Fig. 24D) 350–450 µm across with an erect basal fusion cell bearing dense lobes of ovoid carposporangia 10–15 µm in diameter. Basal nutritive tissue slight, erect filaments mostly disintegrating. Cystocarps on the blade surface, usually angled to the surface, ovoid, basally constricted, 600–900 µm in diameter, pericarp 90–200 (-300) µm and 10–15 cells thick, inner cells periclinally elongate, outer cells in chains; ostiolate. Spermatangia not observed.

Tetrasporangia (Fig. 24E, F) in sori near apices of upper branchlets, on one or both sides, probably intercalary, with outer and mid cortical cells becoming elongate and cutting off small outer cells; tetrasporangia ovoid, 25–50 µm long and (12-) 15–25 µm in diameter, decussately divided.

Type from "Nova Holl. aust." (*J.B. Wilson*); from Back Beach, Sorrento, Vic. (Kylin 1931, p. 21); lectotype (Kylin) in Herb. Agardh, LD.

Distribution: Cape Lannes, S. Aust., to Phillip I., Vic., and Hunter I., Tas.

Selected specimens: Cape Lannes, S. Aust., just above low water in surf (*Kraft* 4411, 10.ii.1973; MELU, 38408). Warrnambool, Vic., low eulittoral on roof of rock overhang (*G. & R. Kraft*, 3.i.1995; MELU, K10414; AD, A64515). Marengo Reef, Apollo Bay, Vic., in shallow water, shaded, rear reef (*Kraft* 6913 & *Ricker*, 21.iv.1979; MELU, 38410). Portsea, Vic., 2–4 m deep on jetty (*O'Brien*, 1.x.1975; MELU, 38415). Near Cat Bay, Phillip I., Vic., lower eulittoral (*M. Warren*, 14.xi.1970; MELU, 38414; AD, A64527). Seal Rocks, Phillip I., Vic. (*Seebeck*, 30.xi.1965; MELU, 2430). Hunter I., NW Tas., sublittoral (*King*, 15.xii.1969; MELU, 20349).

R. stenoglossa is distinguished largely by its habit of clumps of erect, narrow, linear and sparsely branched fronds from a crustose holdfast. It is apparently not a common species and most collections are by Dr G.T. Kraft and his students.

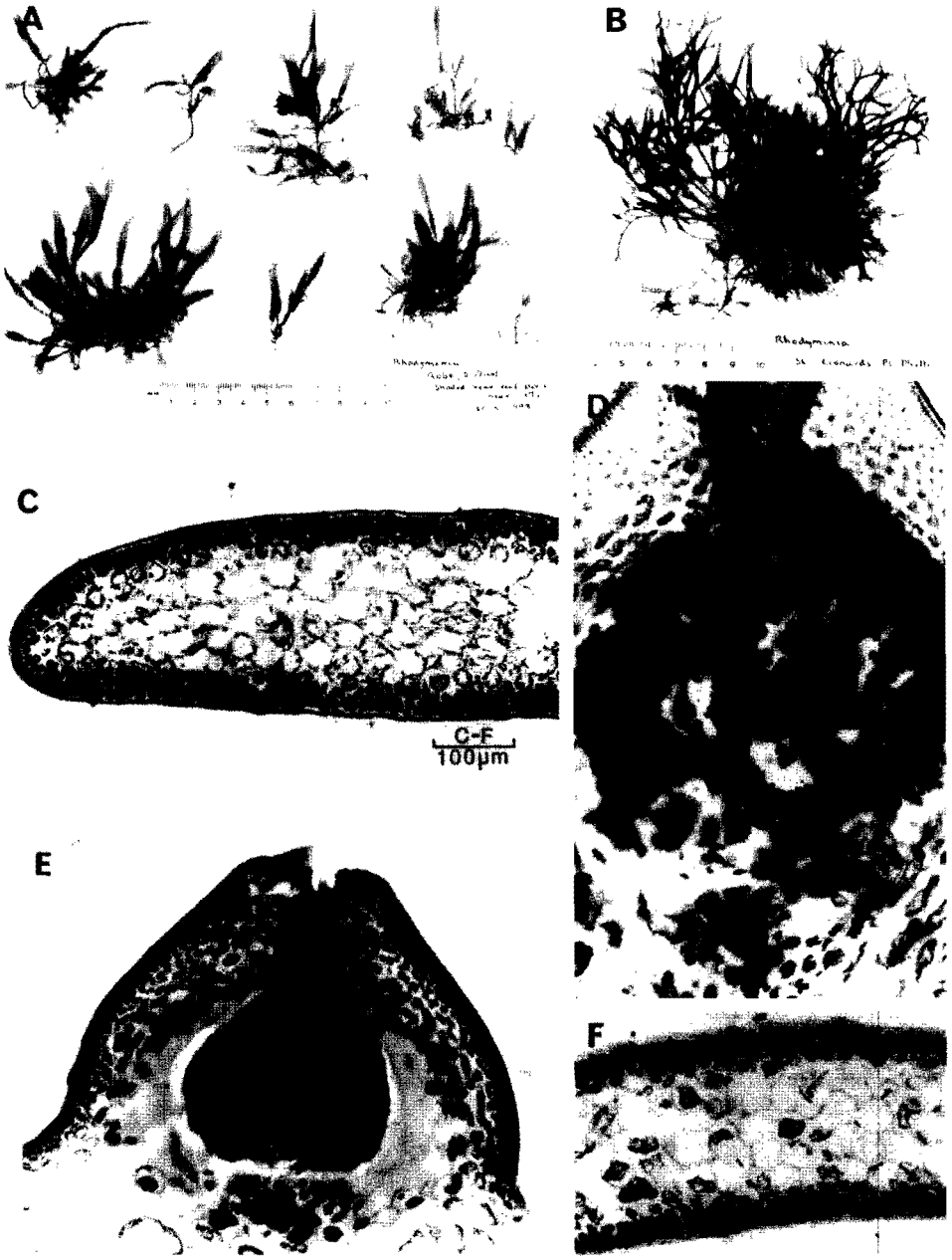


Fig. 25. *Rhodymenia leptophylla* (**A, D,** AD, A63258; **B, C, E, F,** AD, A23103). **A, B.** Habit. **C.** Transverse section of branch. **D.** Section of carposporophyte. **E.** Section of cystocarp. **F.** Transverse section through tetrasporangial sorus.

2. **Rhodymenia leptophylla** J. Agardh 1878: 20. Adams 1994: 231, pl. 83 lower left. Chapman & Dromgoole 1970: 134, pl. 44 lower. Dawson 1941: 143. De Toni 1900b: 519. Kylin 1931: 20, pl. 6 fig. 15. Lucas & Perrin 1947: 201. May 1965: 408. Millar 1990: 368, fig. 27C. Millar & Kraft 1993: 33. Tisdall 1898: 506. Wilson 1892: 178.

PLATE 1 fig. 4; FIG. 25

Thallus (Fig. 25A, B) medium to dark red-brown, fading to grey-red, 4–10 (-30) cm high, with numerous clumped fronds from slender entangled stolons, fronds flat, complanately branched, simple to furcately or palmately branched above with long stipes, branches 2–5 mm broad, usually broadest above, with no or few marginal proliferations, apices rounded when young, tapering in branched apices and often extending as long, subterete, prolongations 10–60 mm long; thallus 300–500 (-800) µm thick; stolons and stipes slender, terete, 5–20 (-60) mm long and 300–1000 µm in diameter, grading upwards to the flat fronds. Holdfasts small digitate pads on the stolons; epilithic. *Structure* multiaxial, developing a cortex (Fig. 25C) 2–3 cells broad, outer cells ovoid and 2–4 µm in diameter, grading to the medulla 4–8 cells broad, cells rather laxly arranged, ovoid, 30–100 µm in diameter; stipe medulla 300–500 µm and 12–16 cells broad. Rhodoplasts discoid.

Reproduction. Gametangial thalli probably dioecious. Carpogonial and auxiliary cell branches not observed. Carposporophytes (Fig. 25D) 250–500 µm across, with branched basal fusion cells bearing a dense mass of ovoid carposporangia 10–15 µm in diameter. Basal nutritive tissue slight, erect filaments absent. Cystocarps (Fig. 25E) on the blade surfaces, often clustered, sessile, not or slightly basally constricted, slightly conical or beaked, 600–850 µm across, pericarp 100–150 (-300) µm and 8–12 (-25) cells thick (thicker around ostiole), inner cells irregularly placed and the outer cells in anticlinal rows of 3–5, ostiole usually depressed. Spermatangia not observed.

Tetrasporangia (Fig. 25F) in sori near branchlet ends, probably intercalary, the cortex slightly thickened with elongate outer cells and some additional small outer cells; tetrasporangia ovoid to elongate, 20–30 (-40) µm long and 10–15 µm in diameter, decussately divided.

Type from the Bay of Islands, New Zealand; lectotype (Kylin 1931, p. 20, fig. 15) in Herb. Agardh, LD.

Distribution: New Zealand; N.S.W.; Qld.

In southern Australia, from West I., S. Aust., to Westernport Bay, Vic., and around Tasmania.

Selected specimens: Oedipus Point, West I., S. Aust., 16 m deep (*Shepherd*, Dec. 1966; AD, A31148). Robe, S. Aust., in shaded pools near jetty (*Womersley*, 30.x.1993; AD, A63258). Cape Lannes, S. Aust., upper sublittoral pool edges (*Womersley*, 31.x.1993; AD, A63255). Port MacDonnell, S. Aust., drift (*Womersley*, 1.xi.1994, AD, A63857 —"Marine Algae of southern Australia" No. 384). St Leonards, Port Phillip, Vic., 1–3 m deep (*Womersley*, 9.viii.1959; AD, A23103). Crawfish Rock, Westernport Bay, Vic., 4 m deep (*Watson*, 29.v.1974; AD, A45402). Georgetown, Tas., upper sublittoral (*Womersley*, 29.i.1949; AD, A10287). Cloudy Lagoon, SE Tas., 1–3 m deep (*Edgar*, 12.ii.1995; AD, A64238).

R. leptophylla is characterised by its habit, with long slender stipes and stolons. Some of the Australian plants agree well with those from New Zealand, but there is considerable variation in size and degree of branching in southern Australian populations, though all have slender stipes and basal stolons. At Port MacDonnell, large entangled clumps up to 50 cm across occur. Millar (1990, p. 369) discussed New Zealand synonyms of this species.

Weber-van Bosse (1928, p. 461) described a f. *minima* of *R. leptophylla* from Indonesia; it seems doubtful if this is related to the southern Australasian taxon.

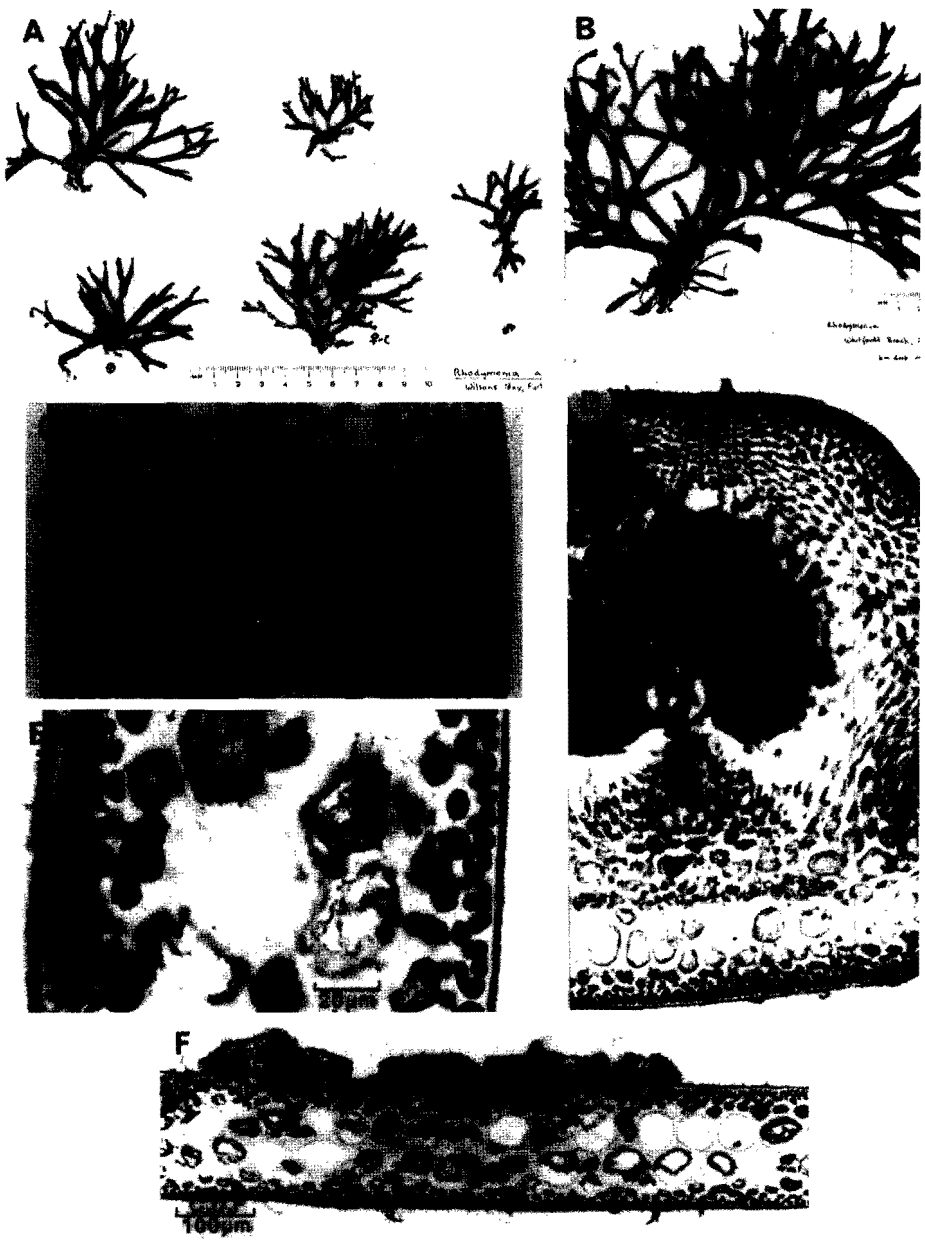


Fig. 26. *Rhodymenia australis* (**A, C–F,** AD, A63580; **B,** AD, A50546). **A, B.** Habit. **C.** Transverse section of older branch. **D.** Section of cystocarp. **E.** Transverse section of male thallus with a spermatangial sorus on left. **F.** Transverse section of tetrasporangial thallus.

3. **Rhodymenia australis** Sonder 1845: 56; 1848: 191; 1881: 18. J. Agardh 1876: 332. Dawson 1941: 139, pl. 18 figs 7, 8. De Toni 1900b: 519. De Toni & Forti 1923: 29. Harvey 1855a: 554; 1860: pl. 146. Huisman & Walker 1990: 416. Kylin 1931: 21. Lucas & Perrin 1947: 201, fig. 65. May 1965: 408. Tisdall 1898: 506. Womersley 1966: 150.
Sphaerococcus australis (Sonder)Kützing 1849: 784.
Acropeltis australis (Sonder)J. Agardh 1852: 609. Kützing 1869: 12, pl. 34c–e.
Rhodymenia foliifera Harvey 1863, synop.: xl. J. Agardh 1876: 331. Chapman & Dromgoole 1970: 133, pl. 43, lower (?). Dawson 1941: 136. De Toni 1900b: 517. Kylin 1931: 21, pl. 7 fig. 17. Lucas 1929a: 18; 1929b: 49. May 1965: 408. Reinbold 1847: 53; 1899: 45. Tisdall 1898: 506. Wilson 1892: 178. Womersley 1950: 175.

FIG. 26

Thallus (Fig. 26A, B) medium to dark red-brown, cartilaginous, 4–10 (-20) cm high, often with basal stolons and developing erect fonds from the stipes and stolons; fronds complanately branched, branches subdichotomous at intervals of 5–30 mm, (2-) 3–5 (-10) mm broad, increasing from the base and usually broadest near the rounded apices but the upper few mm often narrower when fertile, often proliferous from the margin (occasionally from the adjacent surface) of damaged apices; branches 100–200 µm thick (Fig. 26E, F), increasing to 400 µm in lower parts (Fig. 26C); stipes short to medium [2–5 (-20) mm] in length, terete and compressed above, stipes and terete stolons 1–1.4 mm in diameter. Holdfast crustose, 2–10 mm across, stolons with digitate haptera; epilithic or epiphytic on *Amphibolis*. *Structure* multiaxial, developing a cortex (Fig. 26E, F) 2–3 cells broad, outer cells ovoid and 3–5 µm in diameter, grading over 2–4 cells to the medulla (2-) 3–8 (-20) cells broad (Fig. 26C), cells compact, ovoid, 30–70 (-110) µm in diameter, walls 4–7 µm thick, with only small intercellular spaces or occasional smaller cells but sometimes with central compressed cells; cells (especially near the margins) often with globular inclusions; stolon medulla 0.9–1.2 mm and 20–30 cells broad, with a secondary cortex developing. Rhodoplasts discoid to elongate, in chains in inner cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 3-celled, with a 2-celled auxiliary cell branch on an inner cortical (supporting) cell. Carposporophytes 400–700 µm across, with branched basal fusion cells, bearing a dense mass of ovoid to angular carposporangia 10–18 µm in diameter. Basal nutritive tissue moderate (Fig. 26D), with only a few lateral stellate cells remaining. Cystocarps (Fig. 26D) on the blade surfaces, globular to higher than broad, sessile, basally constricted, 700–1000 µm across; pericarp smooth, 180–400 µm and 15–25 cells thick, innermost cells stellate, mid cells ovoid, and outer small cells in anticlinal chains, with a depressed ostiole. Spermatangial sori near branch ends, spermatangia (Fig. 26E) cut off from elongate outer cortical initials, ovoid, 1–2 µm in diameter.

Tetrasporangia (Fig. 26F) in subapical, ovate, nemathecioid sori on one or both sides, the cortex modified with elongate outer cortical cells and additional small outer cells, tetrasporangia ovoid, apparently terminal and pit-connected only basally to inner cortical cells, 25–40 µm long and 15–22 µm in diameter, decussately divided.

Type from "Occid. Nov. Holl." (*Preiss*); lectotype (Millar 1990, p. 367) in MEL, 504193.

Distribution: Rottnest I., W. Aust. (probably further north), to Gabo I., Vic., and around Tasmania.

New Zealand?

Selected specimens: Rottnest I., W. Aust. (*Harvey*, Alg. Aust. Exsicc. 380a; AD, A63558). Wilson Bay, Rottnest I., W. Aust., 15 m deep (*Huisman*, 20.vii.1994; AD, A63580); Whitford Beach, Perth, W. Aust., 6 m deep (*Cook* CS20, 20.viii.1979; AD, A50546). Twin Rocks, Head of Great Australian Bight, S. Aust., 20–22 m deep (*Branden*, 19.i.1991; AD, A61147). Pearson I., S. Aust., 50 m deep (*Shepherd*, 9.i.1969; AD, A33878). Brown Beach, Yorke Pen., S. Aust., 6–12 m deep (*Shepherd*, 14.iv.1963; AD, A26575). Off St Kilda, S. Aust., 3 m deep (*S. Lewis*, 28.viii.1972; AD, A42738). Glenelg, S. Aust., 4.5 m deep (*Cannon*, 29.i.1987; AD, A58571 and 4.vi.1987; AD, A58572). Marino, S. Aust., drift (*Womersley*, 30.vi.1963; AD, A26465). Port Noarlunga, S. Aust., 1.5–3 m deep (*Baldock*, 7.xii.1965; AD, A30498). Port Elliot, S. Aust., drift (*Womersley*, 28.v.1994; AD, A63568).

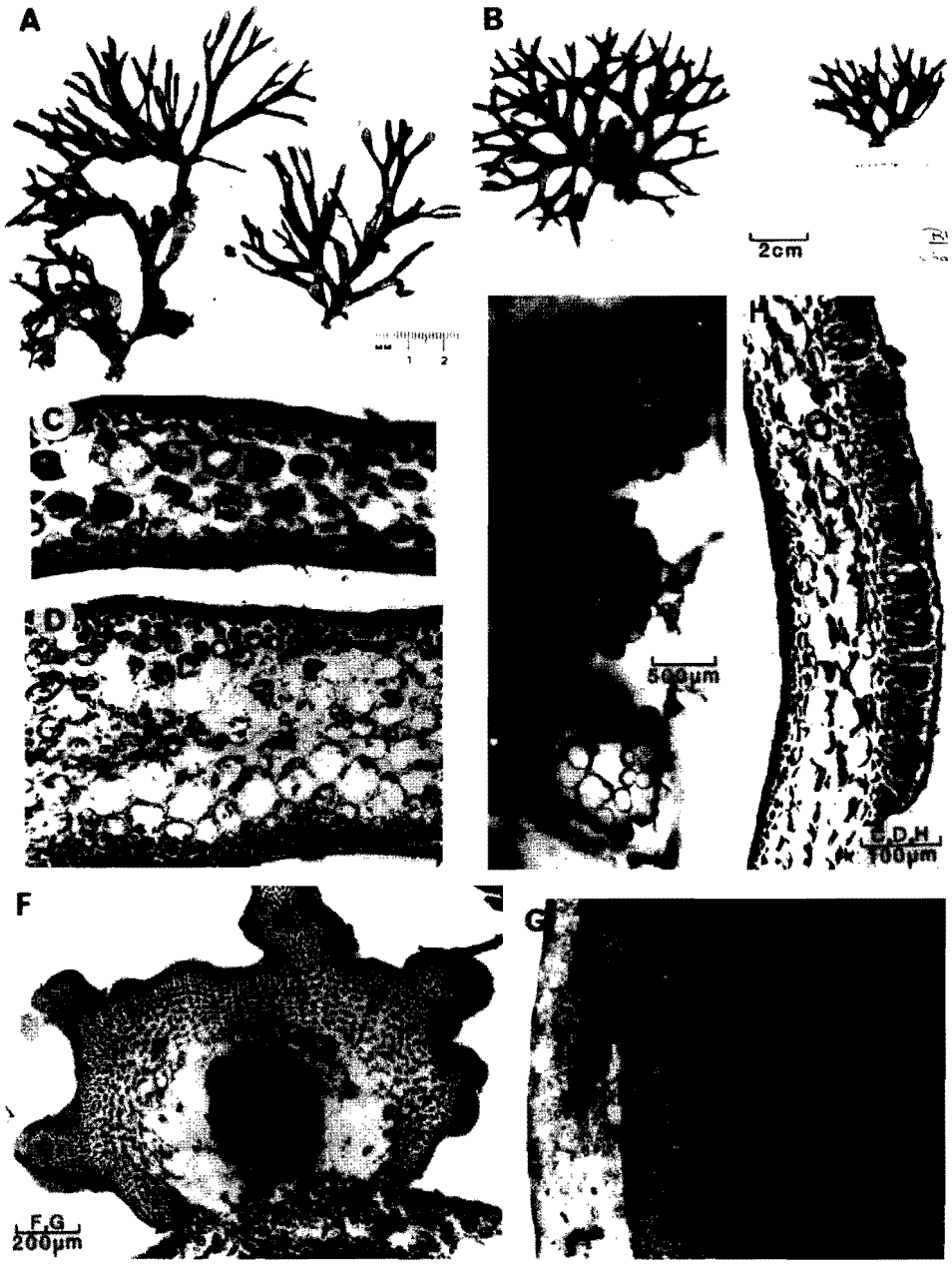


Fig. 27. *Rhodymenia verrucosa* (**A, C–F,** AD, A43500; **B, G, H,** AD, A43332). **A.** Habit, cystocarpic plants. **B.** Habit, tetrasporangial plant on left, cystocarpic on right. **C.** Transverse section of young branch. **D.** Transverse section of older branch. **E.** Verrucose cystocarps. **F.** Section of cystocarp with verrucose pericarp. **G.** Surface view of tetrasporangial nemathecium. **H.** Sectional view of tetrasporangial nemathecium.

Pennington Bay, Kangaroo I., S. Aust., 2 m deep (*Kraft*, 13.iv.1973; AD, A43582). Muston, Kangaroo I., S. Aust., upper sublittoral (*Womersley*, 27.viii.1950; AD, A15373). Young Rocks, S of Kangaroo I., S. Aust., 16–30 m deep (*Branden*, 18.vi.1991; AD, A61465). 9 km off Cape Northumberland, S. Aust., 38 m deep (*Shepherd*, 12.iii.1975; AD, A46198). Dutton Bay, Portland, Vic., drift on *Amphibolis* (*Womersley*, 13.iv.1959; AD, A22697). Off Williamstown, Port Phillip, Vic., 2.5 m deep (*Macpherson*, 15.i.1961; AD, A28820). Walkerville, Vic., drift (*Sinkora* A1544, 23.ii.1972; AD, A42274). Gabo I., Vic., 28 m deep (*Shepherd*, 14.ii.1973; AD, A43348). Eddystone Point., Tas., 30 m deep (*Riddle*, 24.ii.1990; AD, A60404). Marion Bay, Tas., 10–12 m deep (*Shepherd*, 13.ii.1970; AD, A35644). Dead I., Port Arthur, Tas., 9–14 m deep (*McCauley*, 2.iii.1990; AD, A60475).

R. australis is here interpreted broadly as the common species on southern Australian coasts, with basal stolons, short to medium length stipes and branches (2-) 3–5 (-10) mm broad. Proliferations are common from damaged apices of branches and occasionally as small leaflets from the margins or surface. It occurs from low tide level to 50 m deep, and varies considerably in width of branches depending on age, state of growth and degree of water movement.

R. foliifera Harvey is not considered distinct from *R. australis*. The type was from King George Sound, W. Aust. (lectotype *Harvey*, Alg. Aust. Exsicc. 381B in TCD) and was first referred to the South American *R. corallina* by Harvey.

R. australis has been recorded, usually with doubt, from Indonesia by Weber-van Bosse (1928, p. 461), from Bombay, India by Børgesen (1934, p. 41), and from Juan Fernandez I. by Levring (1941, p. 645). These records need verification.

4. **Rhodymenia verrucosa** Womersley, *sp. nov.*

FIGS 27, 30C

Thallus (Fig. 27A, B) medium to dark red-brown, cartilaginous, 3–14 cm high, with one to a few complanately branched fronds, branching subdichotomous to alternate at intervals of 5–20 mm, branches (2-) 3–8 (-10) mm broad, 200–300 (-500) µm thick, usually thicker marginally, stipes terete to compressed, slender, simple or branched, 2–10 mm long, 0.3–1.0 mm thick. Holdfast crustose, 2–5 mm across, with one to a few fronds; epilithic. *Structure* multiaxial, developing a cortex (Fig. 27C, D) 1–2 cells broad, outer cells ovoid and 4–5 µm in diameter, grading abruptly to the medulla 3–5 (-10) cells broad, cells laxly arranged with intercellular spaces, ovoid, inner 2–3 cells often regularly arranged (Fig. 27C) and 45–90 µm in diameter, some cells with globular inclusions; stipe medulla 400–800 µm and 8–12 cells broad. Rhodoplasts discoid to elongate, ribbon like in inner cells.

Reproduction. Gametangial thalli probably dioecious. Carpogonial and auxiliary cell branches not observed. Carposporophytes (Fig. 27F) 600–900 µm across, with branched, elongate, fusion cells bearing a dense mass of ovoid carposporangia 15–25 µm in diameter. Basal nutritive tissue slight, erect filaments of stellate cells disintegrating early but some remaining. Cystocarps protuberant on the blade surfaces, mainly on one side and often clustered, sessile, basally constricted and the surface with prominent verrucose excrescences (Fig. 27E, F), 0.7–1.5 mm across, pericarp 180–360 µm (apart from the excrescences) and 10–20 cells thick, inner cells stellate, mid cells ovoid, outer cells more or less in anticlinal chains, ostiolate. Spermatangia not observed.

Tetrasporangia in sharply defined nemathecia (Fig. 27G, H) near branch ends, with the outer cortical cells becoming elongate and cutting off small outer cells; tetrasporangia (Fig. 30C) terminal, ovoid, 25–35 µm long and 12–22 µm in diameter, decussately or cruciately divided.

Thallus cartilagineus, 3–14 cm altus, una vel paucis frondibus complanatis, subdichotome aut alterne ramosis. Rami (2-) 3–8 (-10) mm lati, stipes teres vel compressus, 2–10 mm longus. Hapteron incrustans, 2–5 mm latum, epilithicum. Structura corticis 1–2 cellulas lata et medulla 3–5 (-10) cellulas lata, 2–3 cellulis interioribus saepe ordinatim dispositis.

Reproductio. Probabiliter dioecia. Carposporophyta 600–900 µm lata, cellulis coalescentibus ramosis et carposporangiis densis. Textura basalis nutritiva levis, filamentis erectis plerumque fatiscentibus. Cystocarpa in laminis, saepe in latere fasciculata, basaliter constricta, superficie manifeste verrucosa. Tetrasporangia in nemathecis discretis prope

extremitates ramorum, cellulis exterioribus corticalibus elongatis, terminalis, ovoideis, 25–35 μm longis et 12–22 μm in diametro, decussate vel cruciatim divisa.

Type from Gabo I., Vic., 18 m deep (*Shepherd*, 17.ii.1973); holotype in AD, A43500, cystocarpic. *Syntype* from Gabo I., Vic., 13 m deep (*Shepherd*, 14.ii.1973); in AD, A43332, tetrasporangial and cystocarpic.

Distribution: Althorpe Is, S. Aust., 15 m deep (*Baker*, 26.x.1993; AD, A64480). West I., S. Aust., to Gabo I., Vic., and eastern Tasmania.

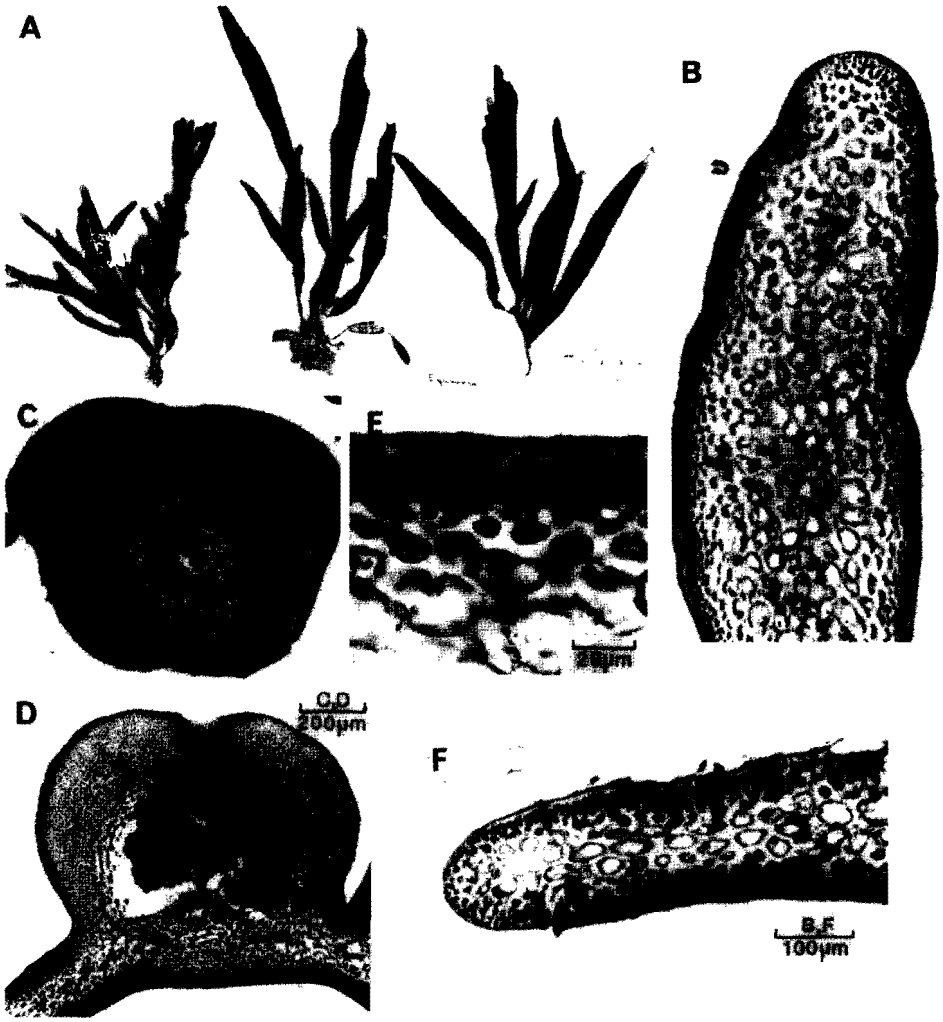


Fig. 28. *Rhodymenia obtusa* (**A–D, F,** AD, A41872; **E,** AD, A57040). **A.** Habit. **B.** Transverse section of branch. **C.** Transverse section of stipe with secondary cortex. **D.** Section of cystocarp. **E.** Transverse section of male thallus with spermatangia. **F.** Transverse section of branch with tetrasporangia.

Selected specimens: Oedipus Point, West I., S. Aust., 16 m deep (*Shepherd*, Dec. 1966; AD, A31142). Nora Creina, S. Aust., in channel between island and headland (*Kraft* 6220, 29.xii.1976; MELU, 38378). Cape Buffon, S. Aust., 2 m deep (*Kildea & Collings*, 27.ix.1992; AD, A62801). Warrnambool, Vic., drift (*Kraft* 7979 & *Herrington*, 6.xi.1989; MELU, 38371). Bicheno, Tas., 20–22 m deep (*Kraft* 9378, 18.xii.1992; MELU). Marion Bay, Tas., 3–5 m deep (*Shepherd*, 13.ii.1970; AD, A35599). Fluted Cape, Bruny I., Tas., 16 m deep (*Shepherd*, 10.ii.1972; AD, A41526).

R. verrucosa is characterised by the prominently verrucose cystocarps which set it apart from all other described species of *Rhodymenia*. The medulla in young branches has two central cells which are more rounded and laxer as a tissue than in most species, and the inner layer of the pericarp also has more stellate cells than is usual in the genus. The above description of tetrasporangial nemathecia is based on two collections (the syntype and MELU, 38371) where tetrasporangial and cystocarpic plants are on the one sheet. Transverse sections of the thalli are similar and it is presumed that they belong to the one species.

5. **Rhodymenia obtusa** (Greville)Womersley, *comb. nov.*

Phyllophora obtusa Greville 1831: 148, pl. 4 figs 1–5.

Phyllophora obtusa var. *crispata* Sonder 1848: 171.

Epymenia obtusa (Greville)Kützing 1849: 787; 1869: 15, pl. 40a, b. J. Agardh 1851: 220; 1892: 93. Etcheverry 1986: 281. Harvey 1863, synop.: xlv. Kylin 1931: 22. Sparling 1957: 350, figs 9a–g, 10, pls 51a, 52, 53.

Epymenia wilsonis Sonder 1855: 516; 1881: 18. Adams 1994: 234, pl. 83 lower right. J. Agardh 1892: 92. Chapman & Dromgoole 1970: 129, pl. 42 (upper). De Toni 1900b: 526. Guiler 1952: 94. Harvey 1863, synop.: xlv. Kylin 1931: 22, fig. 7, pl. 10 fig. 23. May 1965: 407. Sparling 1957: 348. Tisdall 1898: 506.

Epymenia membranacea Harvey 1859a: pl. 89; 1859b: 326. J. Agardh 1876: 334; 1878: 20; 1892: 93. De Toni 1900b: 527. Kützing 1869: 15, pl. 40c–e. Kylin 1931: 23. May 1965: 407. Sonder 1881: 18. Sparling 1957: 348. Tisdall 1898: 506. Wilson 1892: 178.

PLATE 2 fig. 1; FIGS 28, 30D

Thallus (Fig. 28A) dark red to red-brown, (5-) 10–25 cm high, fronds complanately branched with subdichotomous to alternate branches at intervals of mostly 2–6 cm, branches flat, 0.5–1.5 cm broad (broadest in cooler water specimens) with broadly rounded apices and a midrib present in lower fronds; proliferous laterals frequent from the midrib or centre of frond, 1–8 cm long, with small ovate to branched proliferations usually present, often in patches, and which become fertile; stipe compressed, 5–20 mm long and 0.5–1 mm broad. Holdfast crustose, 1–5 mm across, bearing 1–several fronds; epilithic. *Structure* multiaxial, developing a cortex (Fig. 28B) 2–3 cells thick, outer cells ovoid and 3–5 µm in diameter, grading over 2–4 cells to the medulla, 3–5 (-8) cells broad, inner larger cells ovoid and 30–60 µm in diameter, medulla becoming 8–20 cells thick in older parts (Fig. 28B) with intermixed larger and smaller cells. Midrib formed by secondary cortical development; stipe (Fig. 28C) medulla 20–30 cells across, with a secondary cortex. Rhodoplasts discoid to elongate, ribbon like in medullary cells.

Reproduction. All reproductive structures borne on the small proliferations, which are mostly ovate and 2–4 mm long, occasionally irregularly branched. Gametangial thalli dioecious. Carpogonial branches (Fig. 30D) 4-celled, with 3-celled auxiliary cell branches, borne on inner cortical cells. Carposporophyte (Fig. 28D) with a basal, erect, fusion complex of several elongate cells and a dense mass 500–700 µm across of ovoid to angular carposporangia 10–18 µm in diameter. Basal nutritive tissue slight, erect filaments disintegrating early apart from a few stellate cells. Cystocarps (Fig. 28D) on both sides of the proliferations, sessile, basally constricted, 0.75–1.5 mm across, pericarp 180–350 µm and 10–20 cells thick, inner cells stellate, outer cells in anticlinal chains, with a depressed ostiole. Spermatangia (Fig. 28E) covering the surface, cut off from elongate initials on outer cortical cells, ovoid, 2–2.5 µm in diameter.

Tetrasporangia in nemathecia (Fig. 28F) among extended cortical filaments 30–45 µm and 3–4 cells long, intercalary in mid cortical cells with pit-connections to outer cortical cells, ovoid, 20–45 µm long and 10–25 µm in diameter, irregularly decussately divided.

Type from Cape of Good Hope, South Africa (from Bowie); in E?

Distribution: South Africa, New Zealand, southern South America.

In southern Australia, from Topgallant I., S. Aust. (mainly from Robe), to Gabo I., Vic., and around Tasmania.

Selected specimens: Topgallant I., Investigator Group, S. Aust., 27 m deep (*Turner*, 29.iii.1982; AD, A53057). Port Elliot, S. Aust., drift (*Womersley*, 20.ix.1959; AD, A23148). Robe, S. Aust., 3 m deep on jetty piles (*Kildea & Collings*, 26.ix.1992; AD, A62828). Nora Creina, S. Aust., shaded pool (*Womersley*, 1.xi.1993; AD, A63253). Cape Northumberland, S. Aust., completely shaded pool 10–30 cm deep (*Womersley*, 24.ii.1992; AD, A61616 and 1.xi.1993; AD, A63267). Warrnambool, Vic., upper sublittoral (*Womersley*, 13.iv.1959; AD, A22896). Port Phillip Heads, Vic., 10 m deep (*Watson*, 8.iii.1985; AD, A57040). Gabo I., Vic., 13 m deep (*Shepherd*, 14.ii.1973; AD, A43334). Two Mile Creek, St Patricks Head, E Tas., 6 m deep (AIMS-NCI, Q66C 3707-U, 26.ii.1990; AD, A60344). Peggy Point, Bicheno, Tas., upper sublittoral pools (*Wollaston & Mitchell*, 2.iii.1964; AD, A27835). Stapleton Point, Prosser Bay, Tas., 3–6 m deep (*Shepherd*, 10.ii.1970; AD, A35738). Tesselated

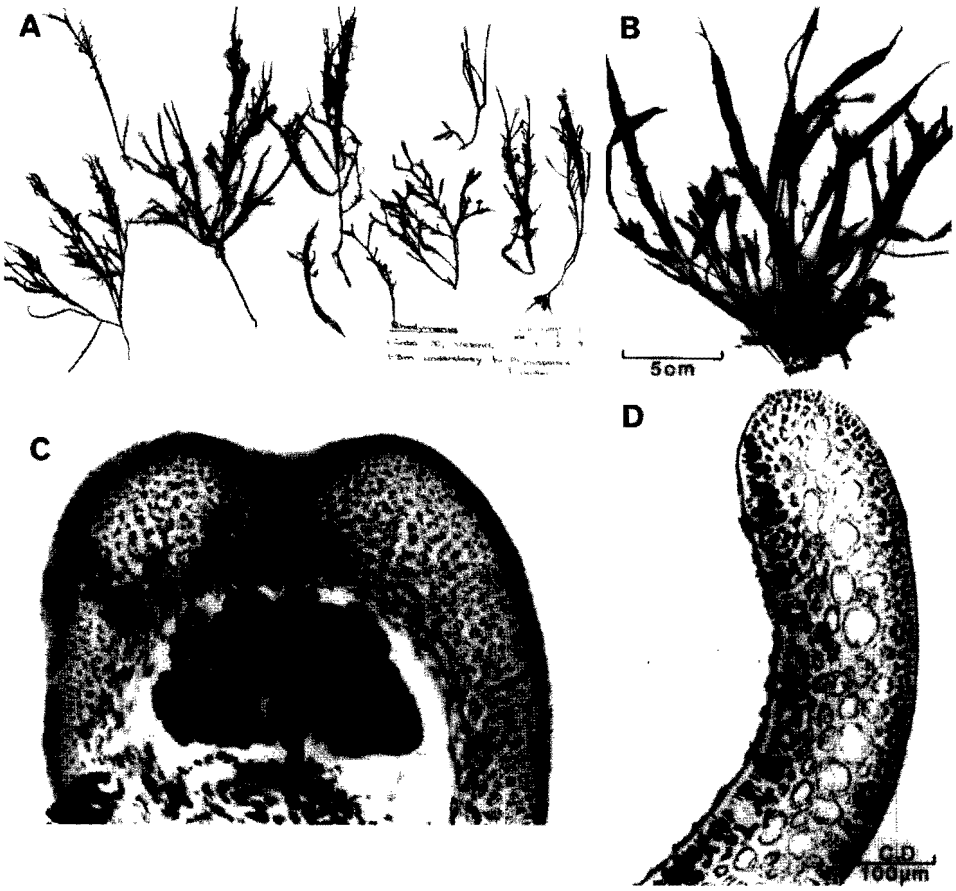


Fig. 29. *Rhodymenia prolificans* (**A, D,** AD, A43377; **B, C,** AD, A41873). **A.** Habit, slender plants. **B.** Habit, broader plant. **C.** Section of cystocarp. **D.** Section of tetrasporangial branch.

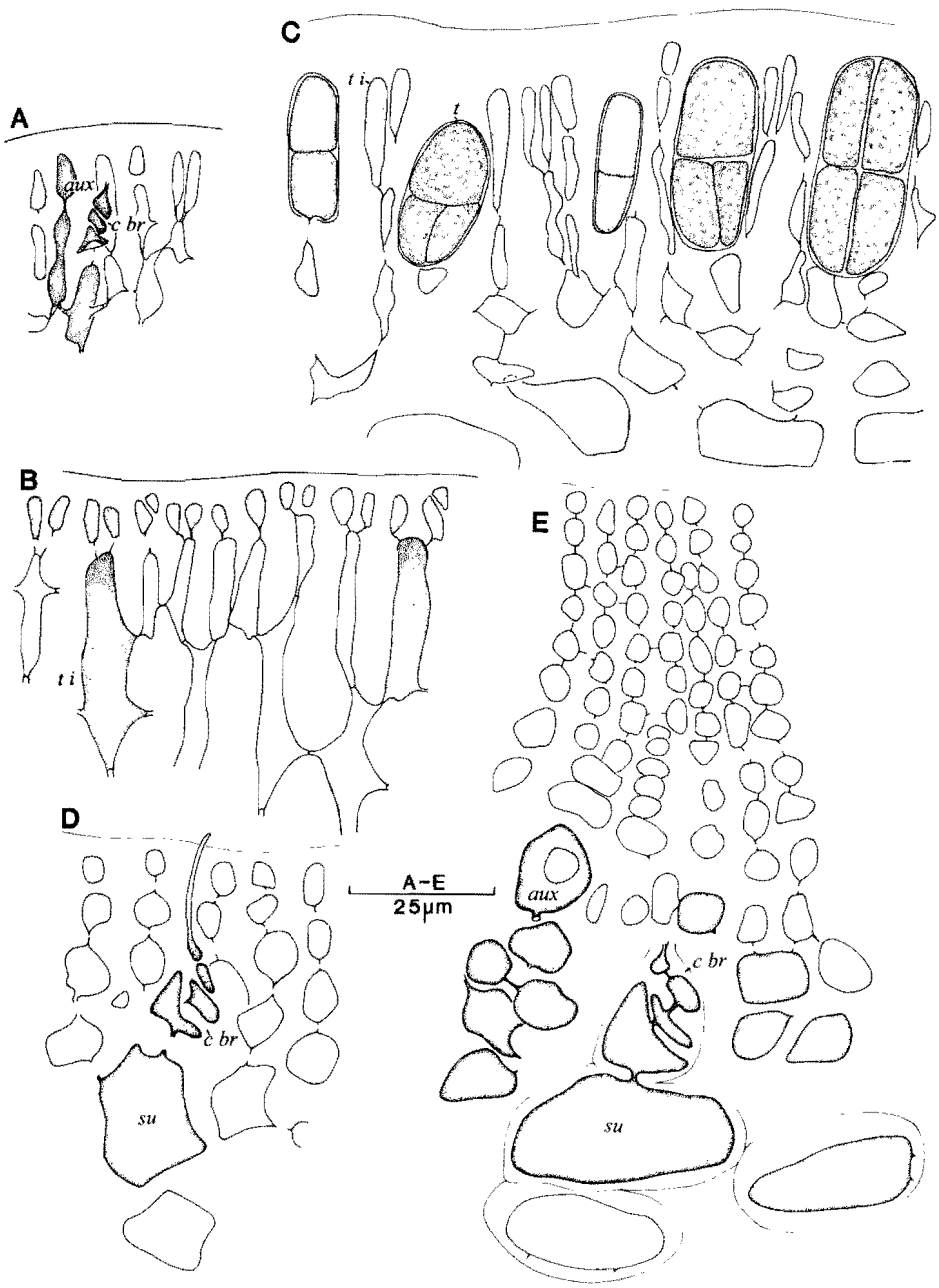


Fig. 30. A. *Cordylecladia furcellata* (AD, A39609). Transverse section of cortex with a carpogonial branch and probable auxiliary cell branch. **B.** *Erythrymenia minuta* (AD, A22254). Transverse section of cortex with developing intercalary sporangia. **C.** *Rhodymenia verrucosa* (AD, A43332). Transverse section of cortex with developing and mature tetrasporangia. **D.** *Rhodymenia obtusa* (AD, A63267). Transverse section of thallus with a carpogonial branch. **E.** *Rhodymenia prolificans* (AD, A49246). Transverse section of thallus post fertilization, with a carpogonial branch and proliferating auxiliary cell branch (auxiliary cell with a globular inclusion).

Pavement, Eaglehawk Neck, Tas., 0–1 m deep (*Brown & Kenchington*, 16.x.1986; AD, A57612). Canoe Bay, Fortescue Bay, Tas., 2–3 m deep (*Gowlett-Holmes*, 22.vi.1995; AD, A64436). Fluted Cape, Bruny I., Tas., 1–5 m deep (*Shepherd*, 11.ii.1972; AD, A41754) and 0–6 m deep (*Shepherd*, 12.ii.1972; AD, A41872).

R. obtusa specimens in south eastern Australia are usually narrower in branch width, especially those specimens towards the extremes of the range; some, however, compare well with South African specimens (i.e. 1–1.5 cm broad) and in view of the structural and reproductive similarities it seems best to interpret *R. obtusa* as variable in branch width and include *E. wilsonis* and *E. membranacea* as synonyms, as did Sparling (1957, p. 348).

The lectotype of *E. wilsonis* Sonder, from Wilsons Prom., Vic., is in MEL, 674904; it is a relatively slender specimen with prominent proliferous laterals from the central thallus. The type of *E. membranacea* Harvey, from Georgetown, Tas., is in Herb. Harvey, TCD, and, as illustrated by Harvey (1859a, pl. 89) has proliferous, fertile, leaflets on the thallus surface.

6. **Rhodymenia prolificans** Zanardini 1874: 499. Dawson 1941: 138. Guiler 1952: 94. Lucas 1929a: 18. Lucas & Perrin 1947: 201. May 1965: 408. Sonder 1881: 18.

FIGS 29, 30E

Thallus (Fig. 29A, B) medium to dark red-brown, 5–20 cm high, with numerous, often clumped, fronds from the holdfast, fronds erect, flat, cartilaginous, gradually broadening upwards from the slender stipe to a narrower rounded apex, 0.5–1 mm broad near the base, 2–6 (-8) mm broad near the apices, with frequent proliferous marginal laterals especially from the upper parts, laterals 5–50 mm long, 0.5–4 mm broad, simple or also proliferous from their margins, basally slender and usually broadest near their apices; proliferations also often present on branch surfaces; thallus branches 180–300 (-350) µm thick, stipe terete to compressed, 400–600 µm thick. Holdfast crustose, 2–20 mm across, with few to numerous fronds; epilithic. *Structure* multiaxial, developing a cortex 3–4 cells thick (Fig. 29D), outer cells ovoid in section and (2-) 3–5 µm in diameter, grading fairly sharply to the medulla (3-) 4–8 cells broad, cells ovoid, 20–45 µm in diameter, stipe medulla becoming 300–450 µm and 12–20 cells broad. Rhodoplasts discoid to elongate.

Reproduction. Gametangial thalli probably dioecious. Carpogonial branches probably 4-celled (Fig. 30E), auxiliary cell branches probably 3-celled, auxiliary cell with a globular inclusion (Fig. 30E). Carposporophytes (Fig. 29C) 270–450 µm across, with erect, branched fusion cells bearing dense masses of ovoid to angular carposporangia 8–14 µm in diameter. Basal nutritive tissue slight, erect filaments soon disintegrating. Cystocarps (Fig. 29C) on the surface (occasionally near margins) of branchlets 400–500 µm thick, medulla 10–15 cells broad, sessile, slightly basally constricted, 0.6–1.2 mm across, pericarp 100–270 µm and 8–20 cells thick, with a depressed ostiole. Spermatangia not observed.

Tetrasporangia (Fig. 29D) in sori near branchlet ends, on one (concave) or both sides, with the cortex slightly extended, cells elongate with small additional outer cells, tetrasporangia ovoid, probably terminal and basally pit-connected only to inner cortical cells, 20–35 µm long and 10–20 µm in diameter, decussately divided.

Type from Georgetown, Tas. (*Goodwin*); lectotype ("paratype" only seen) in Herb. Zanardini, Museo Civico di Storia Naturale, Venice.

Distribution: Lawrence Rock, Portland, Vic., and Gabo I., Vic., and around Tasmania.

Selected specimens: Lawrence Rock, Portland, Vic., in rock pools (*Beauglehole* 663, 15.i.1960; AD, A24789). Gabo I., Vic., 1–3 m deep (*Shepherd*, 15.ii.1973; AD, A43377). Remine, Tas., upper sublittoral pools (*Wollaston & Mitchell*, 25.ii.1964; AD, A27510). Peggy Point, Bicheno, Tas., upper sublittoral pools (*Wollaston & Mitchell*, 2.iii.1964; AD, A27830). Safety Cove, Port Arthur, Tas., lower eulittoral (*Skinner*, 21.ii.1978; AD, A49246). Fluted Cape, Bruny I., Tas., 0–6 m deep (*Shepherd*, 12.ii.1972; AD, A41873).

R. prolificans is distinctive in habit, with slender branches broadening upwards and numerous marginal and usually also surface proliferations. It is usually found just below low tide level or in pools.

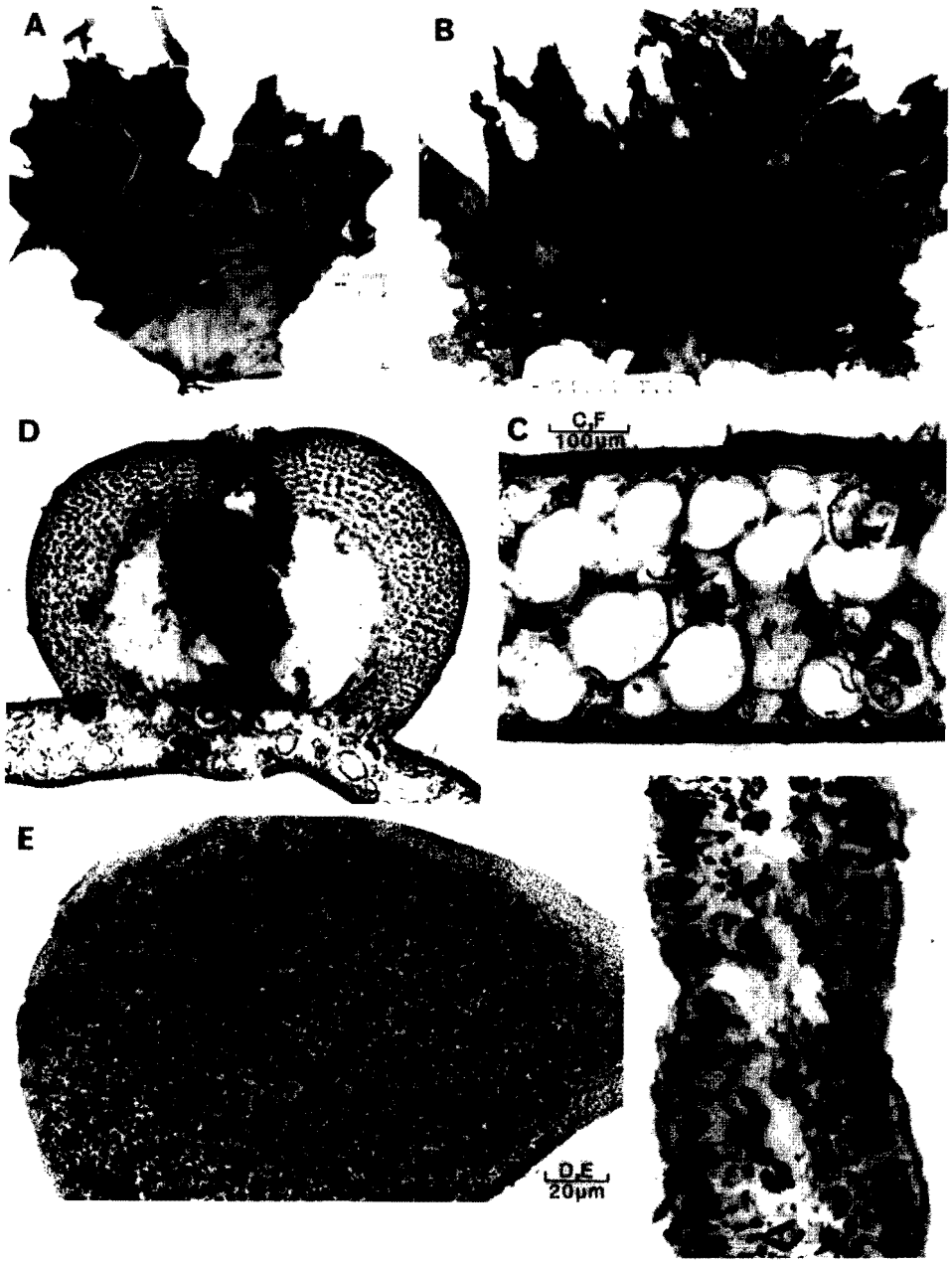


Fig. 31. *Rhodymenia halymenioides* (**A, D,** AD, A63886; **B,** AD, A63792; **C, E, F,** AD, A63868). **A.** Habit, cystocarpic plant. **B.** Habit, tetrasporangial plant. **C.** Transverse section of older thallus. **D.** Section of cystocarp. **E.** Tetrasporangial leaflet. **F.** Section of tetrasporangial leaflet.

7. **Rhodymenia halymenioides** (J. Agardh)Womersley, *comb. nov.*
Epymenia halymenioides J. Agardh 1876: 694; 1892: 91. De Toni 1900b: 525. Guiler 1952: 94. Kylin 1931: 23, pl. 10 fig. 24. Lucas 1929a: 18. May 1965: 407. Sonder 1881: 18. Sparling 1957: 348. Tisdall 1898: 506. Wilson 1892: 178.
Chrysymenia meredithiana J. Agardh 1876: 321. Sonder 1881: 18. Tisdall 1898: 506.
Halichrysis ?meredithiana (J. Agardh)De Toni 1900b: 536. Lucas 1929a: 19.
Erythrymenia meredithiana (J. Agardh)Kylin 1931: 13. Guiler 1952: 94.

FIG. 31

Thallus (Fig. 31A, B) medium red, foliose, 16–20 cm high and 20–25 cm broad, with an ovate thallus irregularly lacerate or perforate, base cuneate with a compressed stipe 4–12 mm long and 1 mm thick. Surface of tetrasporangial thalli (Fig. 31B) covered with numerous ovate, stipitate, proliferations 2–5 (-8) mm long and 2–3 (-5) mm broad. Holdfast discoid, 3–4 mm across; epilithic. *Structure* multiaxial, developing a cortex 1–2 cells thick, outer cells ovoid in surface view and 4–6 µm in diameter, grading sharply to the medulla (Fig. 31C, D) 2–3 cells broad, cells ovoid, 50–90 µm in diameter, with intermixed smaller cells. Rhodoplasts discoid.

Reproduction. Gametangial thalli probably dioecious. Carpogonial branches and auxiliary cells not observed. Carposporophytes (Fig. 31D) 500–800 µm across with an erect, branched, fusion cell bearing dense masses of ovoid to angular carposporangia 12–25 µm in diameter. Basal nutritive tissue moderate, erect filaments disintegrating. Cystocarps scattered on the thallus surface (Fig. 31A), sessile, basally slightly constricted, 1–1.5 mm across, pericarp 200–300 µm and 12–18 cells thick, inner cells stellate, ostiolate. Spermatangia not observed.

Tetrasporangia in sori (Fig. 31E, F) on the proliferations, among cortical filaments 30–40 µm and 2–3 cells long, terminal and basally pit-connected only to inner cortical cells, ovoid, 20–40 µm long and 18–26 µm in diameter, decussately divided.

Type from Orford, Tas. (*Meredith*); holotype in Herb. Agardh, LD, 27057.

Distribution: SE Tasmania.

Selected specimens: Orford, Tas.; holotype of *C. meredithiana*, cystocarpic (*Meredith*; LD, 26474). Gordon, Tas. (*Perrin*, 13.ix.1942; AD, A63792, tetrasporangial and HO, fragment in AD, A63792, cystocarpic). Arch Rock, E of Ninepin Point, Tas., 5–12m deep (*Sanderson*, 21.x.1994; AD, A63886, tetrasporangial and cystocarpic; AD, A63868, tetrasporangial).

Tetrasporangial specimens of *R. halymenioides* are distinctive in habit, the ovate, foliose, thallus bearing fertile proliferations over most of the surface apart from near the stipe. Cystocarps however are borne on the thallus surface and there are no surface proliferations. This difference resulted in J. Agardh in the one publication describing Orford, Tas., tetrasporangial specimens of Meredith as *Epymenia halymenioides* and cystocarpic ones as *Chrysymenia meredithiana*. The latter has been known only from the type, but recent collections of both phases have clarified their synonymy.

Rhodymenia halymenioides is here selected as the name for this species.

8. **Rhodymenia cuneata** Harvey 1859b: 319; 1863: pl. 295. Sonder 1881: 18.
Epymenia ?cuneata (Harvey)J. Agardh 1892: 91. De Toni 1900b: 526. Guiler 1952: 94. Lucas 1929a: 18. May 1965: 407. Sparling 1957: 348.

FIG. 32

Thallus (Fig. 32A) medium to dark red-brown, fading to grey-red, 4–20 cm high, foliose and usually divided above into several lobes 1–8 cm across, membranous to cartilaginous, surface smooth and without proliferations, (150-) 200–350 µm thick, with a slender, terete to compressed, stipe 4–15 mm long tapering to a narrowly to broadly cuneate frond base. Holdfast discoid, 1–3 mm across, with 1–2 fronds; epilithic or on the mollusc *Maoricolpus*. *Structure* multiaxial, developing a cortex 1–2 cells thick (Fig. 32B), outer cells rounded and 5–8 µm in diameter (forming slight rosettes in surface view), grading sharply to the medulla mostly 2 cells broad when young, cells ovoid, 90–140 µm in diameter, walls (3-) 5–10 µm

thick with occasional intercellular spaces or smaller cells between larger cells; medulla becoming 8–12 cells and 600–800 µm broad near and in the stipe, stipe 0.6–1.2 mm in diameter with some secondary cortical development. Rhodoplasts discoid to elongate, becoming ribbon like or reticulate.

Reproduction. Gametangial thalli probably dioecious. Carpogonial branches not observed; auxiliary cell terminating a 2-celled branch on the supporting cell, with a globular inclusion. Carposporophyte (Fig. 32C) dendroid, with an erect branched fusion cell(s) and closely adjacent lobes forming a dense subspherical to ovoid mass of carposporangia 350–600 µm across; all cells forming angular to ovoid carposporangia 10–14 µm across. Basal nutritive tissue relatively slight, erect filaments disintegrating apart from remnant stellate cells. Cystocarps (Fig. 32C) sessile, broad-based (not or slightly constricted), 1.0–1.6 mm across; pericarp 200–300 µm and 10–15 cells thick, ostiolate. Spermatangia unknown.

Tetrasporangia unknown.

Type from East coast, Tas. (*Gunn*); holotype in Herb. Harvey, TCD.

Distribution: East and SE Tasmania.

Selected specimens: Musselroe Bay, Tas. (*Perrin & Lucas*, March 1936; NSW, 10607, 10608). Sloping I., Frederick Henry Bay, Tas., 12 m deep (AIMS-NCI, Q66C 5024-A, 12.ii.1991; AD, A61375). 2 km N of Satellite I., D'Entrecasteaux Ch., Tas., 15 m deep (*Shepherd*, 17.ii.1972; AD, A41667). Simpson Bay, Bruny I., Tas., 11 m deep (*Shepherd*, 11.ii.1972; AD, A41596). Great Taylor Bay, Bruny I., Tas., 10 m deep (*Shepherd*, 7.ii.1970; AD, A35288) and 19 m deep (*Shepherd*, 14.ii.1972; AD, A42162). Sarah I., Bathurst Ch., SW Tas., 2–5 m deep (*Edgar*, 11.iii.1995; AD, A64252).

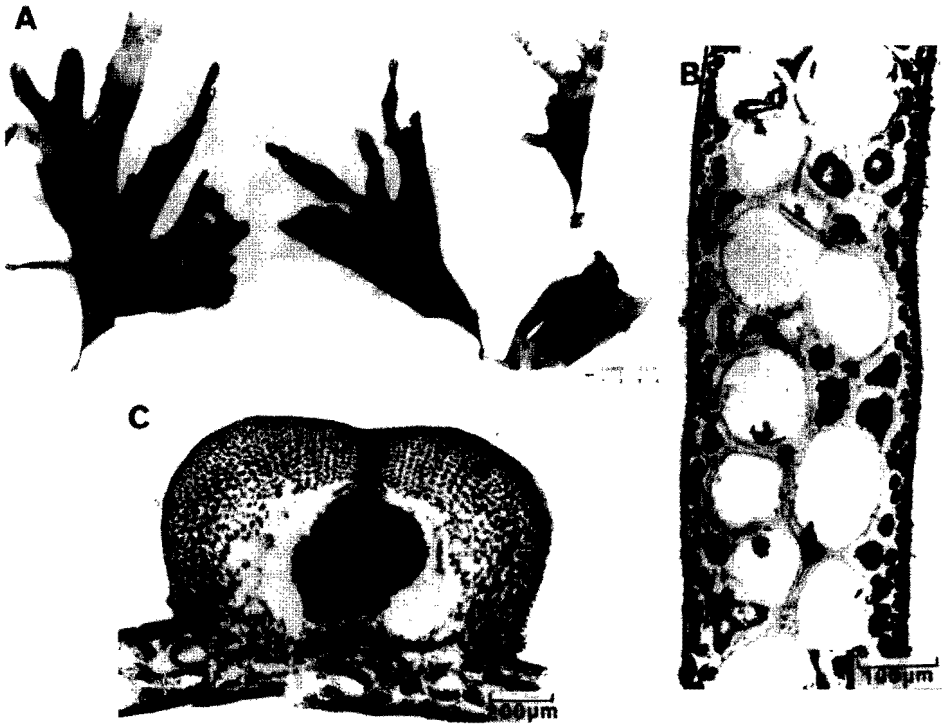


Fig. 32. *Rhodymenia cuneata* (AD, A61375). **A.** Habit. **B.** Transverse section of thallus. **C.** Section of cystocarp.

R. cuneata is distinctive in habit and in cross section with mostly two large, relatively thick-walled medullary cells. The outer cortical cells mostly form slight rosettes around the next inner cells.

Further studies are needed, especially of male and tetrasporangial plants.

Excluded or doubtful species

Rhodymenia corallina (Bory)Greville (1830: xlviii), from South America [type from Chile (*Binder*); lectotype in Herb. Bornet, PC].

Harvey (1859b, p. 319) first ascribed Australian specimens to *R. corallina* (followed by several other authors) but later (1863, synop.: xl) referred them to his *R. foliifera*. The lectotype of *R. corallina* in PC agrees well with the figure of Bory (1828, pl. 16). It is a large plant, about 20 cm high, with a distinct stipe 3–4 cm long, broadening to branches nearly 1 cm broad, then tapering fairly evenly to the apices 2–4 mm broad. While some specimens placed in *R. australis* approach this, they are generally slenderer plants and for the present it seems best to exclude *R. corallina* from the southern Australian flora.

Rhodymenia linearis J. Agardh (1841: 13) was originally recorded from "mari australi; *misit* Hoffman-Bang". Both the locality and the collector are thus unknown. The type sheet (Herb. Agardh, LD, 26970, see Kylin 1931: 20, pl. 6 fig. 16) has relatively linear, subdichotomous branches 2–3 (-4) mm broad, bearing scattered, conical, external cystocarps over most of the branches. One other specimen (26969) from "East coast of New Zealand" in Herb. Agardh is similar in habit, and the species is considered in the New Zealand flora by Chapman & Dromgoole (1970, p. 133, pl. 43, upper). *R. linearis* was credited to "Coast of New Holland" and Tasmania by Sonder (1881, p. 18), Dawson (1941, p. 137) and others but no Australian specimens agree well with the type and it is more likely a New Zealand species only.

Genus **RHODYMENIOCOLAX** Setchell 1923: 394

Thallus 1–4 mm high, forming verrucose or stellate pustules usually with a basal stalk, on species of *Rhodymenia*. *Structure* multiaxial, developing a cortex 1–3 (-6) cells thick and a pseudoparenchymatous medulla of ovoid to elongate cells of varying sizes, with basal filaments penetrating the host medulla.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 4-celled, borne on a multinucleate inner cortical (supporting) cell together with a 2-celled auxiliary cell branch. Carposporophyte developing outwardly, with a basal fusion cell and lobes of carposporangia. Basal nutritive tissue present, erect filaments largely disintegrating. Cystocarps protruding, hemispherical, with a pericarp, ostiolate. Spermatangia in extensive surface sori, cut off from elongate initials on cortical cells.

Tetrasporangia scattered in the unmodified cortex or in extensive nemathecia, decussately or cruciately divided.

Type species: *R. botryoidea* Setchell 1923: 394.

Previous to this, *Rhodymeniocolax* included only the type species from California, U.S.A., though L. Irvine & Guiry (1983, p. 97), suggest that a second species occurs in the British Isles and France. A third species occurs on *Rhodymenia* on southern Australian coasts. Comparisons with the type species are limited by lack of information on it.

Rhodymeniocolax austrina Womersley, *sp. nov.*

FIGS 33, 34A–C

Thallus (Fig. 33A) 1–3 (-4) mm high, light red (drying paler or darker), simple or (usually) with a few irregular branches 1–1.5 (-2) mm long and 300–600 (-1500) μm in diameter, branch ends rounded, branches smooth (male and tetrasporangial) or verrucose (cystocarpic); base (Fig. 33B, C) short and broad; hemiparasitic on *Rhodymenia*.

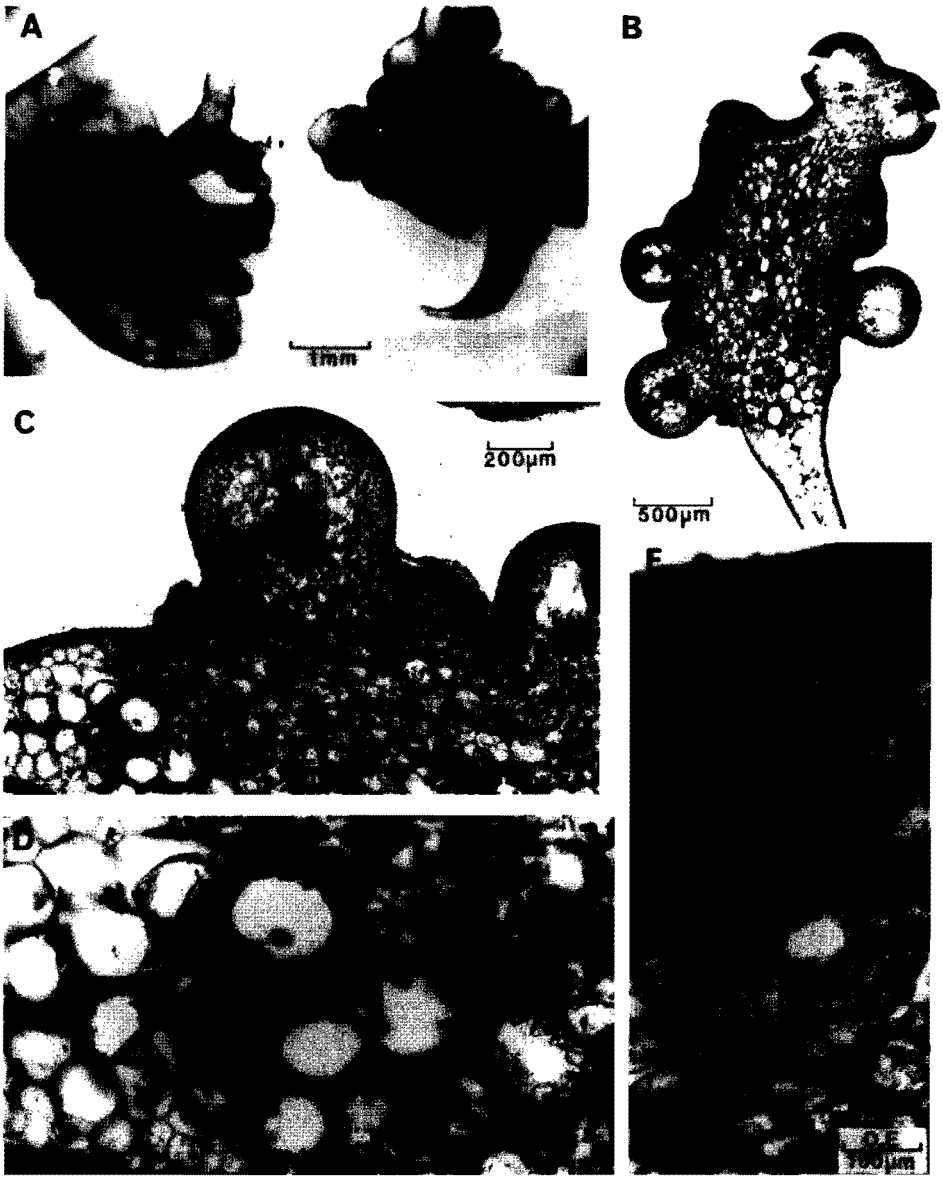


Fig. 33. *Rhodymeniocolax austrina* (AD, A44823). **A.** Habit of thalli on *Rhodymenia* (spermatangial left, cystocarpic right). **B.** Longitudinal section of cystocarpic plant, host at base. **C.** Longitudinal section of attachment to host (on left). **D.** Small-celled filaments of parasite between larger cells of host. **E.** Longitudinal section of *Rhodymeniocolax* through cortex and medulla.



Fig. 34. A–C. *Rhodymeniocolax austrina* (AD, A44823). **A.** Section of cystocarp with carposporophyte. **B.** Section of male thallus with spermatangia. **C.** Section of thallus with tetrasporangia. **D–F.** *Gloiocladia furcata* (AD, A64305; LBMEB, H2538). **D.** Longitudinal section of a cystocarp showing basal nutritive tissue, erect persistent filaments and carposporophyte with elongate fusion cell. **E.** Transverse section of thallus with a tetrasporangial nemathecium. **F.** Transverse section of a tetrasporangial nemathecium.

Structure multiaxial, developing a cortex 2–3 cells thick near branch apices, becoming 4–6 cells thick (Fig. 33E) in mature branches, with anticlinal filaments, outermost cells ovoid, 3–5 (-6) μm in diameter. Medulla 0.5–1.2 mm and (10-) 15–25 cells across, cells of varying sizes, ovoid, larger cells 50–120 μm in diameter. Attachment to host (Fig. 33B–D) many cells broad, with filaments of small ovoid cells (15-) 20–50 μm in diameter penetrating the host medulla (Fig. 33D) and surrounding the medullary cells, often massed, with pit-connections to the host cells. Rhodoplasts discoid to laminate in cortical cells, generally sparse, sometimes ribbon-like in medullary cells.

Reproduction. Gametangial thalli dioecious; probably procarpic. Carpogonial branches 4-celled, borne on inner cortical supporting cells. Auxiliary cell branches not observed. Carposporophytes (Fig. 34A) erect, basal fusion cell branched, all gonimoblast cells forming ovoid to angular carposporangia 6–12 μm in diameter. Basal nutritive tissue moderate, erect filaments largely disintegrating. Cystocarps (Fig. 34A) protruding, hemispherical to slightly basally constricted, often clustered, 400–600 μm across, pericarp 10–15 cells and 100–150 μm thick, cells isodiametric, ostiolate. Spermatangia (Fig. 34B) in dense sori covering most of the surface, cut off from the ends of elongate, branched initials on surface cortical cells, ovoid, 2–4 μm in diameter.

Tetrasporangia (Fig. 34C) in extensive nemathecia, basally pit-connected to inner cortical cells, lying between paraphyses of elongate cells 2–5 μm in diameter, 20–30 μm long and 8–14 μm in diameter, decussately or cruciately divided.

Thallus 1–3 (-4) mm altus, simplex vel paulatim ramosus; rami 1–1.5 (-2) mm longi et 300–600 (-1500) μm in diametro, laeves aut verrucosi ubi cystocarpium; semiparasitius in *Rhodymenia*. Structura multiaxialis, cortice filamentorum verticalium, 4–6 cellulas longorum, medulla 15–25 cellulas lata, cellulis amplitudine variabilibus. Ad hospitem late affixus, filamentis cellularum parvarum ovoidearum medullam hospitis penetrantibus.

Reproductio. Dioecia. Rami carpogoniales 4-cellulas, in cellulis interioribus corticalibus portati. Carposporophyta erecta, cellula basalis coalescens ramosa, carposporangia ovoidea vel angularia, 6–12 μm in diametro. Textura basalis nutritiva moderata, filamentis erectis fatiscentibus. Cystocarpia exserta, saepe fasciculata, 400–600 μm lata, ostiolata. Spermatangia in soris densis in superficie. Tetrasporangia in nemathecis basaliter lacunis iuncta cum cellulis interioribus corticalibus, inter paraphyses cellularum elongatarum, 20–30 μm longas et 8–14 μm in diametro, decussate vel cruciatim divisa.

Type from Crawfish Rock, Westernport Bay, Vic., 8 m deep (*Watson & Womersley*, 16.i.1974); holotype in AD, A44823.

Distribution: Off Outer Harbor, S. Aust., to Westernport Bay, Vic.

Selected specimens: 20 km WSW of Outer Harbor, S. Aust., 22–25 m deep (*McFarlane*, 11.ix.1975; AD, A46618). 1.3 km off Cape Northumberland, S. Aust., 15 m deep (*Shepherd*, 7.vii.1977; AD, A55108). Gloucester Reserve, Williamstown, Vic., 1–3 m deep (*Kraft et al.*, 8.v.1989; MELU, A38627, A38628 and *van Amerongen*, 25.vii.1990; MELU, A38629). Crawfish Rock, Westernport Bay, Vic., 4 m deep (*Watson*, 29.v.1974; AD, A44400).

The species of *Rhodymenia* which are hosts to *Rhodymeniocolax* are uncertain, but may fall within broad concepts of *R. australis*.

R. austrina differs from the type species, *R. botryoidea*, in habit (being more erect), in having a cortex of anticlinal filaments and in having tetrasporangia in nemathecia; *R. botryoidea* has a parenchymatous cortex and tetrasporangia scattered in the cortex (Sparling 1957, p. 362, fig. 13d–f). The Australian species may be more closely related to the unnamed British species (L. Irvine & Guiry 1983, p. 97).

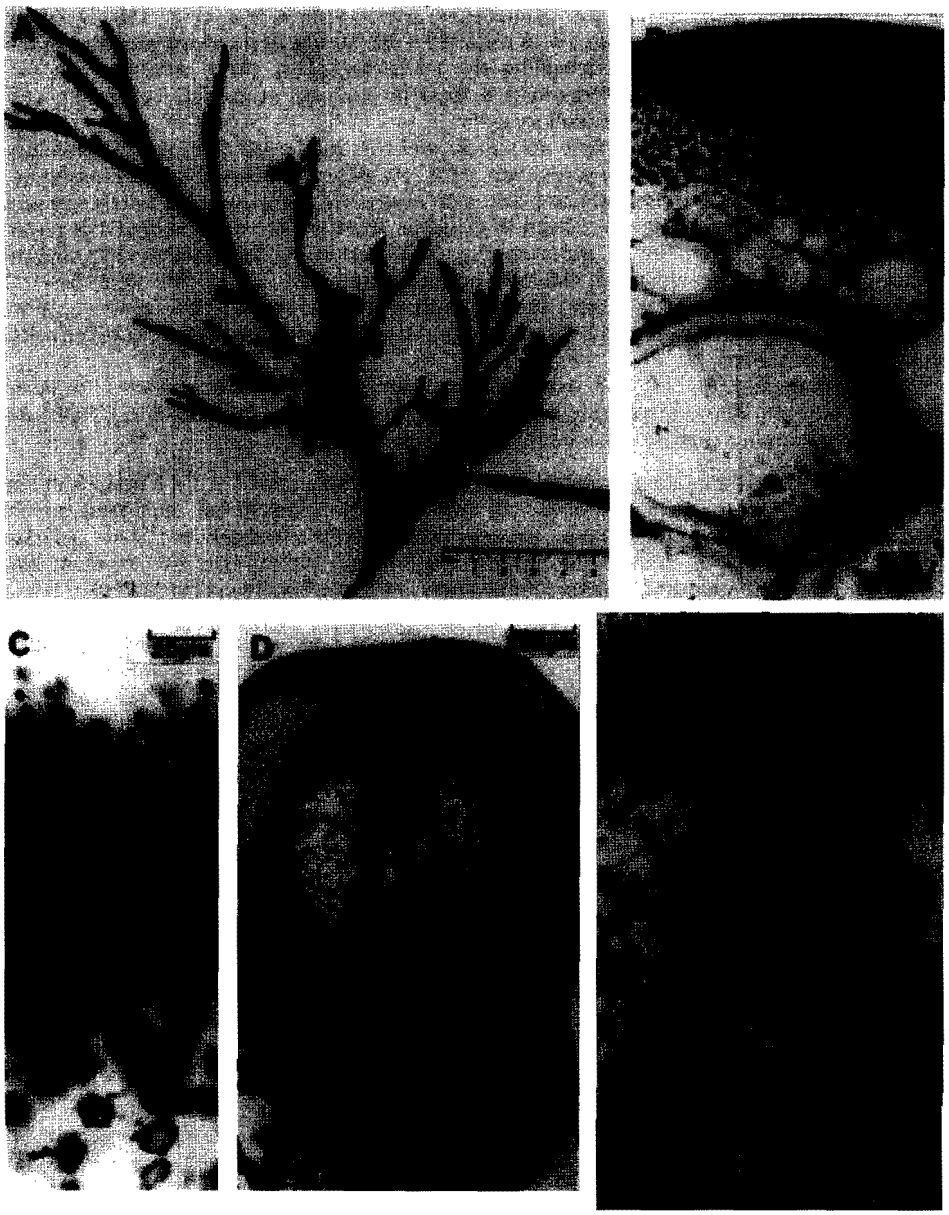


Fig. 35. *Faucheopsis coronata* (AD, A61466). **A.** Habit. **B.** Transverse section of mature thallus. **C.** Auxiliary cell branch (3 cells) with broad lateral pit-connections from the lower two cells of the branch to cortical filaments. **D.** Section of cystocarp with young carposporophyte. **E.** Carposporophyte with branched basal fusion cells, basal nutritive tissue, and relatively persistent erect filaments.

Genus **FAUCHEOPSIS** Kylin 1931: 9

Thallus erect, firm, complanately branched with long, compressed, subdichotomous branches from the margins of lower, broader axes, attached by a discoid holdfast. *Structure* multiaxial, solid, with a compact outer cortex of closely-adjacent anticlinal filaments of small ovoid cells, arising from an inner cortex of periclinally ovoid cells; medulla of large, thick walled cells without secondary pit-connections, with slender rhizoidal filaments forming layers 1–4 cells thick between them.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Early sexual stages unknown. Carposporophyte dendroid, with an erect, branched, fusion cell bearing lobes of carposporangia. Basal nutritive tissue prominent, erect filaments persistent and extending around the carposporophyte. Cystocarps external, sessile on the margins or surfaces of older branches, at first smooth, later developing short horns. Spermatangia unknown.

Tetrasporangia scattered, cruciately divided.

Type (and only) *species*: *Faucheopsis coronata* (Harvey)Kylin 1931: 9.

Faucheopsis is closely related to *Gloiocladia* but for the present it is kept generically separate. *Faucheopsis* is less mucilaginous and firmer than species of *Gloiocladia*, the cortex is thicker and compact, with dense anticlinal filaments of small cells, branched mainly only near where they are attached to the inner cortical cells (in contrast to the laxer, more branched, cortical filaments in *Gloiocladia*), the medullary cells are thick-walled and without the numerous secondary pit-connections of *Gloiocladia*, and the rhizoidal filaments between the medullary cells are far denser and more prominent than in the latter. The cystocarps of *Faucheopsis* are less prominently horned, often smooth until relatively old.

F. tasmanica (J. Agardh)May (1965, p. 352) is *Austrophyllis harveyana* (J. Agardh)Womersley & Norris (1971, p. 30) (see Womersley 1994, p. 252).

Faucheopsis coronata (Harvey)Kylin 1931: 9; 1956: 330. Irvine & Guiry 1986: 292, figs 3–5, pl. 1 figs 1, 2.

Callophyllis coronata Harvey 1859a: pl. 97.

Fauchea coronata (Harvey)J. Agardh 1876: 294; 1879: 126, pl. 19 figs 5–7. De Toni 1900b: 494. Irvine & Guiry 1986: 292, figs 3–5, pl. 1 figs 1, 2. Sonder 1881: 17. Tisdall 1898: 506. Wilson 1892: 180.

FIGS 35, 37A

Thallus (Fig. 35A) medium to dark red-brown, 20–50 cm high, complanately branched with lower (previous season?) parts 1–2.5 cm broad, with frequent marginal, irregularly subdichotomous branches commonly 6–25 cm long and 5–15 mm broad, tapering to 2–4 mm broad near apices. Holdfast discoid; epilithic. *Structure* multiaxial, developing a compact cortex (Fig. 35B) 40–80 (-130) µm thick, the outer cortex of mostly simple (basally branched) anticlinal filaments of 5–8 (-15) ovoid cells 1.5–2.5 µm in diameter, arising from the compact inner cortex of periclinally ovoid cells 4–6 µm in diameter. Medulla 4–6 cells thick, cells ovoid, (50-) 100–300 (-400) µm in diameter, with walls 6–15 (-22) µm thick and mostly without pit-connections; rhizoidal filaments (Fig. 35B) prominent between medullary cells, forming a layer 1–4 cells thick, cells 2–6 µm in diameter and L/D (1-) 2–6 (-8). Rhodoplasts discoid.

Reproduction. Gametangial thalli probably dioecious. Carpogonial branches (Fig. 37A) probably 3-celled, borne on an inner cortical supporting cell. Auxiliary cell branch (Fig. 35C) 3-celled, with prominent lateral pit-connections from the lower two cells to adjacent cells. Carposporophyte dendroid (Fig. 35D), with a basal, erect, elongate fusion cell with upper branches bearing lobes of ovoid carposporangia 15–20 µm in diameter. Basal nutritive tissue prominent, erect filaments persistent (Fig. 35E), with elongate cells around the carposporophyte and short-celled filaments around the ostiole. Cystocarps marginal and over the surface of broader branches, external, sessile, 0.7–1.2 mm across, without horns or developing short horns with age, ostiolate. Spermatangia unknown.

Tetrasporangia scattered, cruciately divided (Guiry, pers. comm.).

Type from Port Phillip Heads, Vic. (*Harvey*); lectotype in Herb. Harvey, TCD (Alg. Aust. Exsicc. 406E).

Distribution. Only known from Port Phillip Heads, Vic., and Port MacDonnell, S. Aust.

Selected specimens: Port MacDonnell, S. Aust., drift (*Kraft* 5960, 21.xii.1975; MELU, 23110; AD, A61466).

F. coronata appears to be a rare species, known only from the type and Port MacDonnell collections; it is probably a deep water species.

The cystocarps are mostly without horns, but develop short ones with age; the latter were illustrated by Harvey (1859a, pl. 97 figs 3, 4).

Chapman & Dromgoole (1970, p. 119, pl. 39 lower) recorded *F. coronata* from Kaikoura and the Bay of Islands, New Zealand, but this record is almost certainly incorrect.

Genus GLOIOCLADIA J. Agardh 1842: 87

Thallus erect, mucilaginous, much branched radially or complanately, main branches subdichotomous or pinnate, branches terete and flanged, or compressed, thallus attached by discoid holdfasts. *Structure* multiaxial, solid, with a cortex of anticlinal branched filaments of slender cells with the inner cells forming a reticulum, and a medulla of large ovoid cells with numerous secondary pit-connections and often rhizoidal filaments between the larger cells.

Life history triphasic, with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli monoecious or dioecious. Carpogonial branches borne on relatively large supporting cells in the inner cortex, 2- or 3-celled, together with 2-celled auxiliary cell branches, the auxiliary cell usually with a globular proteinaceous inclusion. Carposporophyte erect, with a basal, often branched, fusion cell bearing lobes with all cells becoming carposporangia. The supporting cell and the basal cell of the auxiliary cell branch have prominent pit-connections to rows of cells, the lower ones remaining short and darkly staining as the nutritive tissue, the erect cells prominent and elongate with frequent lateral connections but persistent as they are stretched by the developing carposporophyte, and the upper cells remaining short in filaments that surround the ostiole. Cystocarps external, mainly marginal on flat branches, pericarp relatively thick and usually with 1–4 prominent horns. Spermatangia cut off from surface cortical cells.

Tetrasporangia scattered or in sori or nemathecia, pit-connected to mid cortical cells, ovoid-elongate, decussately divided.

Type species: *G. furcata* J. Agardh 1842: 87.

Doubts concerning the separation of *Gloiocladia* J. Agardh (1842, p. 87) and *Gloioderma* J. Agardh (1851, p. 243) [and *Fauchea* Montagne & Bory] were expressed by Irvine & Guiry (1986, pp. 289–291), following earlier comments by Sparling (1957). Irvine & Guiry refrained from uniting these genera in view of the lack of information on the type species of *Gloiocladia*, especially of the female reproduction and cystocarp structure. Norris (1991, p. 592) however, concluded they were generically the same and transferred most of the names used in *Gloioderma* to *Gloiocladia*. Study of cystocarpic and tetrasporangial plants of *Gloiocladia furcata* from Île Lavezzi, Corsica, 37 m deep (*M. Verlaque*, 30.xi.1989; Herb. LBMEB, No. H2538; AD, A64305) show that although a much smaller species than the Australian species placed in *Gloioderma*, they are very similar in structure, cystocarp structure (with basal nutritive tissue and persistent erect filaments around the carposporophyte – Fig. 34D) and tetrasporangial nemathecia (Fig. 34E, F). The four Australian species are therefore placed under *Gloiocladia*.

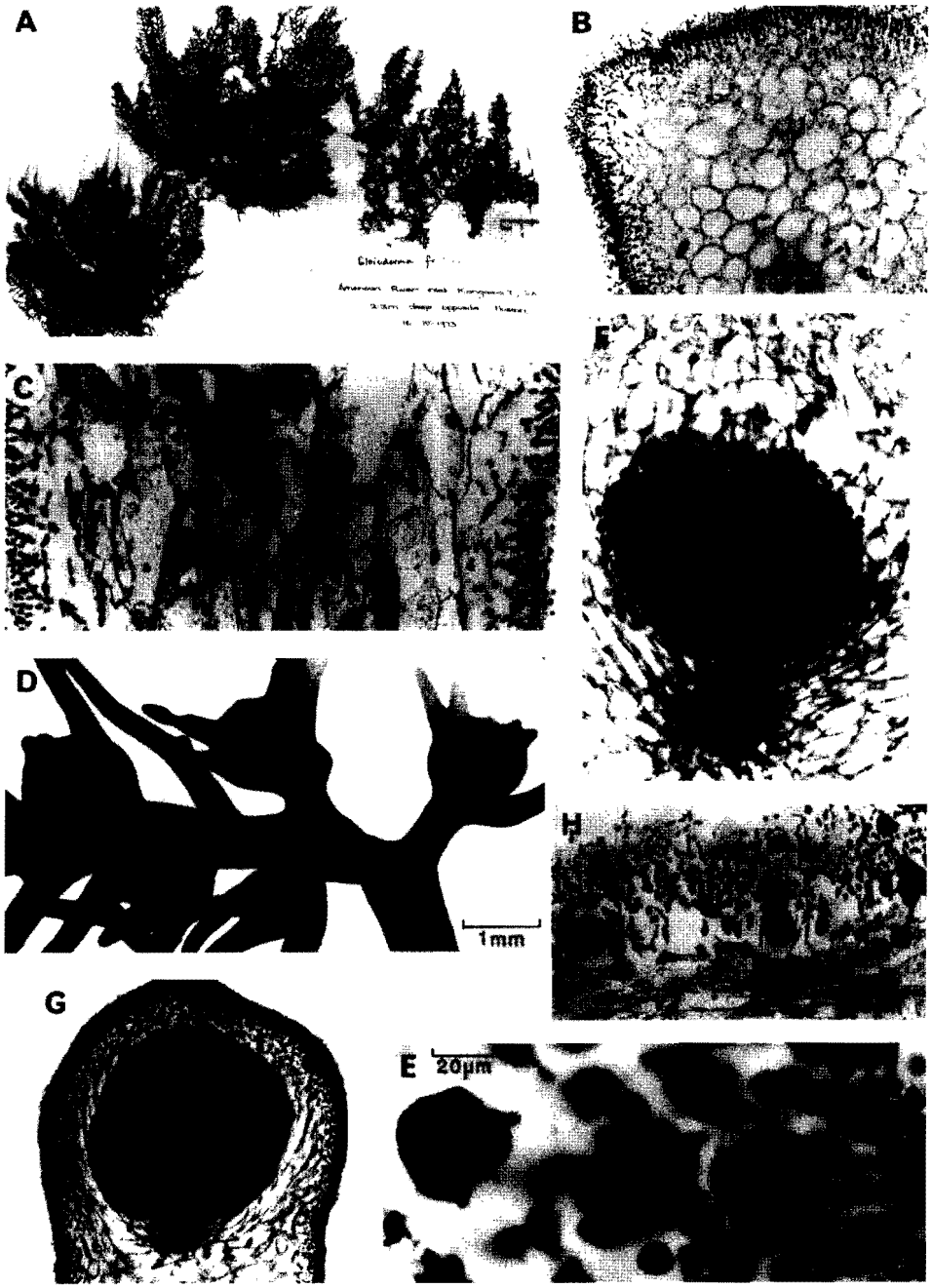


Fig. 36. *Gloiocladia fruticulosa* (**A,** AD, A43739; **D, F, G,** AD, A13360; **B, C, E, H,** AD, A26723). **A.** Habit. **B.** Transverse section of branch. **C.** Longitudinal section of branch. **D.** Branch with cystocarps. **E.** Auxiliary cell branch, auxiliary cell on right. **F.** Carposporophyte with basal nutritive tissue and erect filaments. **G.** Section of cystocarp. **H.** Longitudinal section of branch with tetrasporangia.

KEY TO SPECIES OF *GLOIOCLADIA*

1. Thallus branches terete to flanged, 1–2 mm broad, mainly radially branched ..... 1. *G. fruticulosa*
1. Thallus branches strongly compressed to flat, mostly 4–10 mm broad, complanately and marginally branched 2
    2. Thallus largely subdichotomously branched, 5–10 (-15) mm broad, often developing surface (1–5 mm long) and marginal (mostly 0.5–2 cm long) proliferations, especially on lower parts ..... 2. *G. polycarpa*
    2. Thallus pinnately branched for 1–3 orders, usually without numerous surface proliferations 3
3. Thallus irregularly pinnate, soft and mucilaginous, with discoid adhesive appendages on the ends of some branchlets; usually epiphytic on sea-grasses ..... 3. *G. australe*
3. Thallus regularly pinnate, tapering to branch apices, without discoid, adhesive appendages; usually epilithic ..... 4. *G. halymenioides*

1. **Gloiocladia fruticulosa** (Harvey)Norris 1991: 592.
    Horea fruticulosa Harvey 1860: pl. 156. J. Agardh 1876: 292. Sonder 1881: 17. Tisdall 1898: 505. Wilson 1892: 180.
    Gloioderma fruticulosum (Harvey)J. Agardh 1872: 18. De Toni 1900b: 496. Kylin 1931: 7. Lucas & Perrin 1947: 192. Searles 1984: 220. Sparling 1957: 329, fig. 2e.
    Endosira australis J. Agardh 1899: 106, pl. 1 fig. 3. De Toni 1924: 86. Womersley 1965: 452.

FIGS 36, 37B

Thallus (Fig. 36A) medium to dark red-brown, 5–10 (-15) cm high, much branched radially for 3–4 orders, main branches subdichotomous to lateral, not compressed but flanged below branch bases giving a lobed cross section, 1–2 mm in diameter, with shorter terete laterals 5–10 (-15) mm long, ultimate branchlets 2–5 mm long, terete, 250–500 µm in diameter, often becoming attached to other branches. Holdfast discoid, with branchlet ends forming secondary discoid attachment pads; epiphytic on sea-grasses or possibly epilithic. *Structure* multiaxial, developing a cortex (Fig. 36B, C) 40–80 (-120) µm thick, of 6–9 cells in discrete branch systems arising directly from smaller outer medullary cells, and without lateral secondary pit-connections, cells usually ovoid, (3-) 4–6 µm in diameter and L/D 1–2; medulla (Fig. 36B, C) compact, 4–10 cells thick, cells ovoid to elongate-ovoid, 60–100 µm in diameter, with frequent secondary pit-connections. Rhodoplasts discoid to elongate in cortical cells, becoming elongate or chained in medullary cells.

Reproduction. Gametangial thalli probably dioecious. Carpogonial branches (Fig. 37B) 2-celled, borne on conspicuous supporting (inner cortical) cells together with 2-celled auxiliary cell branches (Fig. 36E), with the supporting cell and the first cell of the auxiliary cell branch developing several thick arms to secondary connections; auxiliary cells ovoid, with granular contents and a globular proteinaceous inclusion (Fig. 36E). Carposporophytes (Fig. 36F, G) compact, 200–400 µm across, all cells forming ovoid to angular carposporangia 20–25 µm in diameter; basal nutritive tissue present, erect filaments surrounding the carposporophyte and remaining relatively persistent (Fig. 36F). Cystocarps (Fig. 36D) 0.7–1.5 mm across, developing 2–3 blunt, elongate horns, ostiolate. Spermatangia unknown.

Tetrasporangia (Fig. 36H) scattered, formed on mid cortical cells, ovoid, 16–35 µm in diameter, decussately divided.

Type from Port Phillip Heads, Vic. (*Harvey*); lectotype (Harvey, Alg. Aust. Exsicc. 440E) in Herb. Harvey, TCD.

Distribution: Port Turton, Yorke Pen., S. Aust., to Westernport Bay, Vic., and the east coast of Tasmania.

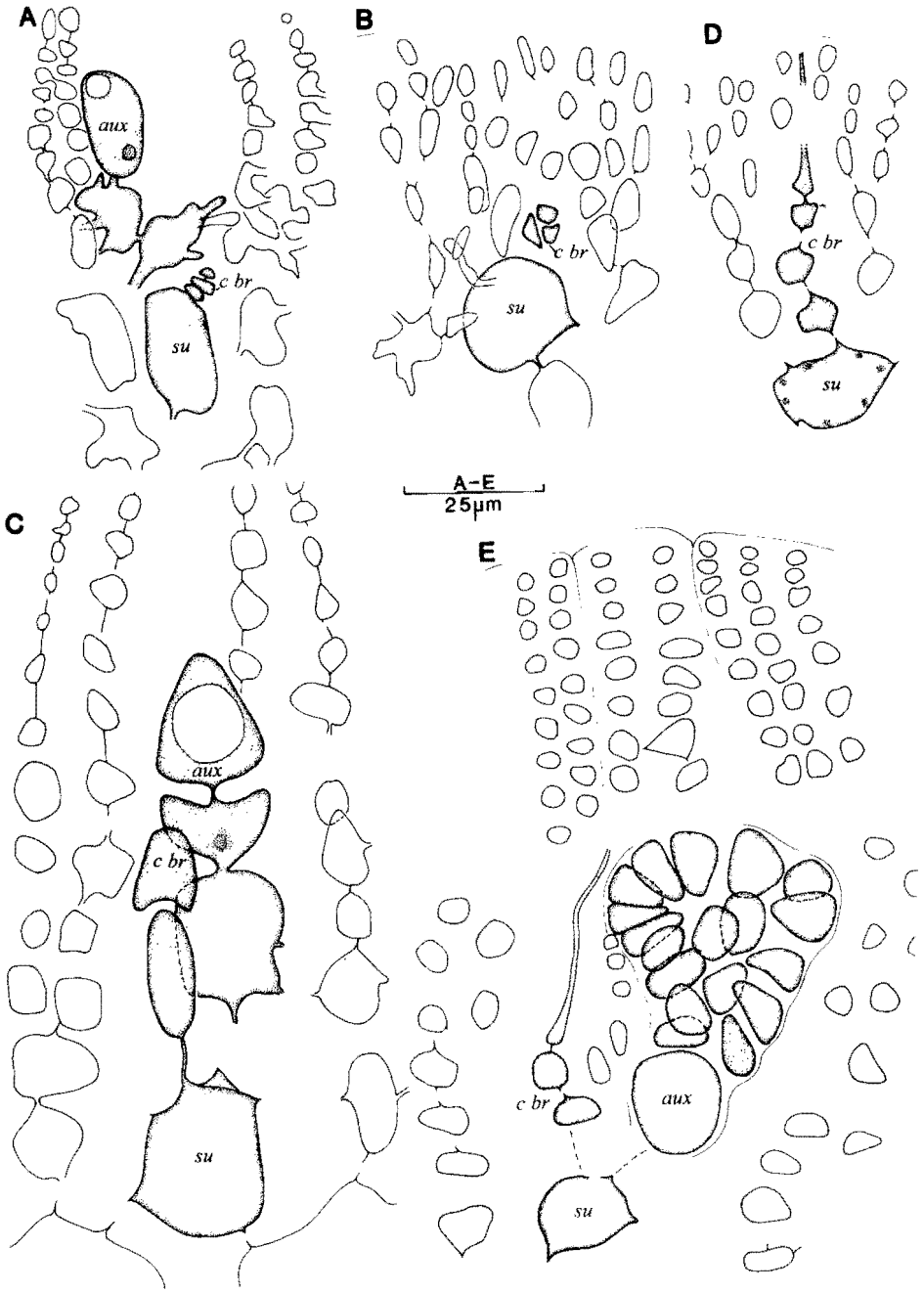


Fig. 37. A. *Faucheopsis coronata* (AD, A61466). Transverse section of cortex (post fertilization) with supporting cell, probable carpogonial branch and auxiliary cell branch. **B.** *Gloiocladia fruticulosa* (AD, A26723). Transverse section of cortex with supporting cell and probable carpogonial branch. **C.** *Gloiocladia australe* (AD, A33408). Transverse section of cortex with a supporting cell bearing probable lower cells of a carpogonial branch and a 3-celled auxiliary cell branch. **D.** *Gloiocladia halymenioides* (AD, A43722). Transverse section of cortex with a 4-celled carpogonial branch. **E.** *Leptosomia rosea* (AD, A63215). Section of cortex with an old carpogonial branch and young carposporophyte.

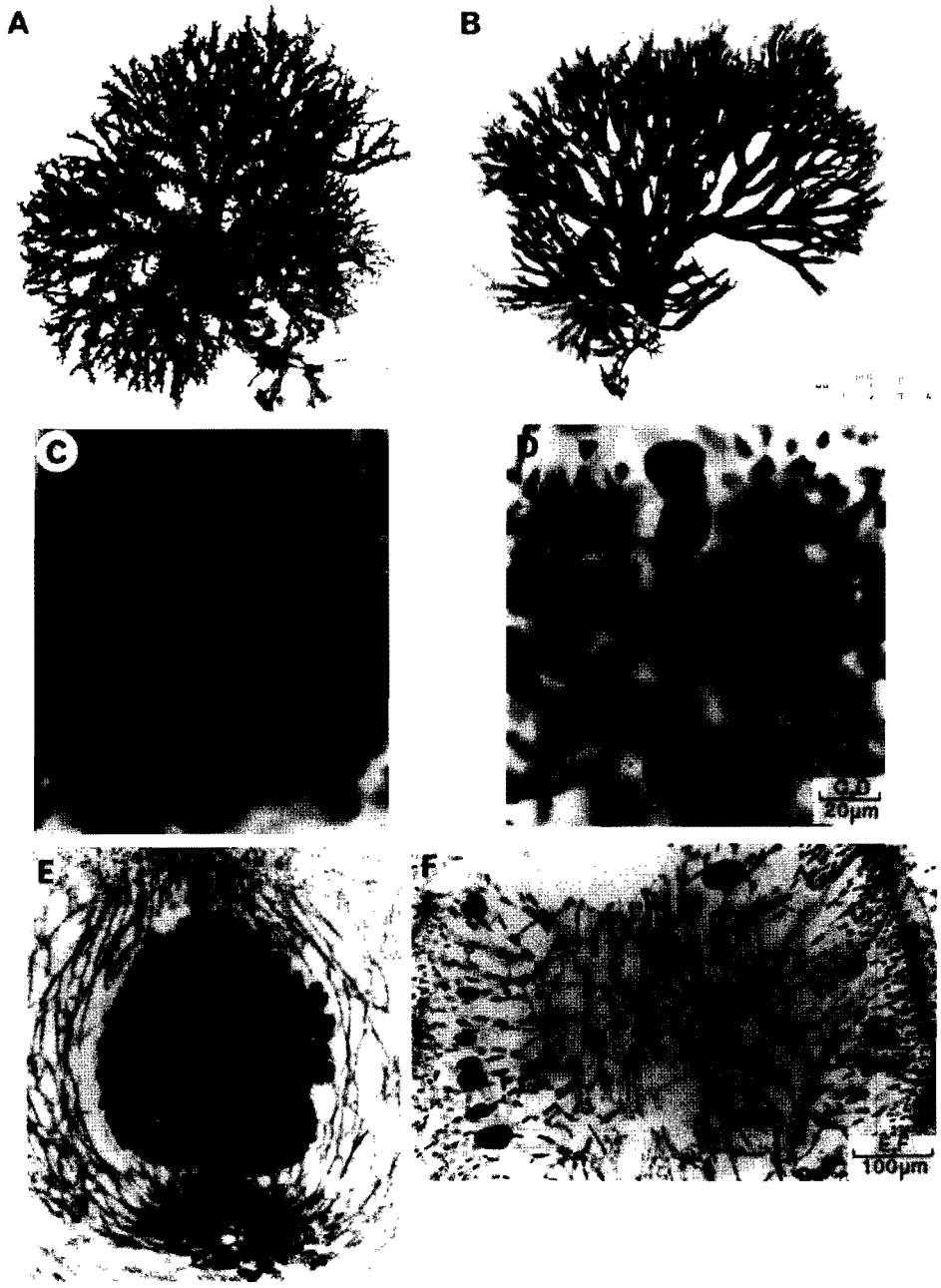


Fig. 38. *Gloiocladia polycarpa* (**A**, AD, A63785; **B–F**, AD, A61753). **A, B.** Habit, tetrasporangial plant on left. **C.** Section of branch with a 2-celled auxiliary cell branch on supporting cell; auxiliary cell with a proteinaceous globule. **D.** Young carposporophyte, with basal supporting cell, first cell of auxiliary cell branch with broad lateral pit-connections, and the auxiliary cell subdividing. **E.** Section of cystocarp with carposporophyte, basal nutritive tissue and prominent erect filaments. **F.** Longitudinal section of branch with tetrasporangia.

Selected specimens: Port Turton, Yorke Pen., S. Aust., 8–10 m deep (*Kald*, 5.ix.1970; AD, A37252). Outside Tapley Shoal (Edithburg), S. Aust., 15 m deep (*Shepherd*, 2.ii.1969; AD, A33503). Port Stanvac, S. Aust., on jetty pylons (*R. Lewis*, 7.iv.1972; AD, A42494). Port Noarlunga, S. Aust., 19 m deep on tyre reef (*Branden*, 26.iii.1987; AD, A57440). Saunders Beach, Eastern Cove, Kangaroo I., S. Aust., drift (*Womersley*, 25.viii.1963; AD, A26723). Rocky Point, Kangaroo I., S. Aust., drift (*Womersley*, 26.viii.1950; AD, A13360). American R. inlet, Kangaroo I., S. Aust., 2–3 m deep opposite Muston (*Kraft et al.*, 16.iv.1973; AD, A43739). Muston, Kangaroo I., S. Aust., 2–3 m deep (*Womersley*, 21.xi.1968; AD, A32935 —"Marine Algae of southern Australia" No. 91). Crawfish Rock, Westernport Bay, Vic., 9 m deep (*Watson*, 30.xi.1968; AD, A33591). Musselroe Bay, Tas. (*Perrin* 762, March 1950; BM). Humbug Point, Georges Bay, St Helens, Tas., 4 m deep (*Riddle*, 25.ii.1990; AD, A60429). Satellite I., D'Entrecasteaux Ch., Tas., 10 m deep (*Shepherd*, 18.ii.1972; AD, A41692).

G. fruticulosa is often common in sheltered conditions but where there is moderate current flow, on *Posidonia* or solid substrates.

Endosira australis J. Agardh was described from the "South Coast of S. Aust." The lectotype is in Herb. Agardh, LD, 32218.

G. fruticulosa was recorded from Juan Fernandez Island by Etcheverry (1986, p. 280), but this record needs verification.

2. **Gloiocladia polycarpa** (Harvey)Womersley, *comb. nov.*

Horea polycarpa Harvey 1859b: 329, pl. 194B; 1863, synop.: xlv. J. Agardh 1876: 293. Reinbold 1897: 53(?). Sonder 1881: 17. Tisdall 1898: 505. Wilson 1892: 180.

PLATE 2 fig. 2; FIG. 38

Thallus (Fig. 38A, B) medium red to red-brown, 8–20 cm high, complanately branched with flat, subdichotomous, main branches 5–10 (-15) mm broad below, tapering to 1–2 mm broad just below apices, with numerous marginal [0.5–2 (-3) cm long] and sometimes surface proliferations(1–5 mm long) from lower and mid branches, less so in cystocarpic plants. Holdfast small, discoid; epilithic or epiphytic. *Structure* multiaxial, developing a cortex (Fig. 38F) 50–90 (-120) µm thick, of anticlinal branched chains of 5–8 cells, inner ones elongate, outer ones ovoid, 2–4 µm in diameter, and a medulla 1–3 cells across, cells ovoid, (50-) 100–200 (-300) µm in diameter, with few to several filaments lying between the medullary cells. Rhodoplasts discoid.

Reproduction. Gametangial thalli dioecious. Carpogonial branches not observed; auxiliary cell branches (Fig. 38C) 2-celled, borne on inner cortical supporting cells, the auxiliary cell with a large globular proteinaceous inclusion and the first cell establishing broad pit-connections (Fig. 38D) to adjacent cells. Carposporophytes (Fig. 38E) ovoid, 180–400 µm across, with all cells forming ovoid carposporangia 20–30 µm in diameter; basal nutritive tissue present with persistent erect filaments (Fig. 38E) and small-celled filaments surrounding the ostiole. Cystocarps mostly on or near the branch margins, 700–1000 µm across with 2–4 well-developed horns, ostiolate. Spermatangia cut off from outer cortical cells, ovoid, 1–2 µm in diameter.

Tetrasporangia (Fig. 38F) scattered or in extensive nemathecia on the thallus branches (few on the proliferations), borne on mid cortical cells, ovoid, 15–25 µm in diameter, decussately divided.

Type from East coast, Tas. (*Gunn*); lectotype (cystocarpic) (here designated), Alg. Aust. Exsicc. 438I, in Herb. Harvey, TCD (isotypes distributed in Alg. Aust. Exsicc. 438).

Distribution: Port Fairy to Western Port, Vic., (probably from Point Avoid, S. Aust., eastwards); N and E Tasmania.

Selected specimens: Port Fairy, Vic. (*Harvey*, Alg. Aust. Exsicc. 438D; Herb. Harvey, TCD). Port Phillip Heads, Vic., (*Harvey*, Alg. Aust. Exsicc. 438E; Herb. Harvey, TCD). Western Port, Vic., (*Harvey*, Alg. Aust. Exsicc. 438H; Herb. Harvey, TCD). Sisters Caves, Rocky Cape, Tas., 5 m deep (*Edgar*, 23.v.1992; AD, A63785). Waubs Bay, Bicheno, Tas., 8–12 m deep, on *Lenormandia* (*Edgar*, 23.x.1994; AD, A63783). Crayfish Point, Taroona, Tas., 0–6 m deep (*Sanderson*, 29.v.1992; A61753). Taroona, Tas., 3–4 m deep (*Edgar*, 4.ii.1995; AD, A64212). Middleton, Tas. (*Perrin*, Nov. 1940; AD, A8949). Roaring Beach, Dover, Tas., drift (*Perrin*, 7.ix.1945; HO, 309250). Southport, Tas., drift

(*Cribb* 77.2, 23.ix.1950; AD, A16255). Adventure Bay, Bruny I., Tas., drift (*Perrin*, 8.xi.1940; HO, 309249).

Herb. Harvey, TCD, contains:

1. Two specimens from "East coast, VDL *R. Gunn.* 438I", one cystocarpic and one tetrasporangial with relatively few, scattered, tetrasporangia, marginal proliferations but few surface proliferations and these only near the base of the specimen.
2. Four specimens from Port Phillip Heads (Vic.), 438E, two cystocarpic, one tetrasporangial (abundant) and with numerous surface proliferations (tetrasporangia in thallus surface, not in proliferations) and one male.
3. One sheet (cystocarpic) from Western Port (Vic.) – 438H.
4. One sheet (cystocarpic) from Port Fairy (Vic.) – 438D.

Since Harvey cited "East coast, *Gunn*" in his publication on the Algae of Tasmania, the cystocarpic specimen is selected as lectotype and the tetrasporangial one as an isolectotype. The Victorian specimens are regarded as syntypes, and Harvey's illustrations (at least of the tetrasporangial plant) may be based on these specimens.

Some literature references (e.g. Kylin 1931, p. 7) give *G. polycarpa* as a synonym of *G. australis*, but the two species are clearly distinct. *G. polycarpa* differs from *G. australis* in having basically subdichotomous branching in contrast to the pinnate form of the latter and in lacking the rounded adhesive discs; it is epilithic or epiphytic whereas *G. australis* is usually epiphytic on seagrasses. While some specimens of *G. polycarpa* have numerous small surface proliferations, the tetrasporangia are not borne in these but in the cortex of the branches where they form extensive sori or nemathecia.

Gloiocladia polycarpa occurs in Tasmania and Victoria. Specimens from Point Avoid, S. Aust., drift (*Womersley*, 2.xii.1975; AD, A46909) and Vivonne Bay, Kangaroo I., S. Aust., drift (*Womersley*, 15.i.1948; AD, A6878 and 2.i.1949; AD, A10619) are now provisionally referred to this species (*Womersley* 1950, p. 174, as *G. australis*) since they show basically subdichotomous branching with small proliferations from both the surface and margins. Reinbold (1897, p. 53) and Lucas (1929b, p. 49), recorded *G. polycarpa* (as *Horea*) from Lacepede and Guichen Bays, S. Aust., but gave *G. australis* as a synonym; this record may apply to the latter species.

3. **Gloiocladia australe** (J. Agardh)Norris 1991: 592.
   Gloioderma australis J. Agardh 1851: 244. De Toni 1900b: 496. Harvey 1863, synop.: xliv. Kylin 1931: 7. Searles 1984: 220.
   Horea speciosa Harvey 1859b: 328, pl. 194A; 1863, synop.: xlv. J. Agardh 1876: 292. Reinbold 1898: 46. Sonder 1881: 17. Tisdall 1898: 505. Wilson 1892: 180.
   Gloioderma speciosa (Harvey)J. Agardh 1872: 18. Guiler 1952: 93. Kylin 1931: 7. Searles 1984: 220. Sparling 1957: 329. Womersley 1950: 174.
   Callophyllis australis Sonder 1848: 175. De Toni 1897: 287. Kützing 1849: 746. Reinbold 1897: 45.
   Haligone rosea Kützing 1866: 23, pl. 66a, b. J. Agardh 1876: 353.
   Gloioderma tasmanicum Zanardini 1874: 503. De Toni 1900b: 497. Kylin 1931: 7. Lucas 1929b: 49. Lucas & Perrin 1947: 194, fig. 62.
   Horea tasmanica (Zanardini)Sonder 1881: 17.
   Bindera ramosa J. Agardh 1894: 129. De Toni 1900b: 549. Kylin 1931: 31, pl. 18 fig. 41.

FIGS 37C, 39

Thallus (Fig. 39A) medium to dark red to red-brown, fading to grey-red, (10-) 20–40 cm high, soft and mucilaginous, complanately branched with flat, irregularly pinnate branches for 3–4 orders, main branches (3-) 6–10 mm broad, bearing marginal pinnate branches 3–10 cm long and also simple branchlets 3–10 mm long, with ultimate branchlets 1–2 mm broad; compact, rounded, potentially adhesive, discs 2–3 mm across, terminate few

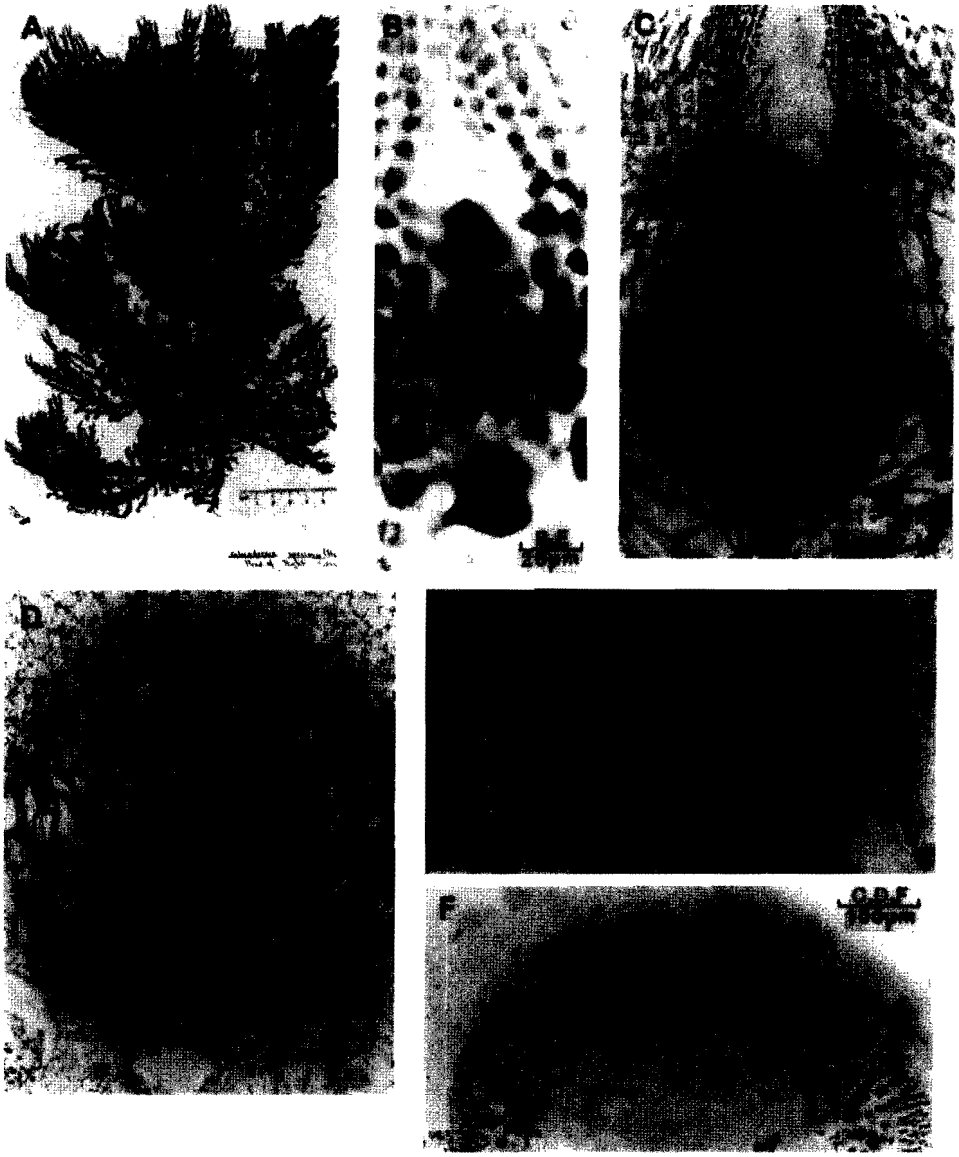


Fig. 39. *Gloiocladia australe* (**A, D, E,** AD, A34193; **B,** AD, A33408; **C,** AD, A32267; **F,** AD, A20060). **A.** Habit. **B.** Auxiliary cell branch and remnant carpogonial branch on supporting cell. **C.** Section of a cystocarp. **D.** Basal nutritive tissue and prominent erect filaments, carposporophyte removed. **E.** Section of cortex with probable spermatangia. **F.** Section of cortex with tetrasporangia.

to numerous branchlets. Holdfast discoid, with adhesions also by the discs of dense, elongate cells; usually epiphytic on sea-grasses or larger algae, or epilithic (?). *Structure* multiaxial, developing a cortex 50–90 µm thick of slender branched filaments 5–8 cells long, with the lower 2–3 cells irregular, 5–10 µm broad, and the upper 3–5 cells ovoid, 2–3 µm in diameter, arising from the lax inner cortex (Fig. 39F) of ovoid cells 15–25 µm in diameter. Medulla 3–5 cells thick, cells large, ovoid, 60–200 (-250) µm in diameter, with frequent secondary pit-connections. Hairs on outer cortical cells common. Rhodoplasts discoid to elongate in cortical cells, ribbon like in medullary cells.

Reproduction. Gametangial thalli monoecious. Carpogonial branches 4(?)-celled, borne on a relatively large globular supporting cell (Fig. 37C) which also bears a 3-celled auxiliary cell branch, the upper auxiliary cell with a large spherical proteinaceous inclusion (Fig. 39B). Carposporophyte (Fig. 39C) ovoid, 250–500 µm across, with an erect fusion cell with erect branches bearing lobes of ovoid carposporangia 20–25 µm in diameter. Basal nutritive tissue of short cells, pit-connected to the supporting cell and auxiliary initial cell, with erect filaments (Fig. 39D) of prominent, persistent elongate cells around the carposporophyte and upper short-celled filaments around the ostiole. Cystocarps mostly marginal (also on the surface of broader branches), 0.7–1.5 mm across, with 2–4 horns, ostiolate. Spermatangia (Fig. 39E) cut off from outer cortical cells, ovoid, 1–2 µm in diameter.

Tetrasporangia (Fig. 39F) scattered, or in nemathecia with extended cortical filaments, pit-connected to mid cortical cells, elongate ovoid, 16–24 µm in diameter, decussately divided.

Type from "Occid. Nov. Holl." (Mus. Paris); holotype in Herb. Agardh, LD, 25674.

Distribution: Point Peron, W. Aust. to Walkerville, Vic., and the N coast of Tasmania.

Selected specimens: Point Peron, W. Aust., drift (*Royce* 482, 28.i.1951; AD, A15470). Head of Great Australian Bight, S. Aust., drift (*Womersley*, 4.ii.1954, AD, A19218 —"Marine Algae of southern Australia" No. 92) and (*Gordon*, 4.xi.1968; AD, A34193). Point Avoid, S. Aust., drift (*Womersley*, 2.xii.1975; AD, A46914). Tiparra Reef, S. Aust., 11–12 m deep (*Shepherd*, 24.ii.1971; AD, A38229). Cable Hut Bay, Yorke Pen., S. Aust., drift (*Woelkerling*, 17.i.1968; AD, A32267). Investigator Strait, S. Aust., 34 m deep (*Watson*, 20.i.1971; AD, A39220). Off Troubridge Light (Edithburg), S. Aust., 17 m deep (*Shepherd*, 4.ii.1969; AD, A33429). Marion Light, Gulf St Vincent, S. Aust., 15 m deep (*Shepherd*, 5.ii.1969; AD, A33408). Vivonne Bay, Kangaroo I., S. Aust., drift (*Womersley*, 30.i.1956; AD, A20174). Pennington Bay, Kangaroo I., S. Aust., drift (*Womersley*, 31.xii.1949; AD, A12816). 1.3 km off Cape Northumberland, S. Aust., 15 m deep (*Shepherd*, 1.ii.1978; AD, A55045). Shoreham, Vic., drift (*Lee*, 5.iii.1961; AD, A24869). Walkerville, Vic., drift (*Sinkora* A2176, 9.iii.1975; AD, A48405). Low Head, Tas. (*Perrin* 764, 25.ii.1942; BM).

The holotype specimen of *G. australis* appears to be a small plant of the species more commonly known as *G. speciosa*, but it is unusual in having small surface proliferations. Only a few specimens with surface proliferations have been seen. The type is from Western Australia, where only two species of *Gloiocladia* are known – *G. australe* (*G. speciosa*) and *G. halymenioides*; of these two, it is certainly not the second.

G. australe differs from *G. halymenioides* in habit, having more irregularly pinnate branching, usually slightly broader main branches, and not tapering evenly to the apices as does the latter, and in possessing the rounded, discoid, ends to branchlets which can apparently adhere to the host as secondary holdfasts. It is usually a deep-water species and commonly (always?) epiphytic on sea-grasses whereas *G. halymenioides* is usually epilithic.

Horea speciosa Harvey, type from Georgetown, Tas., (lectotype in TCD – Alg. Aust. Exsicc. 439) is a well developed specimen of *G. australe*; *G. speciosa* has been the most frequently used name for this species.

Haligone rosea Kützing (1866, p. 23, pl. 66a, b), from Phillip I., Vic. (Mueller), type in L, 941, 61...67, is *Gloiocladia australe*, not *Gloiocladia halymenioides* as given by De Toni (1900b, p. 497).

Gloioderma tasmanicum Zanardini (1874, p. 503) from Georgetown, Tas., type in Museo Civico di Storia Naturale, Venice, is *Gloiocladia australe*.

Bindera ramosa J. Agardh (1894, p. 129) from Western Port, Vic. (*Wilson*, 6.iv.1893), lectotype in Herb. Agardh, LD, 25729, is also *G. australe*.

Callophyllis australis Sonder (1848, p. 175) from W. Aust. (Preiss), holotype (with Sonder's illustrations) in MEL, 1005769, appears to be a fragment of *G. australe*. Although this is the earliest specific epithet, its use is prevented by the use of *G. australe*, by Norris (1991).

4. **Gloiocladia halymenioides** (Harvey)Norris 1991: 592. Huisman 1993: 17.

Horea halymenioides Harvey 1855a: 555; 1859a: pl. 673; 1863, synop.: xlv. J. Agardh 1876: 292; 1879: pl. 19 figs 1–4. Sonder 1881: 17. Tisdall 1898: 505. Wilson 1892: 180.

Gloioderma halymenioides (Harvey)J. Agardh 1872: 18. De Toni 1900b: 497. Huisman & Walker 1990: 415. Kylin 1931: 7. Lucas 1929b: 49. Lucas & Perrin 1947: 194, fig. 61. Reinbold 1899: 45. Searles 1984: 220. Womersley 1950: 174.

Horea flabelliformis Harvey 1855a: 555.

Horea wilsonis J. Agardh 1885: 38. Tisdall 1898: 505.

Gloioderma wilsonis (J. Agardh)De Toni 1900b: 496. Guiler 1952: 93. Kylin 1931: 7, pl. 1 fig. 2. Lucas & Perrin 1947: 192, fig. 60. Searles 1984: 220. Womersley 1950: 174.

Gloiocladia wilsonii (J. Agardh)Norris 1991: 592.

FIGS 37D, 40

Thallus (Fig. 40A) medium to dark red-brown, (2-) 5–15 (-20) cm high, complanately branched with main branches subdichotomous to alternate, flat, 3–10 mm broad, decreasing to 1–2 mm broad near apices; branches pinnate with marginal laterals 2–10 (-20) mm long, often subpinnate; some plants with small surface proliferations. Holdfast discoid, 2–3 mm across; epilithic or on jetty piles. *Structure* multiaxial, developing a cortex 50–95 µm thick, of branched filaments 2–4 µm in diameter and 5–8 cells long, inner cells L/D 4–8, outer cells ovoid, arising from a layer 1–4 cells thick of tangentially ovoid cells 8–15 µm in diameter on the outer side of the medulla; transition from cortex to medulla sudden. Medulla 2–4 cells thick, cells ovoid, 50–200 (-350) µm in diameter, with frequent secondary pit-connections. Rhodoplasts discoid.

Reproduction. Gametangial thalli dioecious. Carpogonial branches (Fig. 37D) very small, 4-celled, borne on mid cortical cells; supporting cells enlarging post-fertilization with numerous thickened arms to cells of the erect filaments and bearing a 2-celled auxiliary cell branch, auxiliary cell ovoid, with a proteinaceous inclusion. Carposporophyte (Fig. 40D) dendroid, 250–360 µm across, with a basal fusion cell producing several erect arms bearing lobes of ovoid carposporangia 12–22 µm in diameter. Basal nutritive tissue prominent, erect filaments well-developed and relatively persistent. Cystocarps (Fig. 40B, C) external, mostly marginal or on short branchlets, 0.7–1.2 mm across with a rim of 2–6 prominent, acute, horns, ostiolate. Spermatangia (Fig. 40E) cut off from initials on outer cortical cells, ovoid, 1–2 µm in diameter,

Tetrasporangia (Fig. 40F) in scattered groups or in nemathecia on the central region of lesser branches, pit-connected to mid cortical cells, ovoid, 10–18 µm in diameter, decussately divided.

Type from Fremantle, W. Aust. (Harvey); holotype (Trav. Set 152) in Herb. Harvey, TCD.

Distribution: Fremantle, W. Aust., to Walkerville, Vic., and around Tasmania.

Selected specimens: Esperance, W. Aust., drift (*Firman*, Dec. 1952; AD, A18944). Elliston, S. Aust., 11 m deep (*Shepherd*, 19.iv.1970; AD, A35863). Kangaroo Reef, Boston I., Port Lincoln, S. Aust., 5–6 m deep (*Womersley*, 28.ii.1959; AD, A22549). Port Stanvac, S. Aust., 12 m deep on pylons (*Hergstrom*, 24.iii.1971; AD, A38265). Port Noarlunga, S. Aust., 19 m deep on tyre reef (*Branden*, 26.iii.1987; AD, A57441); Muston, American R. inlet, Kangaroo I., S. Aust., 4–5 m deep (*Shepherd*, 29.xii.1977; AD, A48960). Vivonne Bay, Kangaroo I., S. Aust., 3–6 m deep on jetty (*Kraft*, 15.iv.1973; AD, A43722). Pennington Bay, Kangaroo I., S. Aust., drift (*Womersley*, 25.i.1946; AD, A3124). Double Corner Beach, Portland, Vic., drift (*Beauglehole*, 22.vi.1952; AD, A21653). Queenscliff, Vic., drift (*Norris*, 21.i.1963; AD, A27485). Walkerville, Vic., drift (*Sinkora* A2171,

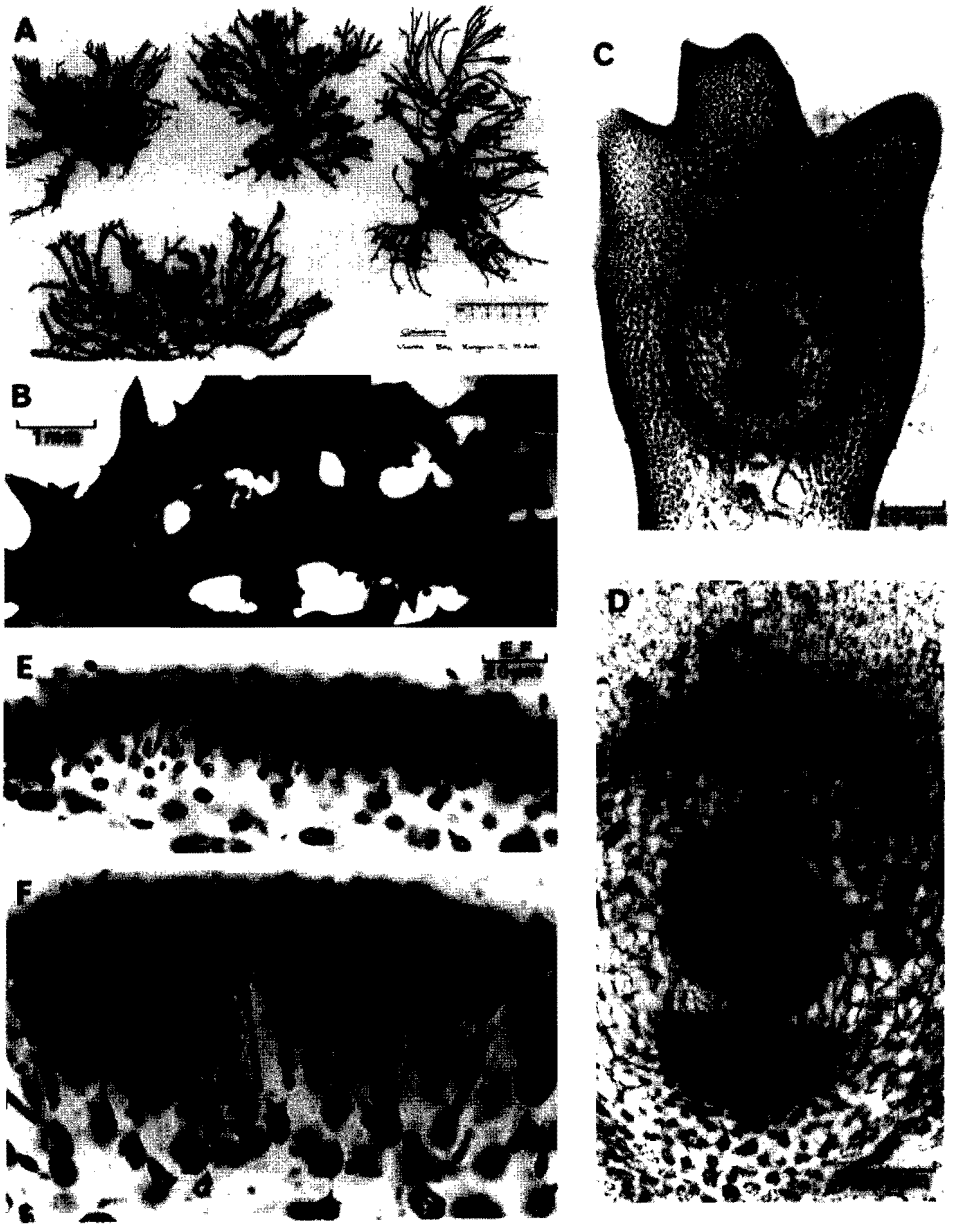


Fig. 40. *Gloiocladia halymenioides* (**A–D, F,** AD, A43722; **E,** AD, A38265). **A.** Habit. **B.** Branches with cystocarps. **C.** Section of cystocarp with pericarpic horns. **D.** Carposporophyte, with basal nutritive tissue and erect filaments. **E.** Transverse section of male branch with spermatangia. **F.** Transverse section of tetrasporangial nemathecium.

1.iii.1975; AD, A48393). Currie R., Tas., drift (*Perrin & Lucas*, March 1935; AD, A49706). Dover, Tas. (*Perrin* 760, 7.ix.1945; BM).

G. halymenioides is distinguished by its regularly pinnate or bipinnate habit with evenly tapering branches. It is found on relatively sheltered coasts, but especially where there is strong current flow, usually in depths of 2–20 m.

Horea flabelliformis Harvey, type from King George Sound, W. Aust., (lectotype in TCD, Harvey, Trav. Set. 341) is almost certainly a young plant of *G. halymenioides*.

G. wilsonis (J. Agardh)De Toni [type from Port Phillip Hds, Vic. (*Wilson*); lectotype in Herb. Agardh, LD, 25664] is regarded as a robust form of *G. halymenioides*.

Genus LEPTOSOMIA (J. Agardh)J. Agardh 1892: 86

Thallus foliose, usually with marginal lobes, delicate, soft and mucilaginous, holdfast discoid or enveloping host stems. *Structure* multiaxial, with a cortex 1–2 cells thick and a medulla of large ovoid cells on either side of a central space within which coarse rhizoids develop, completely filling the space in older parts.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 3-celled, borne on inner cortical cells, with the 2-celled auxiliary cell branch. Carposporophyte erect, with a branched basal fusion cell and all gonimoblast cells becoming carposporangia. Basal nutritive tissue concave, of short cells, with few, inconspicuous or disintegrating erect filaments. Cystocarps scattered, largely immersed in the thallus, with a surface pericarp of small-celled filaments, ostiolate. Spermatangia cut off via initials from surface cortical cells.

Tetrasporangia scattered, transformed from inner cortical cells, intercalary and pit-connected to outer cortical cells, cruciately divided.

Type species: *L. cliftonii* (J. Agardh)J. Agardh 1892: 88 [= *L. rosea* (Harvey)Womersley, *comb. nov.*].

Leptosomia was first described by J. Agardh (1876, p. 319) as a subgenus of *Chrysymenia*, doubtfully including two other species. Later J. Agardh (1892, p. 86) elevated *Leptosomia* to a genus. Kylin (1956, p. 336), followed by Papenfuss (1964, p. 44) and Etcheverry (1986, p. 283) placed four Antarctic species of *Leptosarca* Gepp & Gepp under *Leptosomia* but *Leptosarca* is now regarded as a synonym of *Palmaria*.

The genus is characterised by its vegetative structure, with a central space between large medullary cells, within which rhizoids develop, at first sparse but in older parts filling the space completely. *Leptosomia* is probably monotypic.

Leptosomia rosea (Harvey)Womersley, *comb. nov.*

Rhodymenia ?rosea Harvey 1855a: 554.
Halymenia cliftonii Harvey 1863, synop.: xlvi (in part).
Chrysymenia cliftonii J. Agardh 1876: 319. Sonder 1881: 18.
Leptosomia cliftonii (J. Agardh)J. Agardh 1892: 88. Irvine & Guiry 1986: 297. Kylin 1931: 19, pl. 5 fig. 11. May 1965: 409.
Sebdenia cliftonii (Harvey)De Toni 1900b: 533.
Chrysymenia gelatinosa J. Agardh 1890: 24. Tisdall 1898: 506. Wilson 1892: 179.
Leptosomia gelatinosa (J. Agardh)J. Agardh 1892: 88. Kylin 1931: 20, pl. 5 fig. 12. May 1965: 409.
Sebdenia ?gelatinosa (J. Agardh)De Toni 1900b: 532.

FIGS 37E, 41, 42

Thallus (Fig. 41A) rose-red, delicate, soft and mucilaginous, 15–50 cm high, foliose or usually with axes 3–9 cm broad bearing numerous marginal overlapping lobes for 1–2 orders, lobes 1–15 cm long and 2–8 cm broad, basally broader or somewhat contracted, rounded or tapering to a blunt apex, margin often with minute excrescences; young thallus 90–300 μm thick, becoming 0.5–1 mm thick near the base. Holdfast 2–5 (-10) mm across,

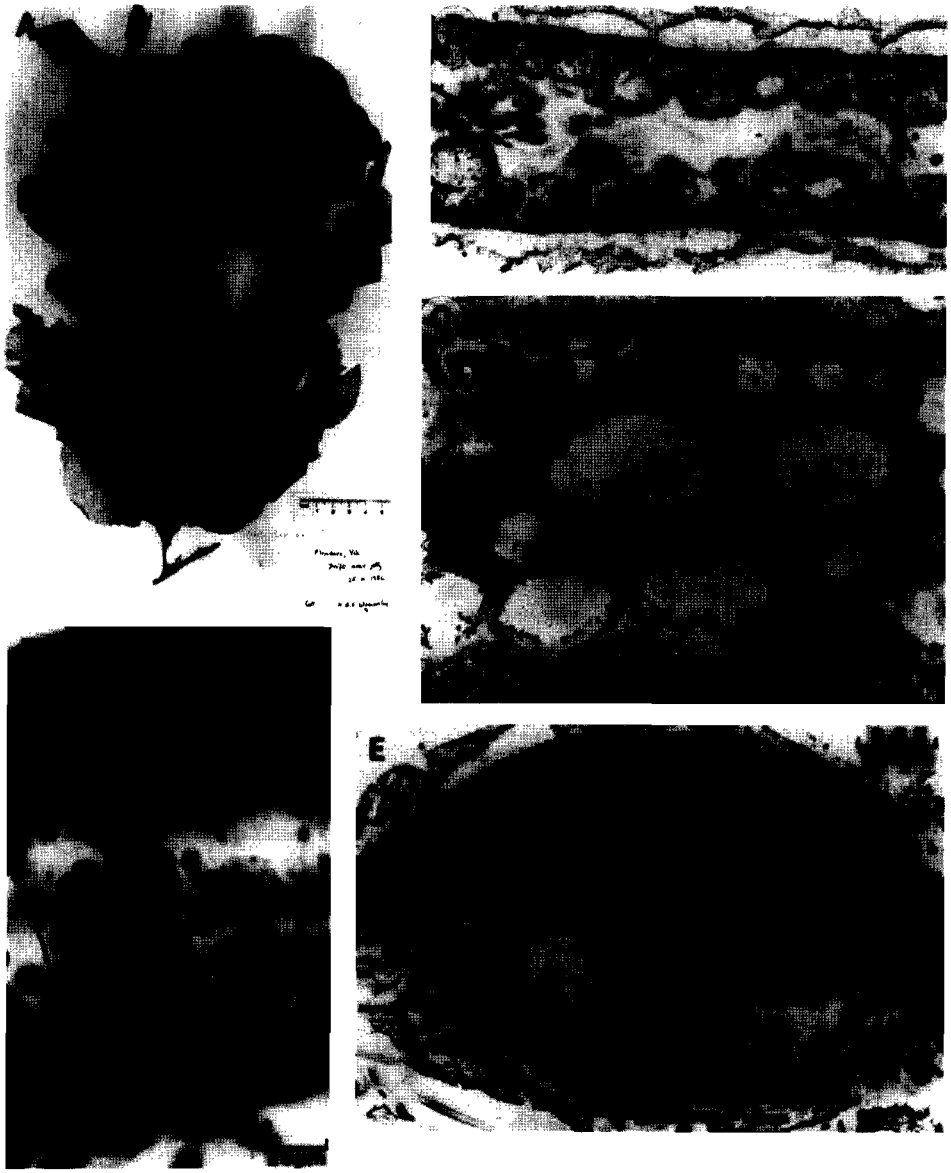


Fig. 41. *Leptosomia rosea* (**A,** AD, A57848; **B, C,** AD, A54302; **D,** AD, A63215; **E,** AD, A44206). **A.** Habit, on stem of *Amphibolis*. **B.** Transverse section of young thallus with central space. **C.** Transverse section of older thallus with central rhizoids and small cells. **D.** Young carposporophyte, with irregular supporting cell, ovoid first cell of auxiliary cell branch, and remnant carpogonial branch with carpogonium and trichogyne. **E.** Section of cystocarp (not through ostiole) with carposporangia, fusion cell, basal nutritive tissue and remnants of erect filaments.

usually surrounding *Amphibolis* stems, with a terete to compressed stipe 0.5–2 cm long; epiphytic or possibly epilithic. *Structure* multiaxial, developing a cortex 1–2 cells thick, outermost cells in slight rosettes over inner cells (Fig. 42A, B, D), cells ovoid, 4–6 µm in diameter and a large-celled medulla with 1 (-2) ovoid cells 50–90 µm in diameter on each side of a central space (Fig. 41B) within which sparse branched rhizoids 7–14 µm in diameter, cells L/D 2–8, develop; in older parts (Fig. 41C) the rhizoids increase to fill the central space with intermixed large and small cells, with the original medullary cells becoming thick-walled (10–20 µm), 120–200 µm in diameter, and with numerous secondary pit-connections. Rhodoplasts ovoid, in chains in inner cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches (Fig. 41D) 3-celled, borne on inner cortical supporting cells (Fig. 37E), together with a 2-celled auxiliary cell branch (Fig. 41D). Carposporophytes (Fig. 41E) with a basal, erect, fusion cell producing 2–4 dense lobes of carposporangia each 20–30 µm in diameter; basal nutritive tissue slightly concave, erect filaments not apparent. Cystocarps (Fig. 42A) scattered, 0.5–1 mm across and 250–600 µm high, immersed in the thallus but slightly protruding, with a distinct surface pericarp (Fig. 41E) of anticlinal rows of 6–10 small cells and a small central ostiole 30–60 µm in diameter. Spermatangia (Fig. 42B, C) covering the thallus, cut off directly or via initials from outer cortical cells, ovoid, 1–2 µm in diameter.

Tetrasporangia (Fig. 42D, E) scattered, intercalary, transformed from inner cortical cells and with pit-connections to outer cortical cells, subspherical to ovoid, 30–55 µm long and 20–45 µm in diameter, cruciately divided.

Type from Fremantle, W. Aust. (*Clifton*); lectotype (here designated) in Herb. Harvey, TCD (Trav. Set 347), with a second specimen in TCD placed (by Harvey ?) under *Halymenia cliftonii*.

Distribution: Yanchep, W. Aust., to Flinders, Vic.

Selected specimens: Yanchep, W. Aust., drift (*Womersley*, 22.ix.1979; AD, A51274). Safety Bay, W. Aust., drift (*Womersley*, 18.viii.1979; AD, A50770 (on *Amphibolis*?) and 29.ix.1979; AD, A50736). Head of the Great Australian Bight, S. Aust., drift on *Amphibolis* (*Parsons*, 4.xi.1968; AD, A34183). Pearson Is, S. Aust., 50 m deep (*Shepherd*, 9.i.1969; AD, A33872). Elliston, S. Aust., 6 m deep in shade (*Shepherd*, 24.x.1969; AD, A34784) and 10 m deep in bay (*Shepherd*, 18.x.1973; AD, A44206). Point Avoid, S. Aust., drift (*Womersley*, 2.xii.1975; AD, A46916). Vivonne Bay, Kangaroo I., S. Aust., 0.5–2 m deep on jetty piles (*Kraft*, 15.vii.1972; AD, A42540). Seal Bay, Kangaroo I., S. Aust., drift (*Womersley*, 29.x.1966; AD, A31062 and 6.i.1990; AD, A60134). Cape Jaffa, S. Aust., drift, epiphytic (*Womersley*, 10.xii.1991; AD, A61563). Robe, S. Aust., 1–2 m deep on *Amphibolis* near jetty (*Womersley*, 12.ix.1983; AD, A54302) and drift on *Amphibolis* (*Womersley*, 30.x.1993; AD, A63215). Flinders, Vic., drift on *Amphibolis* (*Womersley*, 25.x.1986; AD, A57848 —"Marine Algae of southern Australia" No. 371).

Leptosomia rosea is most commonly epiphytic on the stems of *Amphibolis*, rarely on other algae (e.g. *Acrocarpia*), but is probably also epilithic. It is confined to rough-water coasts, usually in deep water or shaded situations.

Rhodymenia? rosea Harvey was described from two specimens of *Clifton* (in Herb. Harvey, TCD) though in his description Harvey refers to "only a single immature specimen" – perhaps it was subdivided. The Trav. Set specimen in TCD is chosen as lectotype and shows the typical sectional structure described above. In TCD there are three large mature specimens of Clifton, dated 1858 and 1859, one of which is also annotated "*Leptosomia rosea*". Thereafter the epithet *rosea* was lost sight of, not being given by Harvey (1863) in his synopsis nor by J. Agardh or De Toni. In describing *Halymenia cliftonii* in 1859, Harvey replaced his earlier name *H. kallymenioides* of 1855 [now *Cryptonemia kallymenioides* (Harvey)Kraft], but in 1863 (synop.: xlvi) he confused plants of *Leptosomia cliftonii* with it. J. Agardh (1876, p. 319) realised this and renamed the latter as *Chrysymenia cliftonii* J. Agardh, transferred in 1892 to *Leptosomia*. Using the earliest name, the species is now to be known as *Leptosomia rosea* (Harvey)Womersley.

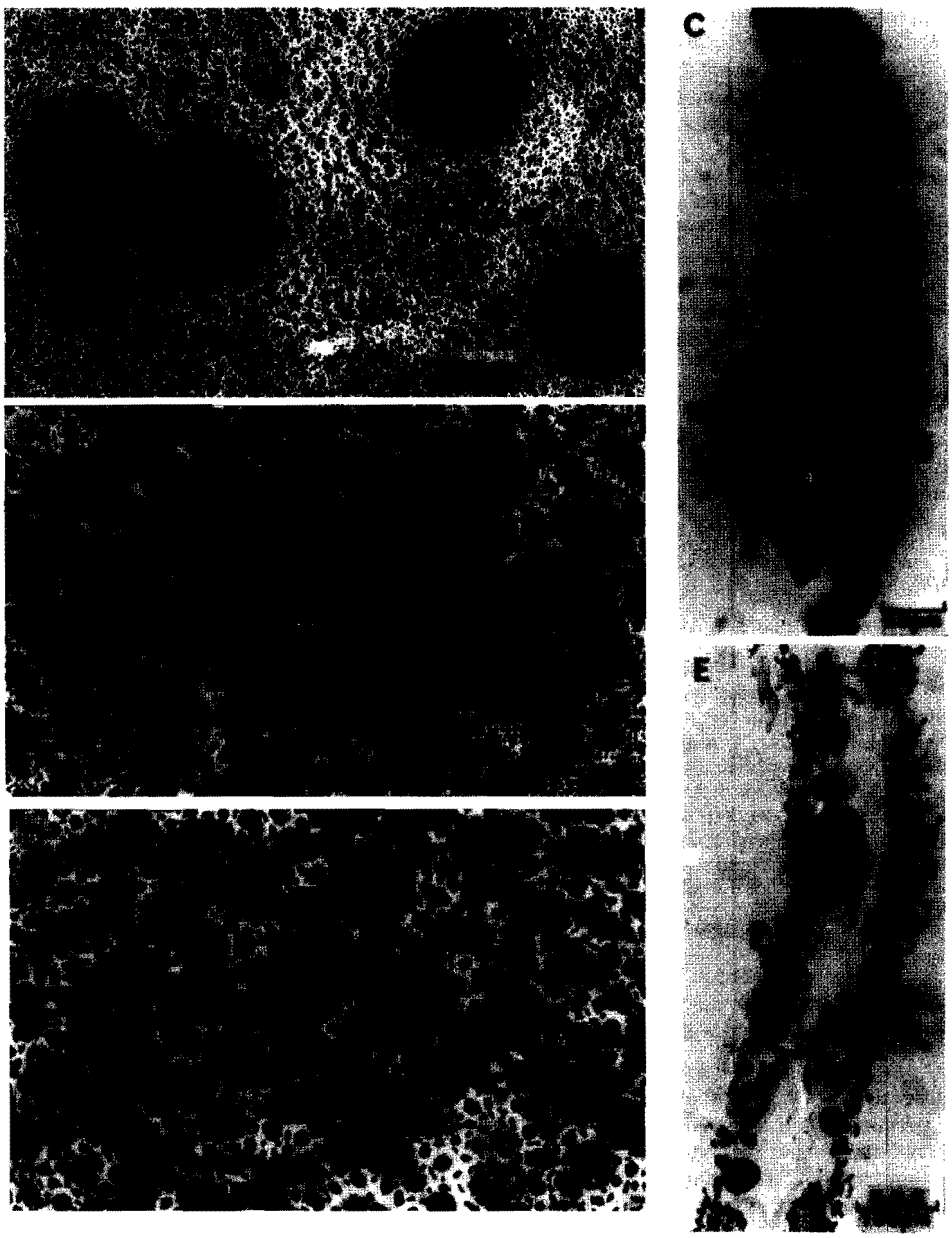


Fig. 42. *Leptosomia rosea* (**A–D,** AD, A57848; **E,** AD, A33872). **A.** Surface view of cystocarpic thallus. **B.** Surface view of spermatangial thallus. **C.** Section of male thallus with spermatangia on cortical cells. **D.** Surface view of tetrasporangial thallus. **E.** Transverse section of thallus with tetrasporangia.

L. rosea is variable in form, and includes the habit of *L. gelatinosa* (J. Agardh) J. Agardh, described from a Wilson specimen from Western Port, Vic. (24.i.1885); the lectotype (Kylin) is in Herb. Agardh, LD, 26637.

Genus HYMENOCLADIA J. Agardh 1852: 772

Thallus erect, variously branched usually complanately, often proliferous from the margins, foliose, pinnate or subdichotomous, branches flat, compressed or terete; holdfast discoid, epiphytic on *Amphibolis* or other algae, or epilithic. *Structure* multiaxial, developing a cortex (1-) 2–6 cells thick and a medulla of large ovoid cells from which smaller cells or filaments are cut off; secretory cells absent in most species.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli monoecious or dioecious; procarpic. Carpogonial branches 4-celled, borne on inner cortical supporting cells together with a 2-celled auxiliary cell branch. Carposporophyte developing outwards, with a basal fusion cell and branched system of lower darkly staining cells, with the upper cells all forming relatively large carposporangia, often with later lobes developing. Basal nutritive tissue well developed, with the erect filaments largely disintegrating but thick-walled remnant cells often remaining near the nutritive tissue. Cystocarps external, hemispherical to conical, with a thick pericarp, ostiolate. Spermatangia in surface sori, cut off from elongate initials on cortical cells.

Tetrasporangia scattered, transformed from intercalary inner cortical or outer medullary cells, relatively large (60–140 μm in diameter), tetrahedrally divided.

Type species: *H. usnea* (R. Brown *ex* Turner)J. Agardh 1852: 772.

A genus of six species, confined to southern Australia, New Zealand and South Africa.

Hymenocladia is characterised by the medullary structure of large and small cells (or filaments) intermixed, and by the very large intercalary, tetrahedrally divided, tetrasporangia (and also large carposporangia).

KEY TO SPECIES OF *HYMENOCLADIA*

1. Thallus foliose to much branched or marginally lobed, mostly 2–10 cm broad ..... 3. *H. chondricola*
1. Thallus much branched, branches terete to flattened, less than 1 cm broad 2
2. Branches slightly compressed, 0.5–1 mm broad ..... 4. *H. filiformis*
2. Branches (at least the axes) compressed, 2–8 mm broad 3
3. Axes 2–8 mm broad, ramuli compressed and 1–2 mm broad ..... 1. *H. usnea*
3. Axes 2–3 (-5) mm broad, ramuli terete or subterete, (100-) 150–250 μm broad ..... 2. *H. divaricata*

1. **Hymenocladia usnea** (R. Brown *ex* Turner)J. Agardh 1852: 772; 1871: 454; 1876: 313. De Toni 1900b: 502. De Toni & Forti 1923: 29. Harvey 1859a: pl. 118; 1859b: 318. Kylin 1931: 24; 1956: 338, fig. 266C. Lucas 1929b: 49. Lucas & Perrin 1947: 197, fig. 63. May 1965: 388. Reinbold 1897: 52; 1899: 45. Sonder 1853: 695; 1881: 17. Sparling 1957: 365, fig. 14a–d. Tisdall 1898: 506. Wilson 1892: 179. Womersley 1950: 176.

Fucus usneus R. Brown *ex* Turner 1819: 70, pl. 225.

Chondria usnea (R. Brown *ex* Turner)C. Agardh 1822: 359.

Halymenia usnea (R. Brown *ex* Turner)Greville 1830, synop.: lxii. Kützing 1849: 717; 1867: 1, pl. 1d, e.

Gracilaria ramalina Harvey 1863: pl. 260.

Hymenocladia ?ramalina Harvey 1855a: 553. J. Agardh 1871: 454; 1876: 313. De Toni 1900b: 502.Kylin 1931: 24, pl. 12 fig. 28. May 1965: 387. Sonder 1881: 17. Sparling 1957: 365. Tisdall 1898: 506.

Chondrococcus squarrosus Kützing 1867: 28, pl. 96a, b. De Toni 1905: 1677.
Hymenocladia gracilarioides J. Agardh 1876: 313. De Toni 1900b: 500. Kylin 1931: 24, pl. 12 fig. 27. May 1965: 387. Sonder 1881: 17. Sparling 1957: 367. Tisdall 1898: 506. Wilson 1892: 179.
Chrysymenia husseyana J. Agardh 1894: 130.

FIG. 43

Thallus (Fig. 43A) erect, medium red to dark red-brown, 10–30 cm high, complanately and pinnately to tri-pinnately branched, branch axes 2–8 mm broad and usually broadest centrally, bearing closely set, compressed, marginal laterals 1–3 mm broad, the ultimate ramuli compressed, 2–10 (-20) mm long and 1–2 mm broad, simple or furcate. Holdfast discoid, around the host stems and 1–3 mm across, bearing one to several fronds; epiphytic

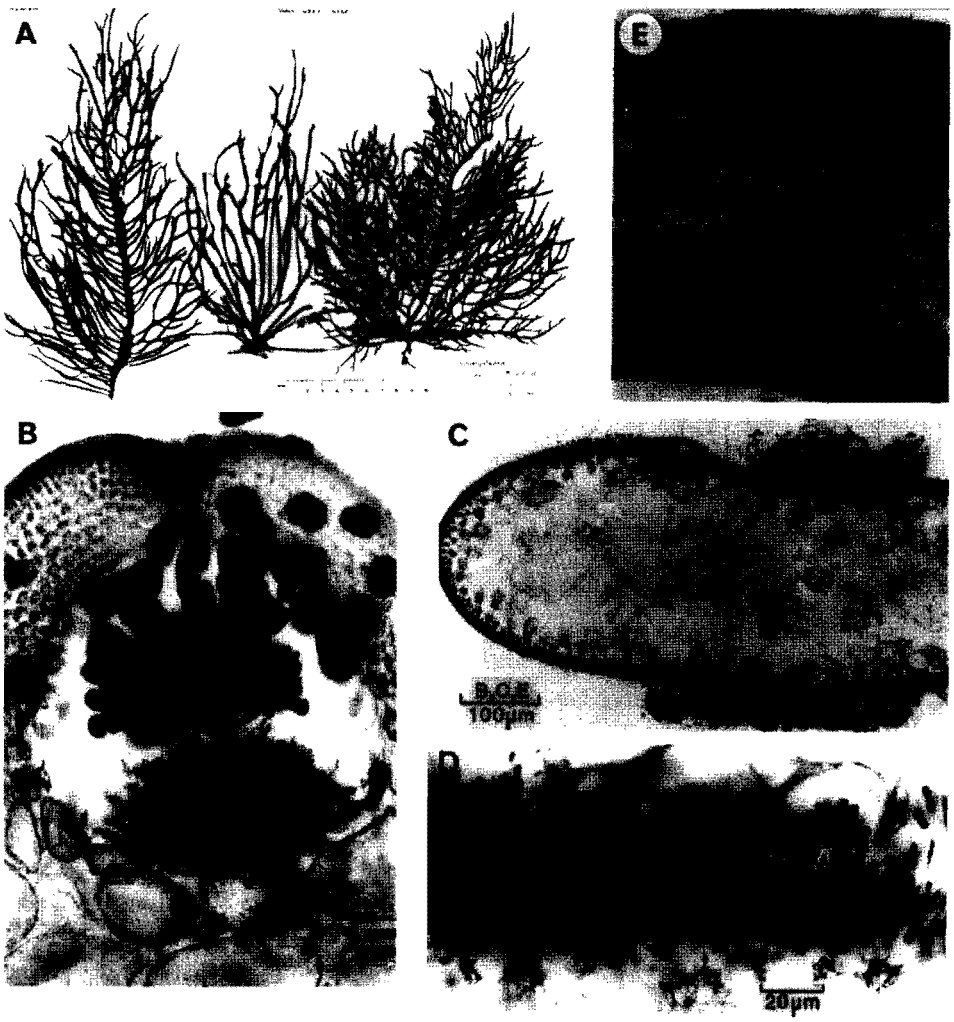


Fig. 43. *Hymenocladia usnea* (**A, B,** AD, A63564; **C, D,** AD, A55423; **E,** AD, A29270). **A.** Habit. **B.** Section of cystocarp, with prominent basal nutritive tissue. **C.** Section of male thallus with spermatangial sori. **D.** Spermatangial sorus. **E.** Section of thallus with two tetrasporangia in inner cortical cells.

on *Amphibolis* and possibly epilithic. *Structure* multiaxial, developing a cortex (Fig. 43C, E) 2–3 (-4) cells thick, outer cells ovoid to elongate and 2–3 μm in diameter, grading over 1–2 cells to the medulla 2–4 cells across, larger inner cells ovoid (in branch transverse section) and 100–150 μm in diameter with walls 4–10 μm thick, with interspersed smaller ovoid cells 20–40 μm in diameter; secondary pit-connections frequent. Rhodoplasts ovoid to elongate, in chains in inner cells.

Reproduction. Gametangial thalli dioecious (or monoecious?). Carpogonial branches 4-celled, borne with a 2-celled auxiliary cell branch on inner cortical cells. Carposporophytes (Fig. 43B) with a basal, branched, fusion cell complex with the upper cells all forming carposporangia, with secondary lobes developed later; carposporangia ovoid to angular, 40–90 μm across. Basal nutritive tissue well developed with vertical chains of cells (Fig. 43B), erect filaments disintegrating early. Cystocarps scattered, hemispherical to conical, 1–1.5 mm in diameter; pericarp 160–200 μm and 8–16 cells thick, cells ovoid (innermost cells slightly stellate), with a prominent ostiole. Spermatangia in discrete surface sori 200–800 μm across (Fig. 43C), with ovoid spermatangia 2–3 μm in diameter cut off from elongate initials on outer cortical cells (Fig. 43D).

Tetrasporangia (Fig. 43E) scattered, transformed from intercalary inner cortical or outer medullary cells, subspherical to ovoid, 70–140 μm in diameter, tetrahedrally divided.

Type from the Kent Is, Bass Strait (*R. Brown*); holotype in BM.

Distribution: Port Denison, W. Aust., to Walkerville, Vic., and Kent Is, Bass Strait. May (1949, p. 296) records it from Tathra, N.S.W., but this record is referred to *Callophyllis rangiferinus* by Millar & Kraft (1993, p. 20).

Selected specimens: Port Denison, W. Aust., drift (*Womersley*, 31.viii.1947; AD, A5858). Israelite Bay, W. Aust., 7 m deep on *Amphibolis* (*Kirkman*, 18.xii.1981; AD, A56672). Smooth I., Isles of St Francis, S. Aust., 22 m deep on *Amphibolis* (*Shepherd*, 29.iii.1980; AD, A52253). Elliston, S. Aust., 7 m deep on *Amphibolis* (*Shepherd*, 25.x.1971; AD, A42589). Tiparra Reef, Spencer Gulf, S. Aust., 11 m deep on *Amphibolis griffithii* (*Shepherd*, 24.ii.1971; AD, A38233). Port Elliot, S. Aust., drift on *Amphibolis* (*Womersley*, 10.viii.1957; AD, A21134 and 28.v.1994; AD, A63564). Vivonne Bay, Kangaroo I., S. Aust., drift (*Womersley*, 17.i.1950; AD, A12650). Cape Jaffa, S. Aust., drift (*Womersley*, 10.xii.1991; AD, A61579). Boatswains Point, Guichen Bay, S. Aust., drift (*Womersley*, 17.v.1965; AD, A29270). Dutton Bay, Portland, Vic., drift (*Womersley*, 13.iv.1959; AD, A22691). Point Lonsdale, Vic., drift (*Sinkora* A1130, 8–12.xi.1970; AD, A62607). Off Point Nepean, Port Phillip Hds, Vic., 5–7 m deep (*Borowitzka & Walker*, 3.xii.1983; AD, A55423). Walkerville, Vic., drift (*Sinkora* A1566, 23.ii.1972; AD, A43173).

Hymenocladia usnea is variable in habit, especially in the degree of development of the distichous ramuli on the laterals, but these are always compressed and broader than those of *H. divaricata*.

The lectotype of *H. ramalina* Harvey, from King George Sound, W. Aust., is in Herb. Harvey, TCD. It is his Trav. Set No. 87 and is a loosely branched form of *H. usnea*.

The holotype of *Chondrococcus squarrosus* Kützing, from Phillip I., Vic. (*Mueller*), is in Herb. Kützing, L, 940, 284...251. It is an old and battered specimen of *H. usnea*, growing on an *Amphibolis* stem.

The lectotype (Kylin 1931, pl. 12 fig. 27) of *H. gracilarioides* J. Agardh, from "Nov. Holl. Occid. (*Mueller*)" is in Herb. Agardh, LD, 26253. It is a slender, regularly subdistichously branched plant of *H. usnea*.

The lectotype of *Chrysymenia husseyana* J. Agardh, from Encounter Bay, S. Aust. (*Hussey*), is in Herb. Agardh, LD, 26299. It is a moderately broad-branched specimen of *H. usnea*.

2. **Hymenocladia divaricata** Harvey 1855a: 553; 1858, pl. 20. J. Agardh 1871: 455; 1876: 314. De Toni 1900b: 502. De Toni & Forti 1923: 28. Kylin 1931: 24. Lucas 1929b: 49. Lucas & Perrin 1947: 198. May 1965: 388. Reinbold 1897: 52. Sonder 1881: 17. Sparling 1957: 367.
Fucus divaricatus R. Brown *ex* Turner 1811: 110, pl. 181, *nom. illegit.*

Chylocladia divaricata (R. Brown *ex* Turner)J. Agardh 1852: 367.

FIG. 44

Thallus (Fig. 44A) yellow-red to red-brown, 5–18 cm high, much branched with compressed branch axes 2–3 (-5) mm broad centrally, bearing marginally and irregularly compressed laterals 2–10 cm long, and 1–2 (-3) mm broad, often with lesser laterals, and all branches densely covered with slender, simple or irregularly branched, subterete ramuli (0.5-) 1–2 (-3) mm long and (100-) 150–250 µm in diameter; ramuli mostly distichously

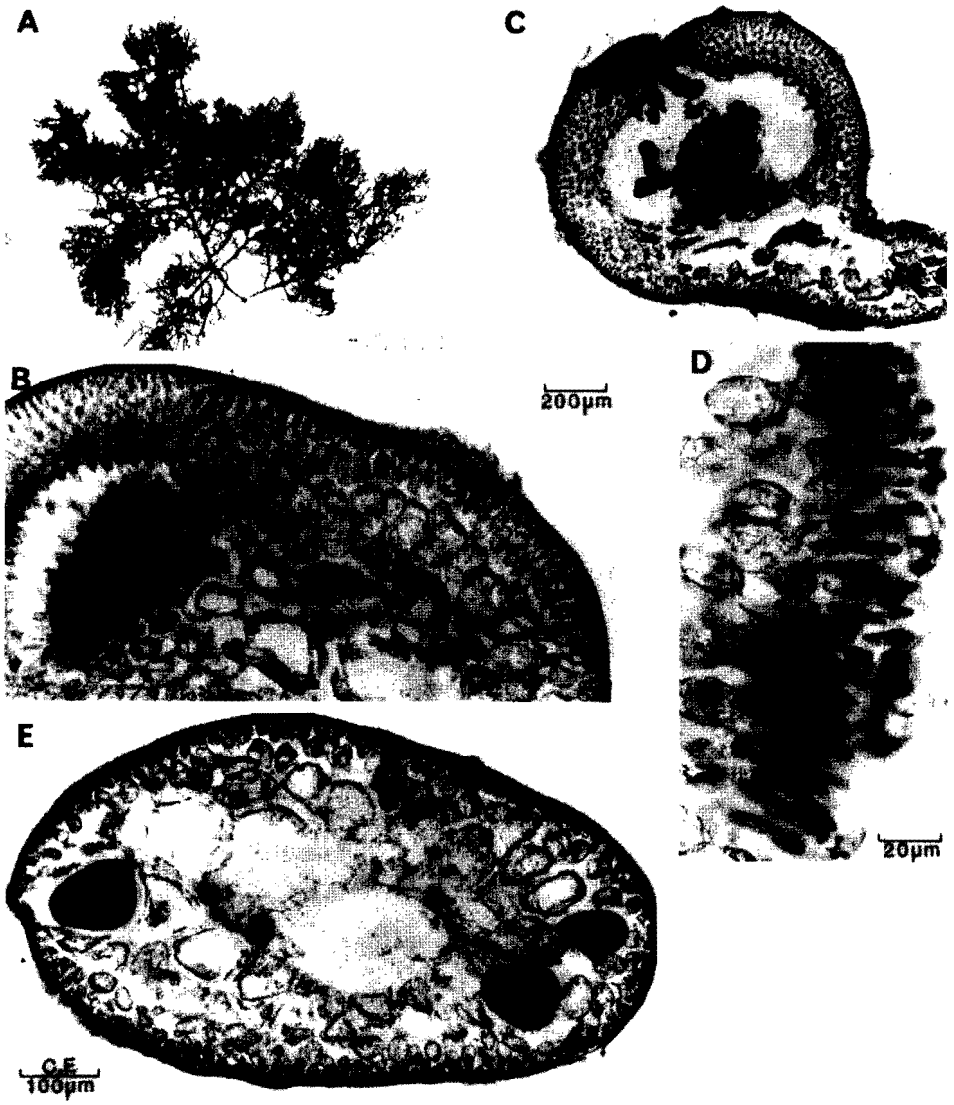


Fig. 44. *Hymenocladia divaricata* (**A, B, D, E,** AD, A61793; **C,** AD, A33471). **A.** Habit. **B.** Transverse section of monoecious branch with a young cystocarp and spermatangial sorus (upper right). **C.** Section of mature cystocarp. **D.** Section of spermatangial sorus. **E.** Transverse section of branch with tetrasporangia in medullary cells.

arranged but flexed out of the plane, with some irregularly placed or from the branch surfaces, apices relatively acute. Holdfast discoid, 1–3 mm across; epiphytic on *Amphibolis*, or epilithic? *Structure* probably multiaxial but apices narrow, developing a cortex (Fig. 44E) 1–2 cells thick, outer cells ovoid and 4–5 µm in diameter, grading over 2–4 cells to the medulla 4–6 cells across, the large inner cells ovoid and 70–140 µm in diameter with walls thin (to 10 µm thick), with intermixed filaments of smaller elongate cells 5–12 µm in diameter; secondary pit-connections frequent. Rhodoplasts elongate, ribbon like in inner cells.

Reproduction. Gametangial thalli monoecious (Fig. 44B). Carpogonial and auxiliary cell branches unknown. Carposporophytes (Fig. 44C) with a basal, branched, fusion complex with the upper cells all forming carposporangia, with secondary lobes developing later; carposporangia ovoid, 45–90 µm in diameter. Basal nutritive tissue prominent (Fig. 44C), with cells of the erect filaments largely disintegrating but some lower thick-walled cells remaining. Cystocarps scattered on lesser branches on the surface or edges, hemispherical and broad based, 1–2 mm in basal diameter, pericarp 130–220 µm and 8–14 cells thick, inner cells ovoid, with a prominent ostiole. Spermatangia in small sori (Fig. 44B), cut off from elongate initials (Fig. 44D), ovoid, 1.5–2 µm in diameter.

Tetrasporangia (Fig. 44E) scattered, transformed from intercalary outer medullary cells, subspherical, 70–100 µm in diameter, tetrahedrally divided.

Type from King George Sound, W. Aust. (*Harvey*, Trav. Set 68); lectotype in Herb. Harvey, TCD.

Distribution: King George Sound, W. Aust., to Cape Jaffa, S. Aust.

Selected specimens: Albany, W. Aust., drift (*Kraft* 4173, 14.xii.1971; AD, A41826). Middleton Beach, Albany, W. Aust., drift (*Wood*, 10.x.1960; AD, A24571). Tiparra Reef, Spencer Gulf, S. Aust., 11 m deep on *Amphibolis* (*Shepherd*, 5.xi.1971; AD, A38341). Stenhouse Bay, S. Aust., drift (*Womersley*, 9.iv.1950; AD, A13203). Sturt Bay, S. Aust. (*Davey* 387; AD, A893). Tapley Shoal, Gulf St Vincent, S. Aust., 10 m deep (*Shepherd*, 2.ii.1969; AD, A33471). D'Estrees Bay, Kangaroo I., S. Aust., drift (*Womersley*, 11.i.1950; AD, A12715). Cape Jaffa, S. Aust., drift on *Amphibolis* (*Womersley*, 25.xi.1992; AD, A61793).

Harvey (1855a, p. 553, followed by 1858, pl. 20), described *H. divaricata* as a new species, independently of *Fucus divaricatus* R. Brown *ex* Turner, which J. Agardh (1852, p. 367) considered was probably a *Chylocladia*; while it is more likely that *F. divaricatus* is the same as Harvey's species, the latter name cannot be transferred to *Hymenocladia* and Harvey must be considered the author of *H. divaricata*. The holotype of *F. divaricatus* is in the BM; it was recorded only from "the coast of New Holland" (R. Brown). There is also an earlier *Fucus divaricatus* Linnaeus (1763, p. 1627) which Turner notes is *Fucus vesiculosus*.

3. **Hymenocladia chondricola** (Sonder)J. Lewis 1994: 9, figs 7–10.

Halymenia chondricola Sonder 1845: 57; 1848: 172; 1881: 13. J. Agardh 1851: 206. De Toni 1905: 1552. Harvey 1863, synop.: xlvi. Kützing 1849: 717; 1866: 33, pl. 92a–d.

Rhodymenia polymorpha Harvey 1859b: 319; 1860: pl. 157.

Hymenocladia polymorpha (Harvey)J. Agardh 1871: 453; 1876: 315. De Toni 1900b: 504. De Toni & Forti 1923: 29, pl. 3 figs 2, 3. Guiler 1952: 94. Kylin 1931: 25. Lucas 1929b: 49. Lucas & Perrin 1947: 198, fig. 64. May 1965: 387. Reinbold 1897: 52. Sonder 1881: 17. Sparling 1957: 367. Tisdall 1898: 506. Wilson 1892: 179. Womersley 1950: 176.

Rhodymenia pinnulata Zanardini 1874: 500. De Toni 1900b: 521.

FIG. 45

Thallus (Fig. 45A, B) medium to dark red, fading to yellow-red, (5-) 10–50 cm high, complanately branched, foliose and often marginally proliferous in an irregular to regular manner with proliferations simple and 1–3 cm long to branched similarly to the main axes. Axes and main branches (1-) 2–8 (-10) cm broad, 350–1000 (-1400) µm thick (margins usually thicker), small or relatively large surface proliferations occasional. Holdfast discoid, 1–4 mm across; epiphytic on *Amphibolis* and various robust algae (e.g. *Acrocarpia*) or



Fig. 45. *Hymenocladia chondricola* (**A, C, F,** AD, A63025; **B, D, E,** AD, A61181). **A.** Habit. **B.** Habit, cystocarpic plant. **C.** Transverse section of thallus with cystocarp. **D.** Cortex with a spermatangial sorus. **E.** Detail of spermatangial sorus with elongate initials. **F.** Transverse section of thallus with tetrasporangia in inner cortical cells.

epizoic, or epilithic. *Structure* multiaxial, developing a cortex (Fig. 45C, F) 2–3 cells broad, outer cells ovoid and 4–6 µm in diameter, grading fairly sharply to a medulla (Fig. 45F) mostly 300–750 µm and 4–10 cells across, larger cells ovoid and 90–170 µm in diameter, walls 5–25 µm thick, with frequent to abundant interspersed smaller ovoid cells or filaments 25–50 µm in diameter; secondary pit-connections frequent, hairs in clusters. Rhodoplasts elongate, in chains or ribbon like in inner cells.

Reproduction. Gametangial thalli dioecious. Carpogonial and auxiliary cell branches not observed. Carposporophytes (Fig. 45C) with a basal, branched, fusion cell complex, with upper cells all forming ovoid carposporangia 45–75 µm in diameter, with later lobes developing. Basal nutritive tissue (Fig. 45C) prominent, erect filaments disintegrating apart from thick-walled remnants near the nutritive tissue. Cystocarps scattered on the surface, protruding, hemispherical, 0.8–1.2 mm in diameter, pericarp 180–300 µm and 8–14 cells thick, inner cells ovoid (innermost stellate), ostiolate. Spermatangia in extensive sori (Fig. 45D), cut off from elongate initials (L/D 6–10) on cortical cells (Fig. 45E), ovoid, 2–3 µm in diameter.

Tetrasporangia (Fig. 45F) scattered, transformed from intercalary outer medullary cells, subspherical to ovoid, 70–100 µm in diameter, tetrahedrally divided.

Type from W. Aust. (*Preiss*); holotype in MEL, 502376.

Distribution: Port Denison, W. Aust., to Walkerville, Vic., and around Tasmania.

Selected specimens: Port Denison, W. Aust., drift (*Womersley*, 31.viii.1947; AD, A5860). Point Peron, W. Aust., drift (*Royce* 886, 2.i.1951; AD, A15472). Elliston, S. Aust., drift (*Womersley*, 27.ii.1959; AD, A22205). Topgallant I., S. Aust., 35 m deep on *Pyura* (*Branden*, 2.vii.1987; AD, A57569). Wanna, S. Aust., drift (*Womersley*, 19.ii.1959; AD, A22414). Between Hopkins and Thistle Is, S. Aust., 6–9 m deep (*Baldock*, 1.i.1964; AD, A27114). Brown Beach, Yorke Pen., S. Aust., drift (*Womersley*, 13.iv.1963; AD, A26636). Port Elliot, S. Aust., drift (*Womersley*, 28.v.1994; AD, A63565). Pelorus Islet, S of Kangaroo I., S. Aust., 10–30 m deep on *Acrocarpia* (*Branden*, 19.vi.1991; AD, A61398). Vivonne Bay, Kangaroo I., S. Aust., drift (*Womersley*, 2.i.1949; AD, A10670). Seal Bay, Kangaroo I., S. Aust., drift (*Womersley*, 29.x.1966; AD, A31016). Pennington Bay, Kangaroo I., S. Aust., reef edge (*Womersley*, 5.i.1947; AD, A4370). Robe, S. Aust., drift (*Womersley*, 15.iv.1994; AD, A63543). Stinky Bay, Nora Creina, S. Aust., drift (*Womersley*, 14.iii.1991; AD, A61181). Port MacDonnell, S. Aust., drift on *Amphibolis* (*Womersley*, 18.ix.1993; AD, A63025). Dutton Bay, Portland, Vic., drift (*Womersley*, 13.iv.1959; AD, A22695). Queenscliff, Vic., drift (*Womersley*, 8.iv.1959; AD, A22853). Walkerville, Vic., drift (*Sinkora* A2297, 7.iii.1976; AD, A48498). Low Head, Tas., (*Perrin*, 19.iii.1945; AD, A8505). Fluted Cape, Bruny I., Tas., 16 m deep (*Shepherd*, 14.ii.1972; AD, A41829).

The holotype sheet of *H. chondricola* consists of two small fragments about 4 cm high, of the species commonly known as *H. polymorpha*. This species is extremely variable in form, from broad, occasionally divided plants to regularly pinnate ones, with main axes 1–10 cm broad. However, the branches are always distinctly broader than those of *H. usnea*.

The holotype of *H. polymorpha*, from Georgetown, Tas. (*Harvey*), is in Herb. Harvey, TCD. This is the only specimen of Harvey's Alg. Aust. Exsicc. 383I in TCD.

The lectotype of *Rhodymenia pinnulata* Zanardini, from Georgetown, Tas. (*Goodwin*), is in Herb. Zanardini, Museo Civico di Storia Naturale, Venice. It is a large, pinnately branched specimen of *H. chondricola*.

The New Zealand *H. sanguinea* (Harvey)Sparling and *H. lanceolata* J. Agardh are within the range of form shown by *H. chondricola*, and are to be considered as synonyms, following Sparling (1957, p. 370) and Chapman & Dromgoole (1970, p. 117).

4. **Hymenocladia filiformis** J. Agardh 1892: 83. De Toni 1900b: 501. Kylin 1931: 24, pl. 11 fig. 26. Lucas & Perrin 1947: 196. May 1965: 387. Sparling 1957: 367.
Hymenocladia subulosa J. Agardh 1896: 91. De Toni 1900b: 501. Kylin 1931: 24, pl. 11 fig. 25. May 1965: 387. Sparling 1957: 367.

FIG. 46

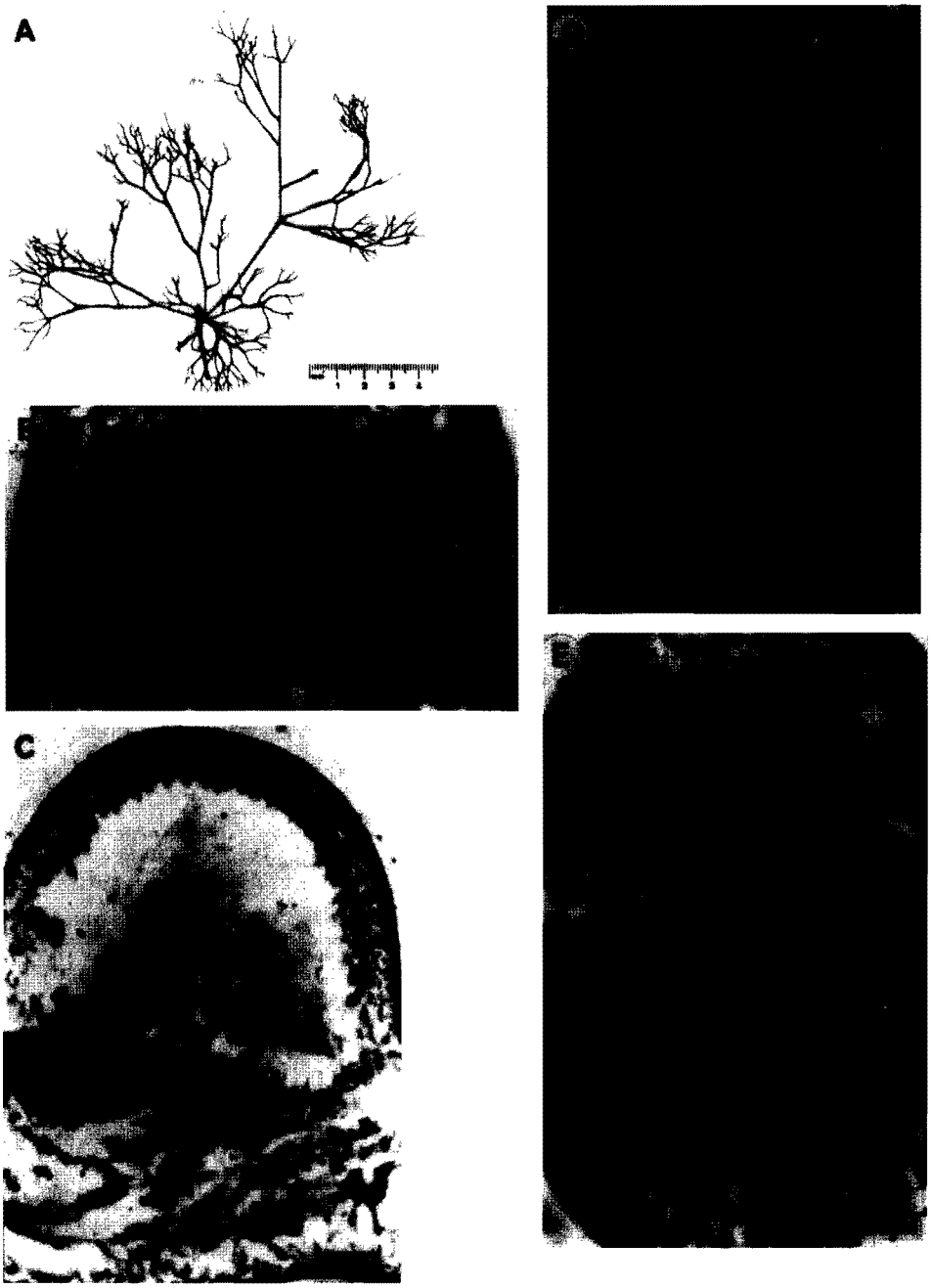


Fig. 46. *Hymenocladia filiformis* (**A, C, D,** AD, A64490; **B, E,** AD, A64491). **A.** Habit. **B.** Transverse section of branch showing small cells between large medullary cells. **C.** Section of a cystocarp with carposporophyte and basal nutritive tissue. **D.** Base of carposporophyte with fusion cell, basal nutritive tissue and cell walls of disintegrated erect filaments. **E.** Transverse section of a branch with two tetrasporangia.

Thallus (Fig. 46A) 4–14 cm high, subdichotomously to laterally branched largely complanately, branches slightly compressed, 0.5–1 mm broad below, tapering slightly to 0.2–0.5 mm broad above, apices rounded. Holdfast discoid; epiphytic on *Amphibolis*. *Structure* multiaxial, with a cortex 2–3 (-4) cells broad, outer cells ovoid and 2–3 µm in diameter, and a medulla (3-) 5–8 cells across (Fig. 46B), inner cells ovoid and 80–150 (-200) µm in diameter, with small-celled filaments lying between the larger cells in older branches. Rhodoplasts discoid, ribbon like in inner cells.

Reproduction. Early reproductive structures unknown. Carposporophytes (Fig. 46C, D) with a basal fusion cell and gonimoblast cells all becoming ovoid carposporangia 45–100 µm in diameter. Basal nutritive tissue (Fig. 46D) well developed, erect filaments disintegrating but cell walls of lower cells remaining. Cystocarps hemispherical, not or slightly basally constricted, 700–1200 µm in diameter, pericarp 100–200 µm and 8–12 cells thick, ostiolate. Spermatangia unknown.

Tetrasporangia (Fig. 46E) scattered in branches, transformed from outer medullary cells, 80–140 µm in diameter, tetrahedrally to cruciately divided.

Type from Champion Bay, W. Aust. (*Spalding*); lectotype in Herb. Agardh, LD, 26217.

Distribution: Champion Bay to Eucla, W. Aust.

Selected specimens: Cervantes, W. Aust., drift on *Amphibolis* (*M. & F. Hommersand*, 20.ix.1995; AD, A64490). Yanchep, W. Aust., drift on *Amphibolis* (*Kraft 8448 & Herrington*, 5.ix.1990; MELU; AD, A64492). Eucla, W. Aust., drift on *Amphibolis* (*Kerry*, Sept. 1975; G.K. 5731; MELU; AD, A64491).

The type specimens are cystocarpic and have the distinctive basal nutritive tissue of *Hymenocladia* (and other Rhodymeniaceae). Tetrasporangial specimens also agree with *Hymenocladia*. The type of *H. subulosa* from Eucla, W. Aust. (*Ryan*); lectotype (Kylin 1931, fig. 25) in Herb. Agardh, LD, 26211, and the Eucla specimen cited above, appear identical with *H. filiformis* from the west coast.

As well as the four species from southern Australia, two other little known species occur on the west coast of Western Australia.

1. **Hymenocladia conspersa** (Harvey)J. Agardh 1871: 452; 1876: 315; 1892: 83. De Toni 1900b: 504. Huisman & Walker 1990: 416. Kylin 1931: 25. J. Lewis 1994: 8, fig. 11. Sparling 1957: 367. Wilson 1892: 179.
   Calliblepharis conspersa Harvey 1855a: 550; 1862: pl. 237 (excl. small ovate plants = *Erythrymenia minuta*). Kützing 1869: 14, pl. 39a, b.

H. conspersa is probably limited to the west coast. The type (Fig. 46C) was from Garden I., W. Aust., [lectotype (Trav. Set 132) in Herb. Harvey, TCD] and the species has been rarely collected. References to *H. conspersa* on southern Australian coasts probably all apply to *Erythrymenia minuta* Kylin, which Harvey incorrectly considered to be juvenile plants of *H. conspersa*.

2. **Hymenocladia dactyloides** (Sonder)J. Agardh 1871: 454; 1876: 312. De Toni 1900b: 500. Huisman & Walker 1990: 416. Kylin 1931: 24. Lucas & Perrin 1947: 196. Sonder 1881: 17. Sparling 1957: 367.
   Gracilaria dactyloides Sonder 1845: 55. J. Agardh 1852: 604; 1871: 454. Harvey 1855a: 550; 1859a: pl. 80. May 1965: 387.
   Plocaria dactyloides (Sonder)Sonder 1848: 190.
   Sphaerococcus dactyloides (Sonder)Kützing 1849: 776; 1869: 8, pl. 22 c, d.

H. dactyloides is based on a *Preiss* specimen (Fig. 46D) from W. Aust.; the holotype in MEL, 698388, was illustrated by Kützing. It is a little known species which needs re-investigation. Harvey's illustration shows the large tetrahedrally divided tetrasporangia typical of *Hymenocladia*, and the holotype has typical *Hymenocladia* cross sectional and cystocarpic structure.

FAMILY CHAMPIACEAE Kützing 1843: 438, 439

Thallus erect, or pulvinate and parasitic, much branched radially or distichously, branches terete to compressed, segmented by monostromatic diaphragms, segments hollow but with longitudinal filaments bearing secretory cells bordering the medulla. *Structure* multiaxial with a distinct group of apical cells producing the longitudinal filaments, diaphragms, and cortex 2–4 cells thick.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious or monoecious; procarpic. Carpogonial branches 3- or 4-celled, with one or two 2-celled auxiliary cell branches, borne on inner cortical cells. Carposporophytes with a basal fusion cell producing a tuft of gonimoblast filaments with only terminal carposporangia, or producing directly large carposporangia; nutritive tissue absent, inner cells of pericarp stellate, persistent or not. Cystocarps protruding, basally constricted, pericarp ostiolate or not. Spermatangia in sori, cut off from initials on outer cortical cells.

Tetrasporangia scattered in the cortex, transformed from cortical cells, tetrahedrally divided; polysporangia in some species of *Gastroclonium*.

A family of four genera, from which the Lomentariaceae is separated by most recent authors, characterised by the segmented, hollow branches with internal longitudinal filaments bearing secretory cells, monostromatic diaphragms, carposporophytes with terminal carposporangia, and scattered tetrasporangia. The stellate inner pericarp cells are often referred to as a tela arachnoidea, but basal nutritive tissue is absent or slight.

KEY TO GENERA OF CHAMPIACEAE

1. Thallus minute (1–2 mm high), lobed, parasitic on *Champia* ..... CHAMPIOCOLAX
1. Thallus 2–50 cm high, much branched, epilithic or epiphytic 2

    2. Carposporophyte with branched, multicellular gonimoblast filaments bearing terminal carposporangia; cystocarps ostiolate ..... CHAMPIA
    2. Carposporophyte with carposporangia formed directly from the fusion cell; cystocarps non-ostiolate ..... CHYLOCLADIA

Genus CHAMPIOCOLAX Bula-Meyer 1985: 429

Thallus 1–3 mm high, lobed, hemiparasitic on *Champia* but pigmented, branches terete with rounded apices, segmented by diaphragms, attached to the host by rhizoids penetrating the cortex. *Structure* multiaxial, developing a cortex 2 cells thick bordered internally by longitudinal filaments bearing secretory cells and with regular, but few, monostromatic diaphragms.

Life history triphasic, with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli monoecious. Carpogonial branches 4-celled, borne on a large cortical (supporting) cell together with a 2-celled auxiliary cell branch. Carposporophyte erect, with branched gonimoblast filaments bearing terminal carposporangia; basal nutritive tissue slight, erect filaments slender. Cystocarps external, ovoid, pericarp thick, inner cells stellate, without or with a very narrow ostiole. Spermatangia cut off from initials on the outer cortical cells, forming extensive sori.

Tetrasporangia scattered, transformed from larger intercalary cortical cells, tetrahedrally divided.

Holotype species: *C. sarae* Bula-Meyer 1985: 429, figs 1–17.

Champiocolax has been known only from the type species from the Caribbean. A second species is now described from southern Australia.

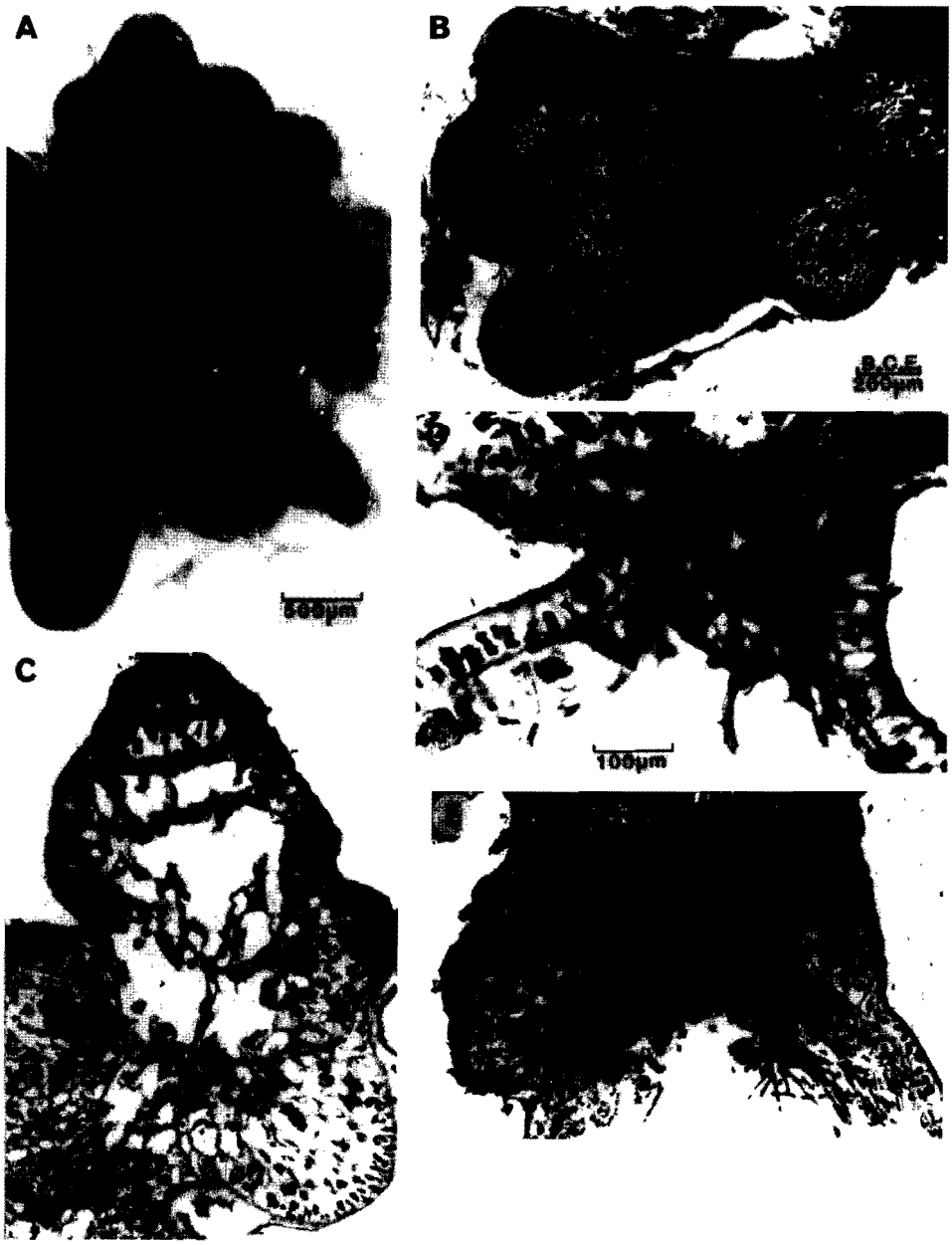


Fig. 47. *Champiocolax lobata* (AD, A39536). **A.** Habit, lowest lobe with septa. **B.** Lobe with septa. **C.** Longitudinal section of lobe with septa and pseudoparenchymatous base. **D.** Attachment to *Champia* (rows of large cells). **E.** Attachment of older thallus to *Champia* (at base of section).

Champiocolax lobata Womersley, *sp. nov.*

FIGS 47, 48A, B

Thallus (Fig. 47A) 2–4 mm high, erect and branched, forming dense clumps with terete, segmented, stubby branches 0.5–1 mm in diameter, arising from a solid stipitate base (Fig. 47C), hemiparasitic on *Champia viridis*. *Structure* multiaxial with a solid, pseudoparenchymatous base attached to the host *Champia* by rhizoidal filaments (Fig. 47D, E), producing above segmented branches (Fig. 47B, C) with a cluster of apical cells, developing a cortex 1–2 cells thick, outer cells anticlinally elongate and 6–12 µm in diameter, with 2–6 monostromatic diaphragms (Fig. 47C) and longitudinal filaments, bearing odd secretory cells, scattered throughout the diaphragms. Rhodoplasts discoid, few in outer cells.

Reproduction. Gametangial thalli monoecious, sexual structures originating on pseudoparenchymatous tissue. Carpogonial branches unknown, auxiliary cell branches probably 2-celled. Carposporophytes (Fig. 48A) with a small basal fusion cell and all cells forming carposporangia 15–25 µm in diameter. Basal nutritive tissue very slight (Fig. 48A), erect filaments present around the carposporophyte. Cystocarps globular, largely external, 700–1000 µm in diameter, pericarp 4–8 cells and 150–300 µm thick, with a narrow ostiole. Spermatangia (Fig. 48B) in small sori, cut off from initials on outer cortical cells, ovoid, 2–3 µm in diameter.

Tetrasporangia unknown.

Thallus 2–4 mm altus, erectus, ramosus, dense fasciculatus, ramis teretibus, segmentatis, 0.5–1 mm in diametro, ex base solida stipitata ortis, semiparasiticus in *Champia viridis*. Structura multiaxialis, basis pseudoparenchymatica et rhizoideis affixa, rami segmentati fasciculo cellularum apicalium corticem 1–2 cellulas crassam, 2–6 diaphragmatibus monostromaticis et filamentis longitudinalibus dispersis formanti.

Reproductio. Monoecia. Carposporophyta cellula coalescenti parva et totis cellulis gonimoblastis carposporangia formantibus. Textura basalis nutritiva perpauca, filamentis erectis. Cystocarpia globularia, plerumque externa, 700–1000 µm in diametro, ostiolo angusto. Spermatangia in soris parvis. Tetrasporangia ignota.

Type from Warrnambool, Vic., on *Champia viridis*, drift (*Womersley*, 1.ix.1971); holotype in AD, A39536.

Distribution: Stenhouse Bay, S. Aust., to Warrnambool, Vic., all on *Champia viridis*.

Known specimens: The type. Stenhouse Bay, S. Aust., 3–7 m deep (*Kraft*, 18.ix.1973; AD, A44564). Guichen Bay, S. Aust., 10–16 m deep (*Womersley*, 1.ix.1949; AD, A10937).

C. lobata differs from the type species in its pseudoparenchymatous base and larger, more lobed, thallus; the type is also reported as non-ostiolate. However further studies are needed on details of thallus structure and reproduction. Kraft & Woelkerling (1981, fig. 4.8H; 1990, fig. 3.9H) figured *C. lobata* as a "dwarf plant" on a species of *Champia*. The Stenhouse Bay specimen occurs on cystocarpic *Champia*.

Genus CHAMPIA Desvaux 1809: 245

Thallus erect or decumbent, some species iridescent, much branched, branches terete to compressed, with regular hollow segments throughout with transverse diaphragms, not or slightly constricted at diaphragms; holdfast discoid or stoloniferous with haptera. *Structure* multiaxial, with a group of apical cells, producing longitudinal filaments bearing secretory cells, and developing outwardly a large-celled cortex with or without outer layer(s) of smaller cells, and inwardly, at regular intervals, the transverse monostromatic diaphragms.

Life history triphasic, with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious; procarpic. Carpogonial branches 4-celled, situated on cortical (supporting) cells with a 2-celled auxiliary cell branch; carposporophyte erect, with a basal fusion cell and branched gonimoblast filaments bearing terminal carposporangia; basal nutritive tissue absent or slight, inner cells of pericarp becoming

stellate and separating. Cystocarps external, globular to urceolate, pericarp 2–6 (-10) cells thick, ostiolate. Spermatangia in surface sori, cut off from rows of initials developed from the small outer cortical cells.

Tetrasporangia scattered, transformed from the larger (primary) cortical cells and protruding inwards, tetrahedrally divided.

Holotype species: *C. lumbricalis* (Linnaeus)Desvaux 1809: 245.

A genus credited with numerous species, many of which need detailed study. The type species, from South Africa, was studied by Reedman & Womersley (1976, p. 76).

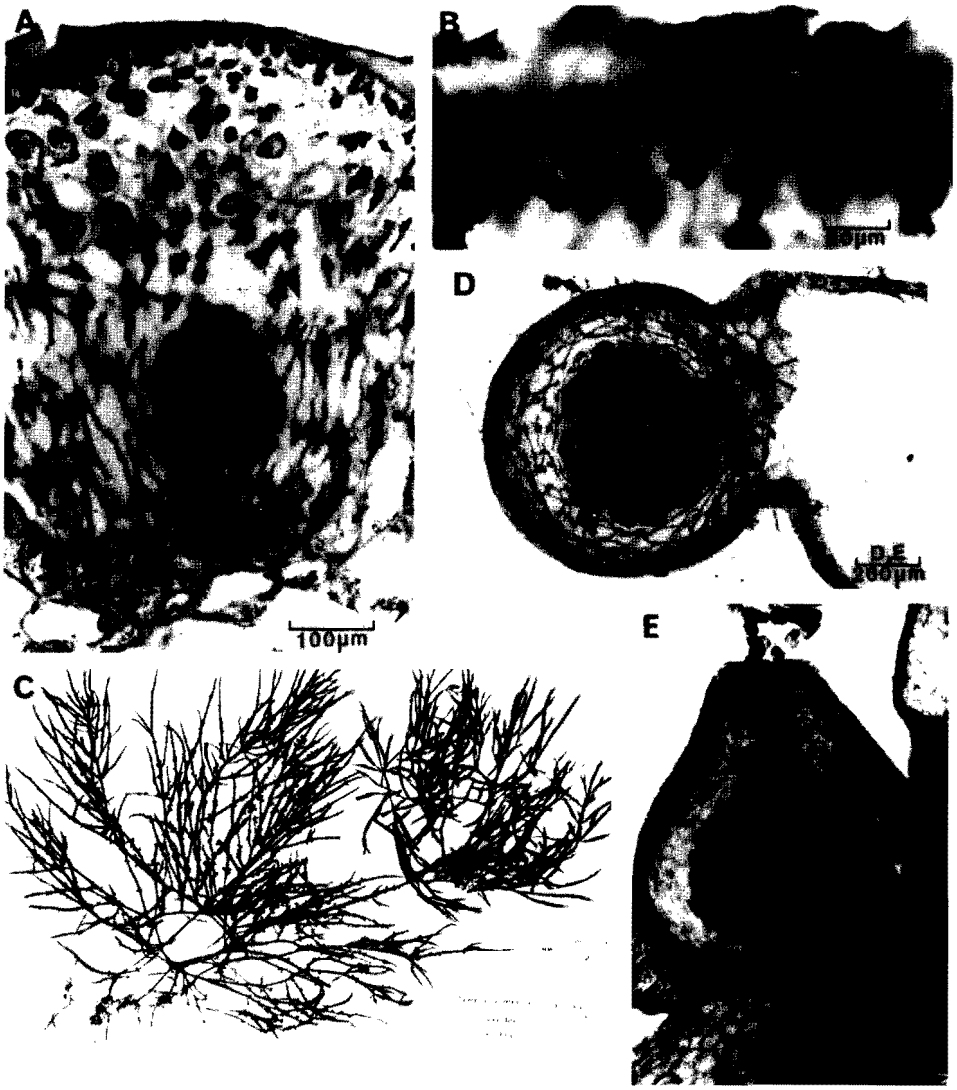


Fig. 48. A, B. *Champiocolax lobata* (AD, A39536). **A.** Section of a cystocarp with carposporophyte, slight basal nutritive tissue and slender erect filaments. **B.** Section of male thallus with spermatangia. **C–E.** *Champia viridis* (**C,** AD, A63830; **D, E,** AD, A44564). **C.** Habit. **D.** Section of a young cystocarp with slight basal nutritive tissue and erect filaments. **E.** A mature cystocarp losing carposporangia.

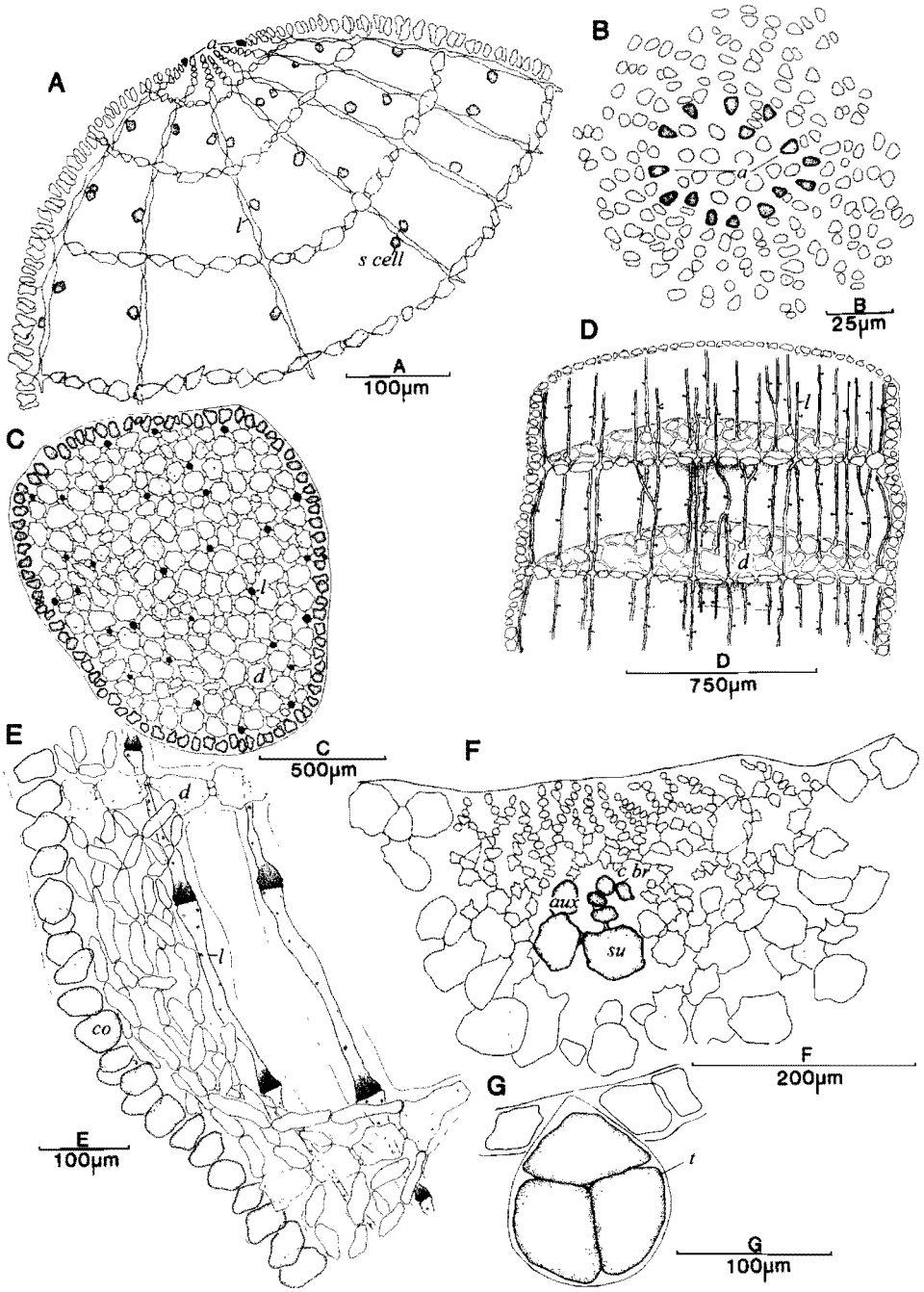


Fig. 49. *Champia viridis* (**A,** AD, A42995; **B–D,** AD, A42991; **E–G,** AD, A30550). **A.** Longitudinal section of a branch apex showing development of cortex, longitudinal filaments and diaphragms. **B.** Surface view of branch apex showing central and peripheral apical cells. **C.** Transverse section of a young branch showing a diaphragm with peripheral and scattered longitudinal filaments. **D.** Three-dimensional view of branch showing diaphragms and longitudinal filaments with secretory cells. **E.** Longitudinal section of older branch showing development of central rhizoids from peripheral diaphragm cells. **F.** Early post-fertilization stage with supporting cell bearing an old carpogonial branch and auxiliary cell branch, with cortical proliferation leading to formation of the pericarp. **G.** Transverse section of cortex with a mature tetrasporangium. [After Reedman & Womersley 1976.]

KEY TO SPECIES OF *CHAMPIA*

1. Thallus with longitudinal filaments scattered through the diaphragms as well as peripheral filaments; branches usually linear, not or only slightly constricted at diaphragms 2
1. Thallus with peripheral longitudinal filaments only; branches usually tapering from base to apices, usually slightly to moderately constricted at diaphragms 3

    2. Branching irregular to verticillate, branches linear, (0.5-) 1–2.5 mm broad ..... 1. *C. viridis*
    2. Branching more or less opposite to becoming clustered, subdistichous and often fairly regularly pinnate; branches 2–5 mm broad, with a slender stalk ..... 2. *C. insignis*

3. Thallus segments obscured except in young branches, with cortical cells becoming covered by an outer cortex 1–3 cells thick; usually epilithic ..... 3. *C. affinis*
3. Thallus segments clear throughout most of thallus, with cortical cells cutting off small cells from their corners but not (or only near the thallus base) forming a continuous layer; usually epiphytic on seagrasses 4

    4. Branches 1–2 mm, branchlets 0.5–1 mm in diameter; cortex single-layered with only a few small cells from each cortical cell throughout; usually one complete longitudinal filament cell between diaphragms; ultimate mature branches often with hooked ends ..... 4. *C. zostericola*
    4. Branches 0.5–1 mm, branchlets 0.3–0.5 mm in diameter; cortex single-layered above, becoming 2–4 cells thick on older axes; usually two complete longitudinal filament cells between diaphragms; ultimate branches rarely hooked ..... 5. *C. parvula*

1. **Champia viridis** C. Agardh 1828: 115. Huisman & Walker 1990: 415. Kützing 1849: 862. Millar & Kraft 1993: 30. Reedman & Womersley 1976: 77, figs 1, 2A–D, 10.
Corinaldia viridis (C. Agardh)Trevisan 1848: 108.
Champia tasmanica Harvey 1844a: 407, pl. 19; 1849: 78; 1859b: 307. J. Agardh 1852: 370; 1876: 306; 1879: 67, pl. 19 figs 10–12. De Toni 1900a: 79; 1900b: 563. Guiler 1952: 95. Hooker & Harvey 1847: 402. Kützing 1849: 861; 1865: 30, pl. 84g. Kylin 1931: 29. Lucas 1929b: 50. Lucas & Perrin 1947: 207, fig. 72. May 1965: 362. Reinbold 1897: 53; 1899: 45. Sonder 1846: 177(?); 1881: 17. Tisdall 1898: 506. Wilson 1892: 180. Womersley 1950: 174; 1966: 151.
C. tasmanica var. *gracilis* Harvey 1863, synop.: xxvii. Sonder 1881: 17.
Corinaldia tasmanica (Harvey)Trevisan 1848: 108.
Champia oppositifolia J. Agardh 1901: 27. Kylin 1931: 29, pl. 16 fig. 37. May 1965: 362.
Champia verticillata J. Agardh 1901: 26. Kylin 1931: 29, pl. 17 fig. 39. May 1965: 362.
Champia compressa sensu Harvey 1863, synop.: xxvii (in part).

PLATE 2 fig. 3; FIGS 48C–E, 49

Thallus (Fig. 48C) dark-red to red-purple, 5–15 (-20) cm high, densely tufted, axes (1-) 2–3 mm broad, with numerous branches for 2–4 orders, irregular, sub-opposite or verticillate. Branches terete to slightly compressed, (0.5-) 1–1.25 mm broad, linear to slightly curved, basally constricted, apices rounded; diaphragms 0.5–1 (-1.5) mm apart, regular and conspicuous in surface view. Holdfasts small, discoid, on stoloniferous basal branches; epilithic or on *Posidonia*. *Structure* multiaxial with central and peripheral initials (Fig. 49B), developing a single-layered cortex (Fig. 49A) of compact, polygonal cells 25–40 µm across with small cells cut off in the outer corners, and in older parts an inner cortex (Fig. 49E) of rhizoidal filaments several filaments thick, derived from the peripheral diaphragm cells; longitudinal filaments (Fig. 49A, D) both peripheral and central with one

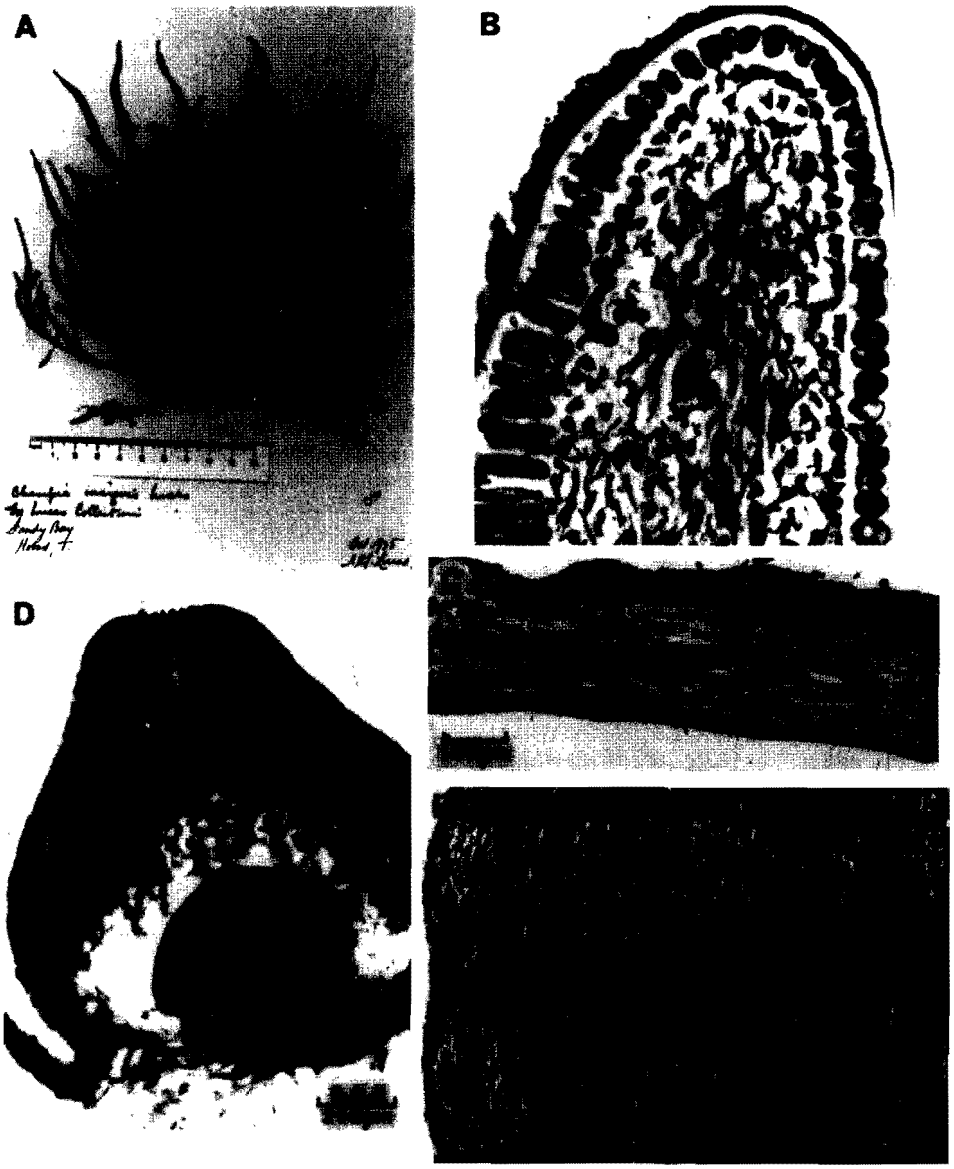


Fig. 50. *Champia insignis*. (**A,** Lectotype; **B, C, E,** AD, A55565; **D,** NSW, 136559). **A.** Habit. **B.** Transverse section of older branch. **C.** Longitudinal section of older branch. **D.** Section of cystocarp. **E.** Surface view of compressed branch with tetrasporangia.

complete and two part cells between the diaphragms, the central cell bearing a secretory cell; diaphragms (Fig. 49C) monostromatic. Rhodoplasts discoid, in chains.

Reproduction. Gametangial thalli probably dioecious. Carpogonial branches 4-celled, auxiliary cell branches 2-celled, borne on a cortical supporting cell (Fig. 49F) with adjacent cortical cells proliferating. Carposporophyte with a basal branched fusion cell and branched gonimoblast filaments bearing ovoid to angular, terminal to subterminal carposporangia 45–60 µm in diameter; basal nutritive tissue slight, erect filaments slender, cells stellate, conspicuous when young (Fig. 48D). Cystocarps (Fig. 48E) scattered, external, globular to urceolate, 0.5–1 mm in diameter. Pericarp 180–280 µm and 4–6 cells thick, inner cells stellate with long arms, ostiolate. Spermatangia not observed.

Tetrasporangia (Fig. 49G) scattered, transformed from cortical cells, 60–90 (-120) µm in diameter, tetrahedrally divided.

Type from W. Aust.; holotype (mica mounts) in Herb. Agardh, LD, 26112.

Distribution: Rottnest I., W. Aust., to Jervis Bay, N.S.W. (Millar & Kraft 1993, p. 30), and around Tasmania.

Selected specimens: Fremantle, W. Aust. (*Clifton*; TCD). Cannan Reefs, S. Aust., 20–25 m deep (*Branden*, 21.i.1991; AD, A61084). Pearson I., S. Aust., 35 m deep (*Shepherd*, 7.i.1969; AD, A34040). Stenhouse Bay, S. Aust., 3–7 m deep (*Kraft*, 18.ix.1973; AD, A44564). Marino, S. Aust., drift on *Posidonia* (*Womersley*, 26.x.1975; AD, A46651). Victor Harbor, S. Aust., drift (*Womersley*, 24.vii.1949; AD, A11183). American R. inlet, Kangaroo I., S. Aust., sublittoral (*Womersley*, 2.xi.1947; AD, A6168). Pennington Bay, Kangaroo I., S. Aust., 0.5–1 m deep (*Kraft*, 13.iv.1973; AD, A42998). Cape Lannes, S. Aust., just sublittoral (*Reedman*, 10.ii.1973; AD, A42991). Nora Creina, S. Aust., just sublittoral (*Reedman*, 12.ii.1973; AD, A42995). Warrnambool, Vic., 4–5 m deep (*Shepherd*, 19.viii.1972; AD, A42626). Popes Eye, Port Phillip Heads, Vic., 2 m deep (*Macpherson*, 5.v.1963; AD, A28822). San Remo, Vic., drift on outer beach (*Sinkora* A467, 14.vi.1970; AD, A62626). Crawfish Rock, Westernport Bay, Vic., 4–5 m deep (*Watson*, 26.iv.1969; AD, A34268). Gabo I., Vic., 28 m deep (*Shepherd*, 19.ii.1973; AD, A43546). Cape Sorell, Tas., low eulittoral (*Bennett*, 4.ii.1955; AD, A20606). Pilot Station, Low Head, Tas., drift (*Womersley*, 23.x.1986; AD, A57778). N end Governor I., Bicheno, Tas., 8–16 m deep (*Edgar*, 23.x.1944; AD, A63830). Stapleton Point, Prosser Bay, Tas., 8–12 m deep (*Olsen*, 21.vi.1966; AD, A30550). Lady Bay, Southport, Tas., 3–5 m deep (*Brown & Womersley*, 28.x.1982; AD, A56521).

The synonymy of *C. viridis* was discussed by Reedman & Womersley (1976, p. 79). It is a distinctive species having central as well as peripheral longitudinal filaments, but specimens from calm water situations are smaller and slenderer than those from rough-water situations.

2. **Champia insignis** Lucas 1931: 409, pl. 25 fig. 1. Guiler 1952: 94. Lucas & Perrin 1947: 207. May 1965: 362. Reedman & Womersley 1976: 81, figs 2E, F, 11A.

FIGS 50, 51A, B

Thallus (Fig. 50A) medium to dark red-brown, 6–18 cm high, with one to several main axes with mostly opposite laterals (occasionally one or three from the segment), lower laterals similarly branched. Axes and main laterals 3–5 mm broad, slightly to moderately compressed, laterals with a slender stalk and a rounded apex; diaphragms evident throughout thallus, 2–3 (-4) mm apart in older parts, 1–2 mm apart in branches, branches slightly constricted at diaphragms. Holdfast discoid to slightly lobed, 2–6 mm across; epilithic. *Structure* multiaxial with peripheral and central initials, developing a single-layered cortex of compact polygonal cells 35–50 µm across, cutting off 1–3 small cells from their outer corners and more numerous such cells near the thallus base; longitudinal filaments both peripheral and central with one or two cells between the diaphragms, usually each cell bearing a secretory cell; diaphragms monostromatic, cells angular, elongate in the compressed branches. Old branches with cortical cells differing on the two sides (Fig. 50B, C) and the space between the diaphragms becoming filled with rhizoids. Rhodoplasts discoid to elongate, ribbon like and branched in inner cells.

Reproduction. Gametangial thalli dioecious. Early female reproduction unknown. Carposporophyte branched, with sterile gonimoblast filaments bearing terminal ovoid carposporangia 30–60 µm in diameter. Cystocarps (Fig. 50D) scattered, conical to urceolate,

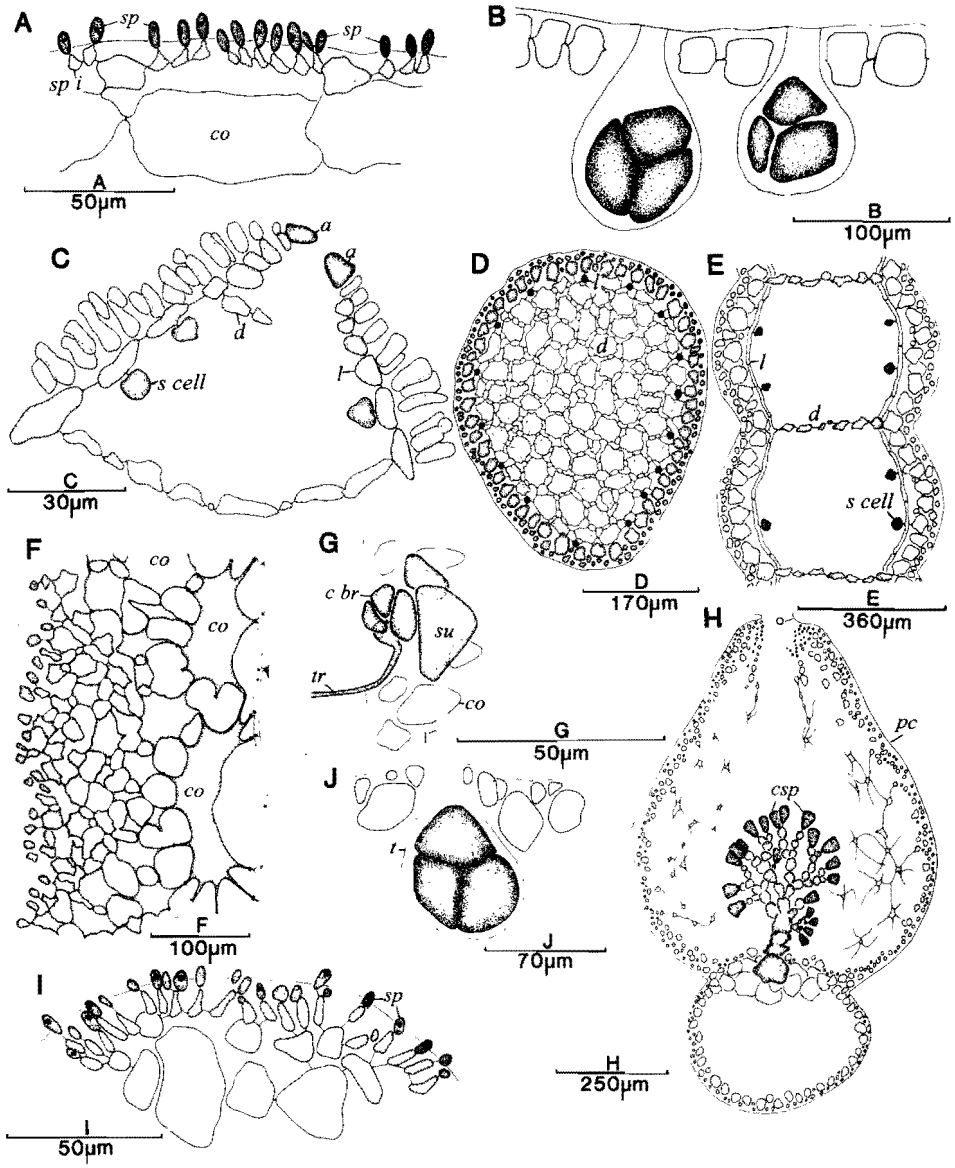


Fig. 51. A, B. *Champia insignis*. (**A,** AD, A12237; **B,** AD, A55565). **A.** Section of male thallus with spermatangia. **B.** Transverse section of thallus with tetrasporangia. **C–J.** *Champia affinis*. (**C, D,** AD, A42994; **E, J,** AD, A42993; **F, H, I,** AD, A42997; **G,** AD, A42990). **C.** Longitudinal section of branch apex showing development of cortex, longitudinal filaments with secretory cells and diaphragms. **D.** Transverse section of a branch with a diaphragm, peripheral longitudinal filaments, and small outer cortical cells. **E.** Longitudinal section of a branch corresponding to **D. F.** Longitudinal section of an old branch with cortex several cells thick. **G.** Supporting cell with a carpogonial branch and auxiliary initial. **H.** Section of an immature cystocarp with gonimoblast from the auxiliary cell and terminal carposporangia. **I.** Transverse section of male thallus with spermatangia. **J.** Transverse section of cortex with a tetrasporangium. [After Reedman & Womersley 1976.]

0.7–1.3 mm in diameter, pericarp 100–300 μm and 6–12 cells thick, ostiolate. Spermatangia (Fig. 51A) in sori on either side of the diaphragms of lesser branches, cut off from chains of initials from the small cortical cells, ovoid and 3–6 μm in diameter.

Tetrasporangia (Fig. 50E) scattered in lesser branches, transformed from cortical cells and protruding inwards (Fig. 51B), 80–100 μm in diameter, tetrahedrally divided.

Type from Sandy Bay, R. Derwent Estuary, Tas. (*Lucas*, Oct. 1925); lectotype in Herb. Lucas, NSW, 136559, isolectotypes in NSW 136558 and AD, A12237.

Distribution: SE Tasmania.

Selected specimens: Bicheno, Tas., 6 m deep at Cod Rock (*Brown, McGeary & Womersley*, 5.xi.1982; AD, A55565). Browns R., Tas. (*Lucas*, Oct. 1923; NSW, 136562). Snug, Tas. (*Lucas*, Aug. 1925; NSW, 136560).

C. insignis is similar to *C. viridis* in having central as well as peripheral longitudinal filaments, but differs in the broader, compressed branches which are mostly distichously branched and have longer, slender, bases.

3. **Champia affinis** (Hooker & Harvey)J. Agardh 1876: 304. Chapman & Dromgoole 1970: 145. De Toni 1900a: 75, pl. 5 fig. 2; 1900b: 559. Guiler 1952: 94. Harvey 1855a: 545; 1859b: 307; 1863, synop.: xxvii. Kylin 1931: 28. Lucas 1929b: 50. Lucas & Perrin 1947: 206, fig. 71. May 1965: 362. Reedman & Womersley 1976: 82, figs 3, 4, 11B, 12. Reinbold 1897: 53; 1899: 45. Sonder 1881: 17. Tisdall 1898: 506. Wilson 1892: 180. Womersley 1950: 176.
Chylocladia affinis Hooker & Harvey 1847: 402. Harvey 1849: 79, pl. 29 lower.
Lomentaria affinis (Hooker & Harvey)Kützing 1849: 863; 1865: 31, pl. 86d–f. J. Agardh 1852: 730. Sonder 1853: 693.
Gastroclonium affine (Hooker & Harvey)Kützing 1849: 866.
Champia obsoleta Harvey 1859b: 307; 1863, synop.: xxvii. J. Agardh 1876: 304. De Toni 1900a: 75, pl. 5 fig. 3; 1900b: 559. Guiler 1952: 94. Kylin 1931: 28, pl. 15 fig. 35. Lucas 1929b: 50. Lucas & Perrin 1947: 206. May 1965: 362. Reinbold 1898: 46. Sonder 1881: 17. Tisdall 1898: 506. Womersley 1950: 176; 1966: 150.

FIGS 51C–J, 52A–C

Thallus (Fig. 52A) grey-red to purple, 4–15 (-40) cm high, with one to several main pyramidal fronds, axes densely and irregularly radially branched for 3–4 orders, often denuded below; axes 1–3.5 mm in diameter, laterals 0.5–1.5 mm and lesser branches 0.2–0.5 mm in diameter, all basally constricted and tapering to rounded apices, terete to slightly compressed; diaphragms distinct in lesser branches, obscured in older parts, (0.5-) 1–1.5 (-2) mm apart, branches constricted at diaphragms except when old. Holdfast discoid, 1–4 mm across, becoming stoloniferous; epilithic or on *Amphibolis* (rarely *Posidonia*). *Structure* multiaxial with a ring of initials, developing a cortex (Fig. 51C) of large inner cells (20-) 25–40 (-60) μm across, cutting off small outer cells which become continuous on older parts and 2–4 cells thick (Fig. 51F) near the thallus base; longitudinal filaments peripheral only (Fig. 51D), usually with two complete cells (each with a secretory cell) and two part cells between the diaphragms(Fig. 51E); diaphragms monostromatic. Rhodoplasts discoid, in chains or ribbon like in inner cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches (Fig. 51G) 4-celled, borne on inner cortical supporting cells together with a 2-celled auxiliary cell branch. Carposporophyte erect, with a basal fusion cell and branched gonimoblast filaments (Fig. 51H) with terminal ovoid to angular carposporangia 30–55 μm in diameter. Cystocarps (Fig. 52B) scattered, external, subspherical to urceolate and basally constricted, 0.7–1.3 mm in diameter; pericarp (40-) 90–180 μm and (4-) 6–10 cells thick, inner cells stellate (Fig. 51H) and separating, ostiolate. Spermatangia in sori (Fig. 52C), spreading from near the diaphragms, cut off from chains of initials (Fig. 51I) on outer cortical cells, ovoid, 3–5 μm in diameter.

Tetrasporangia (Fig. 51J) scattered, transformed from inner cortical cells, 60–80 μm in diameter, tetrahedrally divided.

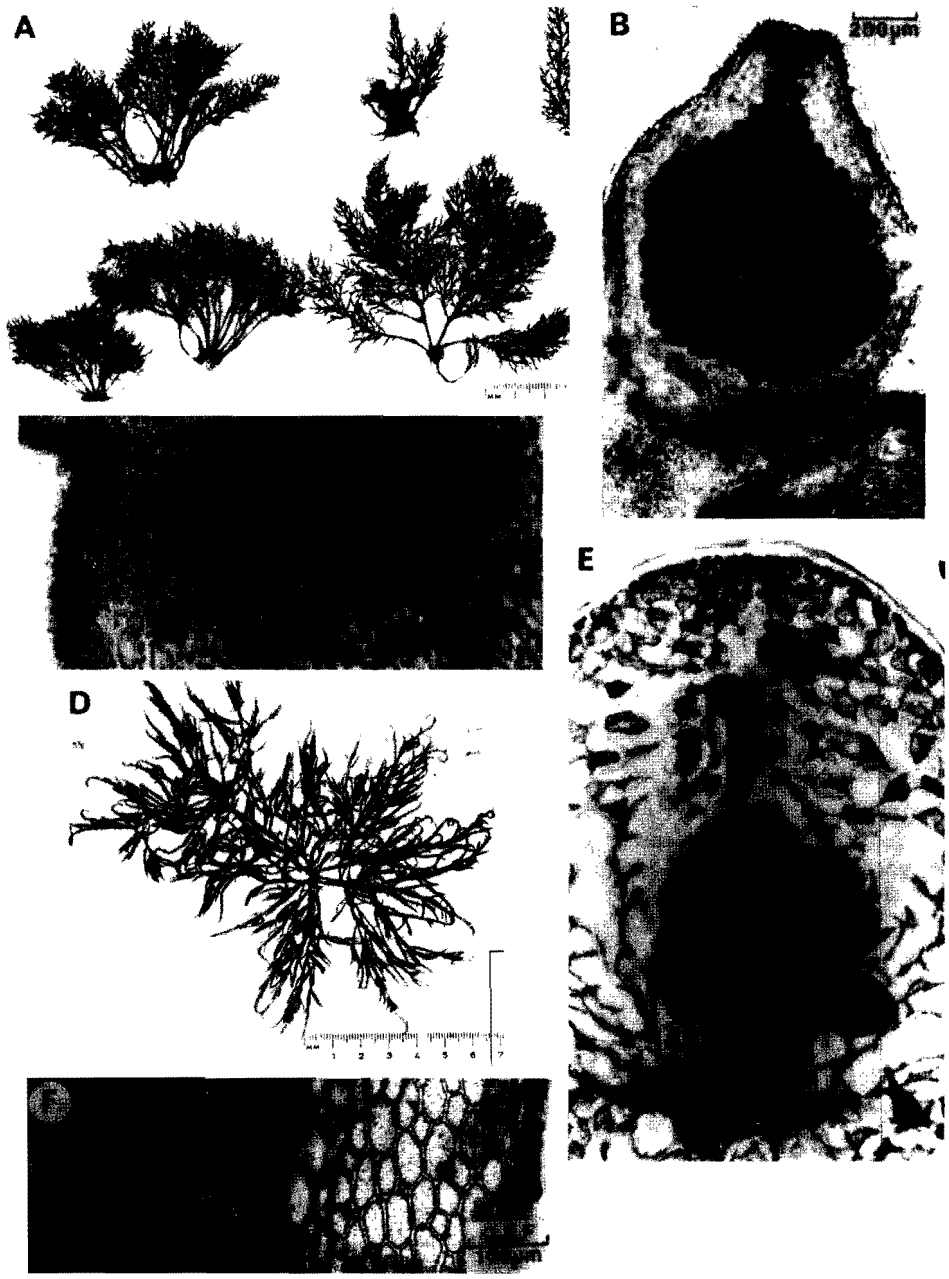


Fig. 52. A–C. *Champia affinis*. (**A**, AD, A42993; **B**, AD, A42990; **C**, AD, A42997). **A.** Habit. **B.** Mature cystocarp. **C.** Surface view of thallus with spermatangial sorus. **D–F.** *Champia zostericola* (AD, A46646). **D.** Habit. **E.** Section of cystocarp. **F.** Surface view of thallus with a spermatangial sorus.

Type from Georgetown, Tas. (*Gunn*); lectotype (Reedman & Womersley 1976, p. 84) in BM.

Distribution: Rottnest I., (*Harvey*), W. Aust., to Western Port, Vic., and around Tasmania. New Zealand.

Selected specimens: Point Sinclair, S. Aust., reef surface (*Womersley*, 26.i.1951; AD, A15213). Streaky Bay, S. Aust., reef pools (*Parsons*, 25.viii.1967; AD, A31930). Wanna, S. Aust., low eulittoral pools (*Womersley*, 21.viii.1967; AD, A31810). Petrel Cove, Victor Harbor, S. Aust., on *Sargassum* leaves, low tide level (*G. & C. Kraft*, 13.xii.1970; AD, A46026). Pennington Bay, Kangaroo I., S. Aust., on reef (*Reedman*, 13.iv.1973; AD, A42997). Muston, Kangaroo I., S. Aust., upper sublittoral (*Womersley*, 27.viii.1950; AD, A15380). Antechamber Bay, Kangaroo I., S. Aust., drift on *Heterozostera* (*Womersley*, 18.viii.1948; AD, A8660). Robe, S. Aust., reef surface (*Womersley*, 5.x.1970; AD, A37319 —"Marine Algae of southern Australia" No. 160). Cape Lannes, S. Aust., on rock platform (*Reedman*, 10.ii.1973; AD, A42990, A42993). Nora Creina, S. Aust., low intertidal (*Reedman*, 12.ii.1973; AD, A42994). Bridgewater Bay, Vic., lower eulittoral (*Beauglehole*, 26.xii.1950; AD, A15639). Apollo Bay, Vic., on pipeline 0–0.5 m deep (*Owen*, 1.ix.1971; AD, A39509). Point Lonsdale, Vic., in pools (*Sinkora* A930, 8.xi.1970; AD, A62613). Flinders, Vic., drift (*Womersley*, 25.x.1986; AD, A57837). Pilot Station, Low Head, Tas., drift (*Womersley*, 23.x.1986; AD, A57779). Bluestone Bay, Freycinet Pen., Tas., 10–12 m deep (*Brown, McGeary & Womersley*, 4.xi.1982; AD, A53979). Lady Bay, Southport, Tas., 3–5 m deep (*Brown & Womersley*, 28.x.1982; AD, A56525).

The synonymy of *C. affinis* has been discussed by Reedman & Womersley (1976, p. 84). It usually occurs commonly on the surface or in pools on rough-water rock platforms at low tide level, occasionally in deeper water or in relatively calm-water situations.

4. **Champia zostericola** (Harvey)Reedman & Womersley 1976: 87, figs 5, 6, 12C, 13. Huisman & Walker 1990: 415. Millar & Kraft 1993: 30.
Lomentaria zostericola Harvey 1855a: 545; 1863, synop.: xxvi. J. Agardh 1876: 632.
Gastroclonium ?zostericolum (Harvey)De Toni 1900b: 567.
Chylocladia zostericola (Harvey)Kylin 1931: 30. May 1965: 362.
Chylocladia affinis var. *arcuata* Hooker & Harvey 1847: 402.
Champia affinis var. *arcuata* (Hooker & Harvey)Womersley 1966: 150.
Lomentaria affinis sensu Kützing 1865: 31, pl. 86d–f. Sonder 1855: 523.
Champia affinis sensu King *et al.* 1971: 122. Lucas & Perrin 1947: 206, fig. 71. May 1965: 362. Womersley 1950: 176.
Champia parvula sensu Harvey 1855a: 545 (in part).

FIGS 52D–F, 53A–G

Thallus (Fig. 52D) grey-red to medium red, forming irregular spreading clumps 6–20 cm high, with one to several erect axes or main branches from an entangled base. Branching irregularly radial, main branches terete, 1.5–3 (-5) mm in diameter, laterals only slightly slenderer, branchlets 0.5–2 mm in diameter, slightly basally constricted, apices rounded, young and mid branches constricted at diaphragms (which are distinct throughout), less so in oldest parts; mature plants with some to many branches ending in recurved tips. Holdfasts small, discoid, or as multicellular pads; epiphytic on seagrasses (*Posidonia, Heterozostera* and *Amphibolis*) or epilithic(?). *Structure* multiaxial with peripheral initials (Fig. 53A, B), developing a single-layered cortex of relatively large angular cells 40–60 (-75) µm across and mostly (1.5-) 2–4 times as long as broad, arranged more or less in longitudinal rows (Fig. 53D) with most cutting off a small corner cell when young and further such cells when older, but maintaining an essentially single-layered cortex; longitudinal filaments peripheral only (rarely with odd ones more centrally), with one complete cell (with a secretory cell) and two half cells between the monostromatic diaphragms (Fig. 53C). Rhodoplasts discoid, in chains or ribbon like in older cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches (Fig. 53E) 4-celled, borne on a cortical cell together with a 2-celled auxiliary cell branch. Carposporophyte (Fig. 53F) erect, with a basal fusion cell, branched ovoid-celled gonimoblast filaments and terminal ovoid to obconical carposporangia 20–40 µm in diameter; basal nutritive tissue slight, erect filaments of stellate cells. Cystocarps (Fig. 52E) scattered, subspherical to slightly conical, 0.7–1 mm in diameter; pericarp 90–160 µm and 2–4 cells thick, inner cells

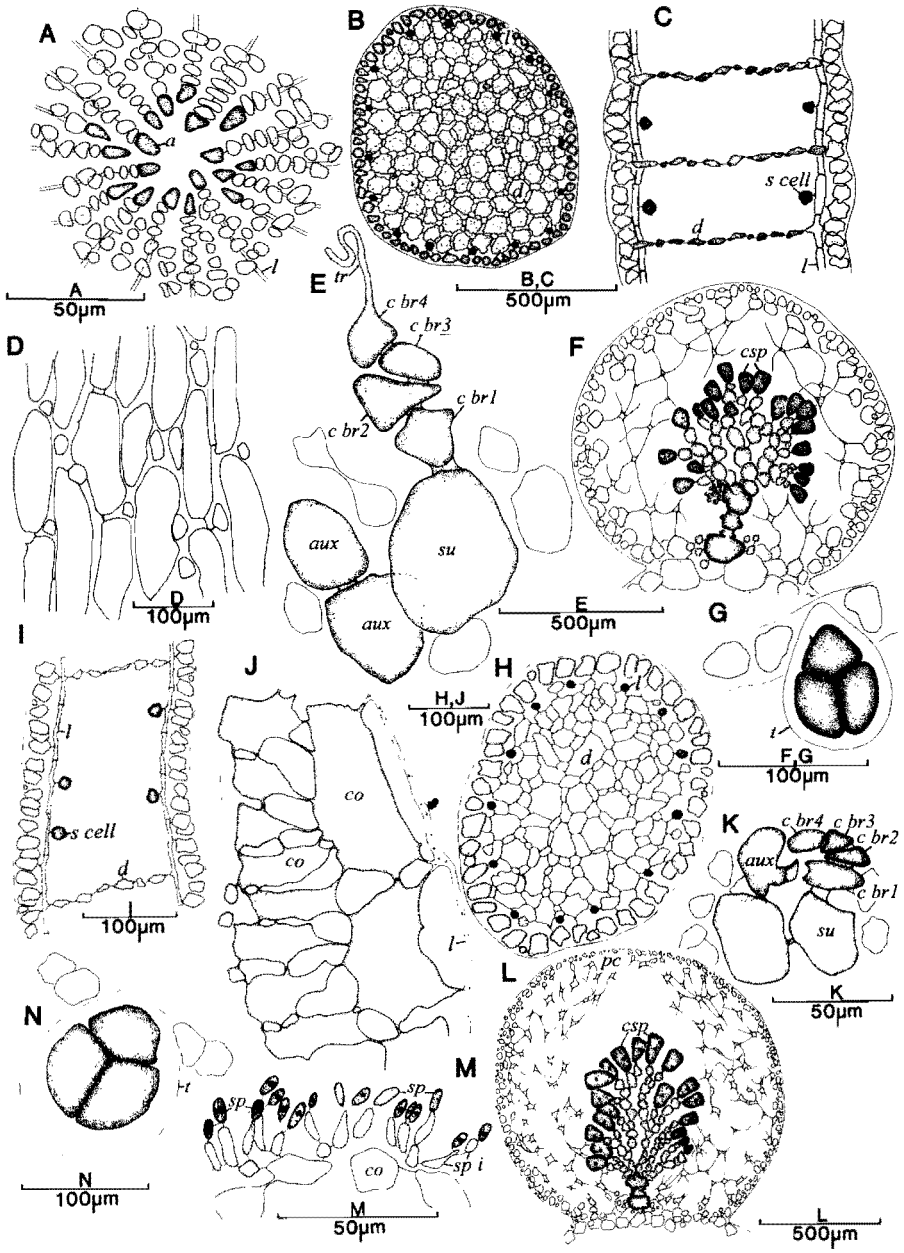


Fig. 53. A–G. *Champia zostericola*. (**A–C, E, F,** AD, A43556; **D,** AD, A46646; **G,** AD, A34256). **A.** Surface view of branch apex with ring of apical cells. **B.** Cross section of a branch with diaphragm and peripheral longitudinal filaments. **C.** Longitudinal section of branch showing cortex, diaphragms and longitudinal filaments with secretory cells. **D.** Surface view of cortical cells. **E.** Supporting cell with 4-celled carpogonial branch and 2-celled auxiliary cell branch. **F.** Young cystocarp and carposporophyte. **G.** A mature tetrasporangium. **H–N.** *Champia parvula* var. *amphibolis*. (**H, I, M,** AD, A41276; **J, N,** AD, A37291; **K, L,** AD, A38255). **H.** Transverse section of branch showing diaphragm, cortex and peripheral longitudinal filaments. **I.** Longitudinal section of branch with single-layered cortex, longitudinal filaments with secretory cells and diaphragms. **J.** Longitudinal section of older axis with a two (-3) layered cortex. **K.** Post-fertilization stage with union between auxiliary cell and carpogonial branch cell. **L.** Cystocarp with young carposporophyte. **M.** Section of male thallus with spermatangia. **N.** Mature tetrasporangium in cortex. [After Reedman & Womersley 1976.]

stellate and separating, ostiolate. Spermatangia in sori (Fig. 52F), often collar like, on smaller branches, cut off from chains of initials derived from the cortical cells, elongate, 2–4 μm in diameter.

Tetrasporangia (Fig. 53G) scattered, transformed form cortical cells, 60–100 μm in diameter, tetrahedrally divided.

Type from Rottnest I., W. Aust. (*Harvey*, Trav. Set 195); lectotype (Reedman & Womersley 1976, p. 87) in Herb. Harvey, TCD.

Distribution: Houtman Abrolhos, W. Aust., to Port Stephens, N.S.W. (*Millar & Kraft* 1993, p. 30), and around Tasmania.

Selected specimens: Coronation Group, Abrolhos Is, W. Aust. (*Sammy*, 24.viii.1970; AD, A43835). Point Peron, W. Aust., drift (*Gordon*, 15.xi.1968; AD, A34256). Egg I., Isles of St Francis, S. Aust., 32–38 m deep (*Shepherd*, 11.i.1971; AD, A38048). Waldegrave I., S. Aust., 22 m deep (*Shepherd*, 23.x.1970; AD, A37408). Off Crag Point, N Spencer Gulf, S. Aust., 15 m deep (*Shepherd*, 6.xi.1974; AD, A46046). Marino, S. Aust., drift (*Womersley*, 26.x.1975; AD, A46646 —"Marine Algae of southern Australia" No. 174). Port Noarlunga, S. Aust., 7 m deep on pylons (*Kraft*, 15.iii.1973; AD, A43556). Vivonne Bay, Kangaroo I., S. Aust., 0–5 m deep (*Kraft & Min-Thein*, 4.xii.1971; AD, A41404). American R., Kangaroo I., S. Aust., drift at jetty (*Womersley*, 25.viii.1963; AD, A26766). Robe, S. Aust., 8 m deep (*P. Womersley*, 24.viii.1973; AD, A43967). Point Roadknight, Vic., drift (*Sinkora* A1406, 29.xi.1971; AD, A43196). Point Lonsdale, Vic., drift (*Sinkora* A1175, 8.xi.1970; AD, A62612). Flinders, Western Port, Vic., drift (*Sinkora* A1727, 16.xi.1972; AD, A53436). Walkerville, Vic., drift (*Sinkora* A2653, 23.xi.1979; AD, A61052). Low Head, Tas. (*Perrin*, Feb. 1940; AD, A8944). Lady Bay, Southport, Tas., 3–5 m deep (*Brown & Womersley*, 28.x.1982; AD, A56522).

C. zostericola is a common species in regions of moderate water movement, usually epiphytic on *Amphibolis, Posidonia* and *Heterozostera*, from shaded shallow areas to 40 m deep. The synonymy was discussed by Reedman & Womersley (1976, p. 87).

5. **Champia parvula** (C. Agardh)Harvey 1853: 76; 1863, synop.: xxvii. J. Agardh 1876: 303. De Toni 1900b: 558. L. Irvine & Guiry 1983: 78, fig. 23A, B. Millar 1990: 371, fig. 29G, H. Reedman & Womersley 1976: 89.
Chondria parvula C. Agardh 1824: 207.

Thallus red to red-brown, erect and spreading, 2–11 cm high, much branched with one to several axes irregularly radially branched for 3 or 4 orders. Axes and branches terete, 1–1.5 mm in diameter below, tapering gradually to branchlets 0.3–0.5 mm in diameter, young branches slightly constricted at diaphragms, segments L/D 1–1.5, ends straight, apices rounded; diaphragms distinct throughout most of thallus, obscured near older bases. Holdfast small, discoid, with occasional haustorial pads; epilithic or epiphytic on *Amphibolis*. *Structure* multiaxial, with 10–15 apical cells, developing a cortex of angular cells mostly 20–50 (-60) μm across and mostly L/B (1-) 2–3, with small cells cut off from their corners and forming a more prominent outer cortex (up to 2–3 cells thick) on older axes; longitudinal filaments peripheral only, usually with two (-3) complete cells (with secretory cells) and two part cells between the diaphragms. Rhodoplasts discoid, usually in chains.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 4-celled, borne on a cortical (supporting) cell together with a 2-celled auxiliary cell branch. Carposporophyte with a basal fusion cell, branched gonimoblast filaments of ovoid cells and terminal, ovoid to obconical, carposporangia (40-) 50–90 μm in diameter. Basal nutritive tissue slight, inner cells of pericarp stellate and separating. Cystocarps scattered, subspherical to urceolate, 0.7–1.3 mm in diameter, pericarp 60–130 μm and 3–5 cells thick, ostiolate. Spermatangia covering segments near apices of young branches, cut off from branched filaments of initials, ovoid, 3–5 μm in diameter.

Tetrasporangia scattered, transformed from cortical cells, (50-) 60–120 μm in diameter, tetrahedrally divided.

Type from Cadiz, Spain; lectotype (Irvine & Guiry 1983, p. 78) in Herb. Agardh, LD, 26022.

Distribution: Widely reported from most temperate waters, but many records need verification.

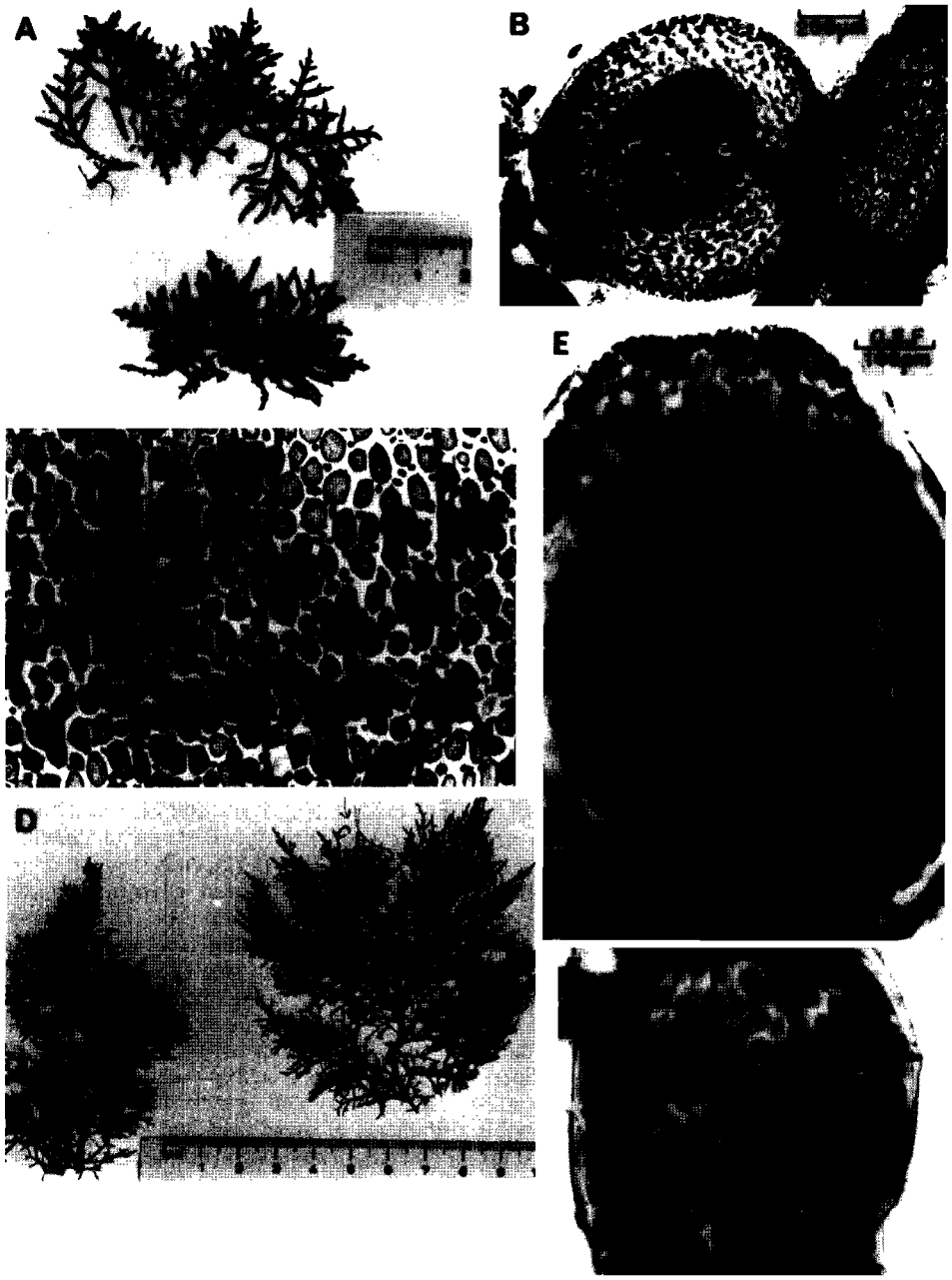


Fig. 54. A–C. *Champia parvula* var. *parvula*. (AD, A48966). **A.** Habit. **B.** Cystocarp. **C.** Tetrasporangia and surface cell pattern. **D–F.** *Champia parvula* var. *amphibolis* (AD, A38255). **D.** Habit. **E.** Cystocarp with mature carposporangia. **F.** Segment with longitudinal filaments and tetrasporangia.

KEY TO VARIETIES OF *CHAMPIA PARVULA*

1. Thallus 2–4 cm high; epilithic..... 5a. *Champia parvula* var. *parvula*
1. Thallus 3–11 cm high, densely radially branched, epiphytic on *Amphibolis* ..... 5b. *Champia parvula* var. *amphibolis*

5a. **Champia parvula** var. **parvula**

FIG. 54A–C

Thallus (Fig. 54A) red-brown, 2–4 cm high, spreading, moderately branched irregularly radially to subopposite, main branches 1–1.5 mm in diameter, branchlets 0.5–1 mm in diameter. Holdfast discoid; epilithic. *Structure* multiaxial, with 10–15 apical cells, developing a cortex of angular cells (15-) 20–50 (-60) µm across and L/B (1-) 1.5–2 (-3), with small cells cut off from their corners, sparse on younger branches, more frequent on older axes; longitudinal filaments peripheral only, usually with two (-3) complete cells (with secretory cells) and two part cells between the diaphragms; hairs common. Rhodoplasts discoid, usually in chains.

Reproduction. Gametangial thalli dioecious. Carposporophyte with a basal fusion cell, branched gonimoblast filaments of ovoid cells and terminal ovoid to obconical, carposporangia (40-) 50–90 µm in diameter. Basal nutritive tissue slight, inner cells of pericarp stellate and separating. Cystocarps (Fig. 54B) scattered, subspherical to urceolate, 0.7–1.0 (-1.3) mm in diameter, pericarp 60–130 µm and 3–5 cells thick, ostiolate. Spermatangia covering segments near apices of young branches, cut off from branched filaments of initials, ovoid, 3–5 µm in diameter.

Tetrasporangia (Fig. 54C) scattered, transformed from cortical cells, (50-) 60–120 µm in diameter, tetrahedrally divided.

Type from Cadiz, Spain; lectotype in Herb. Agardh, LD, 26022.

Distribution: Widely reported from most temperate waters, but many records need verification. Reedman & Womersley (1976, p. 91) listed several dubious references to the species in southern Australia, and it has recently been recorded from N.S.W. by Millar & Kraft (1993, p. 29). However one collection appears to agree with the type variety.

Selected specimen: Muston, American R. inlet, Kangaroo I., S. Aust., 3–4 m deep (*Shepherd*, 29.xii.1977; AD, A48966).

The above description is based on the Muston specimen.

5b. **Champia parvula** var. **amphibolis** Reedman & Womersley 1976: 91, figs 7, 14A.

FIGS 53H–N, 54D–F

Thallus (Fig. 54D) red to red-brown, erect and spreading, 3–11 cm high, much branched with one to several axes irregularly radially branched for 3 or 4 orders. Axes and branches terete, 1–1.5 mm in diameter below, tapering gradually to branchlets 0.3–0.5 mm in diameter, young branches slightly constricted at diaphragms, segments L/D 1–1.5, ends straight, apices rounded; diaphragms distinct throughout most of thallus, obscured near older bases. Holdfast small, discoid, with occasional haustorial pads; epiphytic on *Amphibolis*. *Structure* multiaxial, with 10–15 apical cells, developing a cortex of angular cells 25–50 (-60) µm across and mostly L/B (1.5-) 2–3, with small cells cut off from their corners and forming a continuous outer cortex (to 3 cells thick) on older axes (Fig. 53J); longitudinal filaments (Fig. 53H) peripheral only, usually with two (-3) complete cells (with secretory cells) and two part cells between the diaphragms (Fig. 53I). Rhodoplasts discoid, usually in chains.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 4-celled, borne on a cortical (supporting) cell together with a 2-celled auxiliary cell branch (Fig. 53K). Carposporophyte (Fig. 53L) with a basal fusion cell, branched gonimoblast filaments of ovoid cells and terminal ovoid to obconical carposporangia (40-) 50–90 µm in diameter. Basal nutritive tissue slight, inner cells of pericarp stellate and separating. Cystocarps (Fig. 54E) scattered, subspherical to urceolate, 0.7–1.0 (-1.2) mm in diameter, pericarp 60–130

μm and 3–5 cells thick, ostiolate. Spermatangia covering segments near apices of young branches, cut off from branched filaments of initials (Fig. 53M), ovoid, 3–5 μm in diameter.

Tetrasporangia (Fig. 54F) scattered, transformed from cortical cells, (50-) 60–120 μm in diameter, tetrahedrally divided (Fig. 53N).

Type (of variety) from Tiparra Reef, Spencer Gulf, S. Aust., 11 m deep (*Shepherd*, 23.xii.1970); holotype in AD, A38255.

Distribution: The var. *amphibolis* only known from Tiparra Reef, S. Aust.

Selected specimens: The type and Tiparra Reef, S. Aust., 5 m deep (*Shepherd*, 30.ix.1970; AD, A37291) and 11 m deep (*Shepherd*, 13.xii.1971; AD, A41276).

The Tiparra Reef plants were considered distinct as a variety by Reedman & Womersley, characterised by dense radial branching, size and being epiphytic on *Amphibolis*.

Genus CHYLOCLADIA Greville *in* Hooker 1833: 256, 297, *nom. cons.*

Thallus erect, much branched, branches terete, with regular hollow segments throughout with transverse monostromatic diaphragms, slightly constricted at diaphragms; holdfast discoid, with or without a perennial base to the axes. *Structure* multiaxial, with peripheral and often central longitudinal filaments bearing secretory cells, developing outwardly in young parts a single layered cortex which becomes multilayered in older branches, and inwardly the monostromatic diaphragms.

Life history triphasic, with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious; procarpic. Carpogonial branches on cortical (supporting) cells, 4-celled, with two 2-celled auxiliary cell branches; carposporophytes with a basal fusion cell bearing large, wedge-shaped carposporangia directly. Basal nutritive tissue absent or slight. Cystocarps external, pericarp a few cells thick, inner cells stellate and separating, non-ostiolate. Spermatangia in superficial sori, cut off from outer cortical cells via initials.

Tetrasporangia large, scattered, transformed from primary cortical cells, tetrahedrally divided.

Type species: *C. kaliformis* (Goodenough & Woodward)Greville [= *C. verticillata* (Lightfoot)Bliding 1928: 69].

A genus of about 10 species, with one species on southern Australian coasts.

Chylocladia grandis Reedman & Womersley 1976: 94, figs 8, 9, 14B.

FIGS 55, 56A, B

Thallus (Fig. 56A) red-brown to red-purple, 20–50 cm high, with one to several percurrent terete axes 2–7 mm in diameter, often denuded below, from a hard, branched, perennial base to 5 cm high and 3–7 mm thick, bearing opposite or usually whorled laterals to 10 cm long, similarly branched to a second or third order; laterals 1.5–2.5 mm in diameter, tapering to 0.7–1 mm in diameter in branchlets; branch bases slightly constricted, apices rounded; segments conspicuous throughout, L/D 0.5–1.5, slightly constricted at diaphragms. Holdfast discoid, 0.5–1.5 cm across; epilithic. *Structure* multiaxial with a group of 12–16 central and 15–20 peripheral apical cells (Fig. 55A), developing a cortex one cell thick in branchlets, cells ovoid and 25–35 (-40) μm in diameter, becoming up to 8 cells thick (Fig. 55D) in older axes; longitudinal filaments scattered throughout diaphragms (Fig. 55B), usually with two complete cells and two part cells between diaphragms, with each peripheral filament cell connected to the cortical cells by a lateral filament (Fig. 55C); most such cells bearing a secretory cell; hairs prominent. Diaphragms monostromatic. Rhodoplasts discoid to ribbon like, in chains in older cells.

Reproduction. Gametangial thalli probably dioecious. Carpogonial branches (Fig. 55E) 4-celled, with two 2-celled auxiliary cell branches, borne on primary cortical (supporting) cells in pit-connection with a peripheral longitudinal filament. Carposporophyte (Fig. 55F)

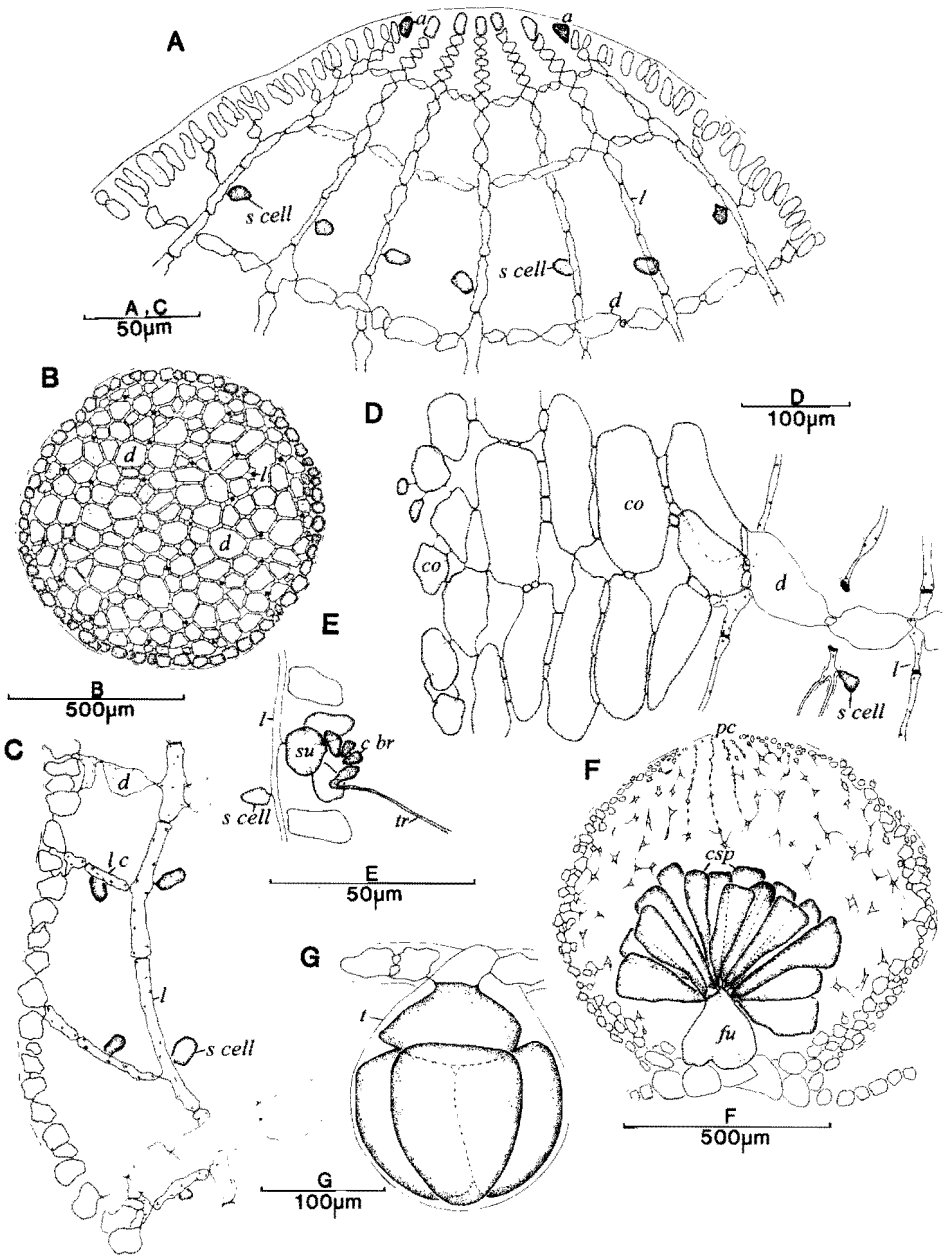


Fig. 55. *Chylocladia grandis* (**A–F**, AD, A33515; **G**, AD, A39197). **A.** Longitudinal section of branch apex showing development of cortex, diaphragms and longitudinal filaments with secretory cells. **B.** Transverse section of branch at a diaphragm, with peripheral and central longitudinal filaments. **C.** Longitudinal section of outer part of a mature branch showing a longitudinal filament with connections to cortex and secretory cells. **D.** Longitudinal section of old axis with a multi-layered cortex. **E.** Supporting cell with carpogonial branch and auxiliary initial cells. **F.** Young cystocarp with carposporangia formed directly from the fusion cell. **G.** Mature tetrasporangium in the cortex. [After Reedman & Womersley 1976.]

with a basal fusion cell producing directly clavate to obconical carposporangia 130–200 μm in diameter; basal nutritive tissue moderate, with numerous slender erect filaments, outer cells stellate. Cystocarps (Fig. 56B) scattered, subspherical to slightly ovoid, 0.7–1 (-1.3) mm in diameter, broad based; pericarp 40–90 μm and 3–6 cells thick, inner cells stellate; non-ostiolate. Spermatangia not observed.

Tetrasporangia (Fig. 55G) scattered, transformed from primary cortical cells and protruding inwardly, 150–200 (-250) μm in diameter, tetrahedrally divided.

Type from Tapley Shoal, Edithburg, S. Aust., 15 m deep (*Shepherd*, 2.ii.1969); holotype in AD, A33515, with isotypes.

Distribution: Tapley Shoal and Investigator Strait, S. Aust.

Selected specimens: Known from the type and Investigator Strait, S. Aust., 34 m, 23 m and 11 m deep (*Watson*, 20.i.1971; AD, A39197, 28.i.1971; AD, A41010, and 20.i.1971; AD, A40995 resp.). Ironstone Point (E of Penneshaw), Kangaroo I., S. Aust., 15 m deep (*Lavers*, 27.xi.1995; AD, A64550).

This distinctive species appears to be rare and from deep water.

FAMILY LOMENTARIACEAE J. Agardh 1876: 606, 630, *nom. cons.*

Thallus erect or decumbent, much branched radially or distichously, branches terete to compressed, hollow and usually irregularly segmented by multilayered partitions or plugs without distinct longitudinal filaments in the medulla; monostromatic septa absent. *Structure* multiaxial, with a group of apical cells producing a cortex 3–6 cells thick and a medulla consisting of a network of filaments bearing secretory cells.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious; procarpic. Carpogonial branches 3-celled, borne on inner cortical cells together with one or two 2-celled auxiliary cell branches. Carposporophytes with or without basal nutritive tissue, with a basal fusion cell and most gonimoblast cells forming carposporangia, surrounded by stellate cells of the inner pericarp. Cystocarps protuberant, sessile, pericarp ostiolate. Spermatangia in surface sori, cut off from initials on the outer cortex.

Tetrasporangia in small, depressed, sori, terminal on cortical cells, tetrahedrally divided.

A family of five genera, now usually separated from the Champiaceae by multilayered partitions separating the segments, irregular medullary filaments rather than discrete longitudinal ones, carposporophytes with most cells forming carposporangia, and tetrasporangia in small, depressed sori, cut off (rather than transformed) from outer cortical cells.

KEY TO GENERA OF LOMENTARIACEAE

1. Cystocarps protuberant, with a well-developed pericarp 3–6 cells thick derived from the outer cortex ..... LOMENTARIA
1. Cystocarps immersed, surrounded by a filamentous involucre derived from inner cortical cells ..... SEMNOCARPA

Genus LOMENTARIA Lyngbye 1819: 101

Thallus erect or forming entangled clumps, much branched, with or without percurrent axes, branches terete or compressed, hollow, basally constricted with solid septa; holdfast discoid or hapteroid. *Structure* multiaxial, with a cluster of apical cells developing an inner cortex 2–3 cells thick and an outer cortex of small cells sometimes forming rosettes, and a medulla of a network of interconnected filaments bearing secretory cells; basal branch septa pseudoparenchymatous.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 3-celled, borne on inner cortical (supporting) cells together with a 2-celled auxiliary cell branch. Carposporophyte with a relatively massive, erect, fusion cell producing slender gonimoblast filaments and clusters of cells, all becoming carposporangia; basal nutritive tissue present, erect filaments disintegrating. Cystocarps external, globular to urceolate, pericarp 3–6 cells thick, ostiolate. Spermatangia cut off via initials on outer cortical cells.

Tetrasporangia in depressed sori, cut off thallus inwardly from small cells lining the depression, tetrahedrally divided.

Holotype species: *L. articulata* (Hudson)Lyngbye 1819: 101.

A genus of about 40 species, with three species known from southern Australia, characterised by thallus structure, external cystocarps and depressed tetrasporangial sori.

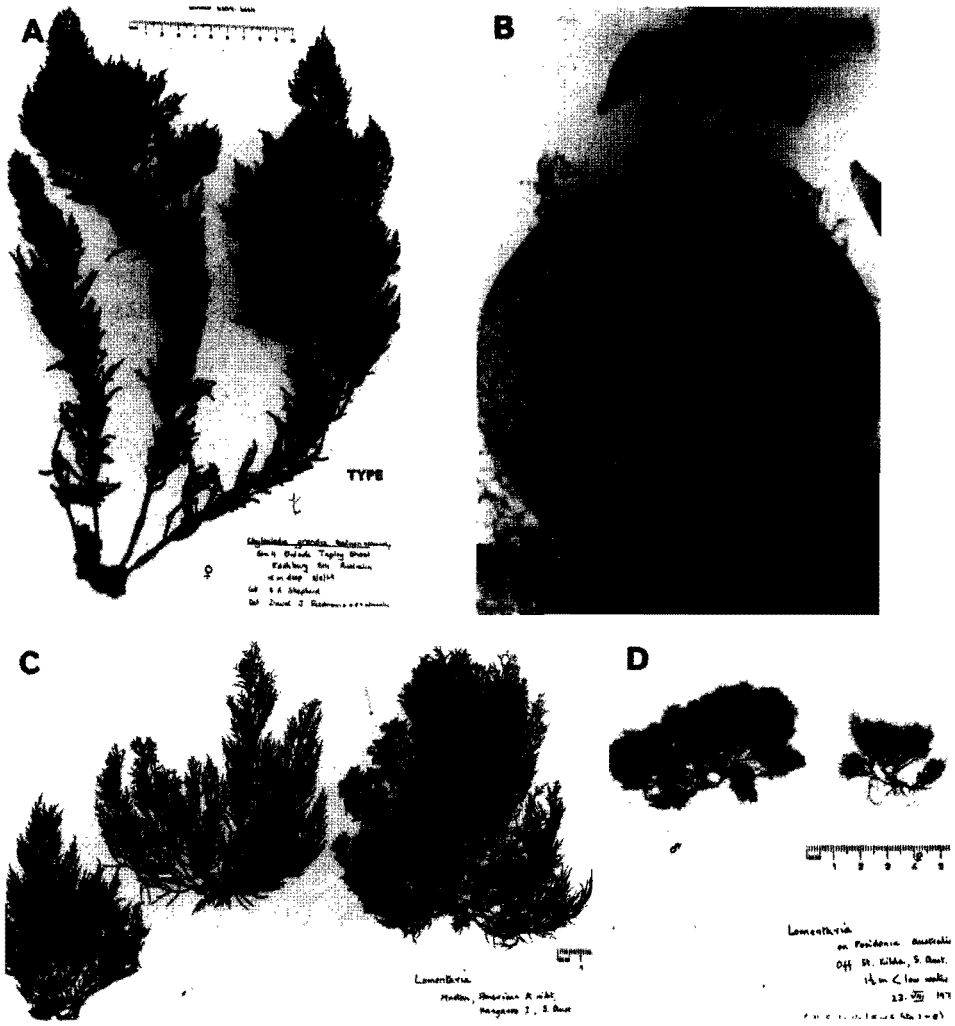


Fig. 56. A, B. *Chylocladia grandis* (AD, A33515). **A.** Habit. **B.** Cystocarp with mature carposporangia and slight basal nutritive tissue with slender erect filaments of stellate cells. **C, D.** *Lomentaria australis* (**C**, AD, A48959; **D**, AD, A42714). **C.** Habit of medium size plants. **D.** Habit of small plants.

KEY TO SPECIES OF *LOMENTARIA*

1. Branching irregularly radial, branches terete except for larger ones which may be slightly compressed; inner cortical cells mostly L/B 1.5–2.5, with outer cells forming distinct rosettes ..... 1. *L. australis*
1. Erect branches compressed, simple or pinnate and largely distichous, inner cortical cells of younger branches more or less isodiametric, outer cells few, scarcely forming rosettes 2
    2. Erect fronds pinnate, 2–20 (-45) cm high, axes (2-) 3–4 (-5) mm broad ..... 2. *L. pyramidalis*
    2. Erect fronds simple, 0.5–2 mm broad, arising from entangled stolons in clumps 2–5 cm high ..... 3. *L. monochlamydea*

1. **Lomentaria australis** (Kützing)Levring 1946: 223. Chapman & Dromgoole 1970: 141. May 1965: 361. Womersley 1950: 176.
Chondrothamnion australe Kützing 1865: 29, pl. 82d–f.
Chrysymenia clavellosa sensu Harvey 1849a: 77.
Chylocladia clavellosa sensu De Toni 1900b: 573. Guiler 1952: 95.Harvey 1859b: 327. Lucas 1929a: 19. Sonder 1881: 17. Tisdall 1898: 506. Wilson 1892: 180.
Lomentaria fruticulosa Reinbold 1899: 46.
Chylocladia fruticulosa (Reinbold)De Toni 1900b: 576. Lucas & Perrin 1947: 208. May 1965: 362.

FIGS 56C, D, 57

Thallus (Fig. 56C, D) light to dark grey-red to red-brown, mucilaginous, 5–20 cm high, usually forming spreading tufts, much branched irregularly radially for 3–4 orders, with or without percurrent axes. Branches terete, becoming compressed in larger branches, hollow, basally constricted and tapering to a subacute to rounded apex, main branches 1–2 mm in diameter, decreasing to branchlets 200–500 µm in diameter. Holdfast discoid, 1–2 mm across, sometimes stoloniferous, bearing one to several fronds; epilithic or epiphytic on *Posidonia, Amphibolis* or larger algae. *Structure* multiaxial with a cluster of apical cells producing longitudinal filaments which branch and interconnect to form a lax medullary network on the inside of the cortex, filaments 5–12 (-15) µm in diameter, producing directly small, ovoid to subspherical, secretory cells 6–12 (-18) µm in diameter; in older segments, the medulla becomes 3–5 filaments thick, moderately dense near the thallus base. Cortex cut off outwardly from the subapical cells, at first as odd cells, becoming 2 cells thick above and 3–6 cells thick below, with a continuous inner cortex of larger, ovoid to elongate cells mostly L/B 1.5–2.5 and 20–60 µm in diameter, and an outer cortex of smaller cells cut off around the inner cells, subdividing below to form rosettes (Fig. 57A) 2–3 cells broad and 2 cells thick, outer cells 2–5 µm in diameter; on older parts the outer cortex becomes continuous. Branch constrictions solid (Fig. 57B), pseudoparenchymatous, with filaments growing into the branch cavity. Hairs frequent. Rhodoplasts ovoid to elongate, irregularly shaped in inner cells, often in chains.

Reproduction. Gametangial thalli dioecious. Carpogonial branches unknown. Carposporophyte (Fig. 57C) erect, with a basal fusion cell, branched above with several appressed lobes of ovoid or clavate to cuneate carposporangia each (25-) 40–60 µm broad; basal nutritive tissue present, erect cells becoming stellate and disintegrating. Cystocarps external, scattered and often borne near branch bases, globular to urceolate and slightly basally constricted, 300–800 µm in diameter, ostiolate, pericarp 40–80 µm and 3–5 cells thick (more around ostiole), inner cells stellate. Spermatangial initials produced from cells of outer cortical rosettes (Fig. 57D), spermatangia ovoid, 2–3 µm in diameter.

Tetrasporangia in scattered, round to elongate, depressed, sori (Fig. 57E) 80–500 µm across, cut off thallus inwardly (Fig. 57F) from small cells lining the depression, few to numerous per sorus, subspherical, (35-) 40–70 µm in diameter, tetrahedrally divided.

Type from "Nova Hollandia"; holotype in Herb. Kützing, L, 940, 284 ... 259.



Fig. 57. *Lomentaria australis* (**A, C,** AD, A43784; **B, E,** AD, A39522; **D, F,** AD, A42714). **A.** Surface pattern of rosettes of outer cortical cells. **B.** Longitudinal section through a constriction. **C.** Section of a cystocarp showing basal nutritive tissue, fusion cell and carposporangia. **D.** Surface view of spermatangial sorus. **E.** Branch with tetrasporangial sori. **F.** Section of thallus with a displaced tetrasporangial sorus.

Distribution: Elliston, S. Aust., to Port Phillip, Vic., and around Tasmania. New Zealand?

Selected specimens: Waldegrave I., S. Aust., 22 m deep (*Shepherd*, 23.x.1970; AD, A37401). Elliston, S. Aust., 4 m deep on *Codium galeatum* (*Shepherd*, 22.x.1970; AD, A37519). Outside Kellidie Bay, Coffin Bay, S. Aust., upper sublittoral (*Womersley*, 22.viii.1967; AD, A31853). Yatala Harbour, N Spencer Gulf, S. Aust., 7 m deep on *Posidonia sinuosa* (*Johnson*, Nov. 1975; AD, A54940). Off St Kilda, S. Aust., 1.5 m deep on *Posidonia australis* (*S. Lewis*, 23.viii.1972; AD, A42714) and 3–4 m deep (*Wickes*, 3.viii.1973; AD, A43784). Gypsum wharf, Ballast Head, Kangaroo I., S. Aust., 0–5 m deep (*Kraft*, 16.vii.1972; AD, A42483). Muston, American R. inlet, Kangaroo I., S. Aust., 4–5 m deep (*Shepherd*, 29.xii.1977; AD, A48959). Pennington Bay, Kangaroo I., S. Aust., drift (*Womersley*, 22.viii.1954; AD, A19764). Port MacDonnell, S. Aust., drift (*Womersley*, 15.v.1982; AD, A53166). Apollo Bay, Vic., 0–0.5 m deep on pipeline (*Kraft & Owen*, 1.ix.1971; AD, A39522). Swan Bay, Port Phillip, Vic., 0.5 m deep (*Watson*, 30.ix.1973; AD, A44128). Low Head, Tas., drift (*Perrin*, 11.ix.1937; AD, A8501). Lady Bay, Southport, Tas., 7 m deep (*Brown & Kenchington*, 14.x.1986; AD, A57690).

The type of *Lomentaria australis* is a relatively robust specimen, similar to those from Tasmania.

Lomentaria australis Areschoug mscr., referred to by Sonder 1853, p. 693 as possibly *Chylocladia tasmanica* Harvey (1844, p. 444) is a *nomen nudum*. The latter is an earlier name for *Coeloclonium opuntioides* (Harvey)J. Agardh, which is correctly known as *Coeloclonium tasmanicum* (Harvey)Womersley, *comb. nov.* [Basionym *Chylocladia tasmanica* Harvey 1844b, p. 444.]

L. australis has been credited to N.S.W. but these records are referred to *L. catenata* by Millar & Kraft (1993, p. 30). However, a slender, irregularly branched *Lomentaria* does occur on the N.S.W. coast and may well be *L. australis*.

L. fruticulosa Reinbold (1899, p. 46) is based on a collection by A.E. Davey from Sturt Bay, S. Aust. An isotype specimen in AD (A1533) is epiphytic on *Posidonia australis* and appears to be a small plant of *L. australis*.

2. **Lomentaria pyramidalis** Kraft & Womersley, *nov. sp.*

FIG. 58

Thallus (Fig. 58A) medium to dark red, mucilaginous, (2-) 5–20 (-45) cm high, more or less pinnately branched for 3–4 orders but not strictly distichous, with scattered branchlets from the face of parent branches, with percurrent axes and main branches. Larger and mid branches compressed, basally constricted and tapering to a rounded apex, main branches (2-) 3–4 (-5) mm broad and 300–500 µm thick, lesser branches 1–2 mm broad, branchlets subterete and 300–600 µm broad. Holdfast discoid, 1–3 mm across, bearing 2–5 fronds; epiphytic on *Posidonia* or *Amphibolis* (or *Acrocarpia*) or possibly epilithic. *Structure* multiaxial, with a cluster of apical cells producing filaments which interconnect to form a lax medullary network on the inside of the cortex (Fig. 58B), filaments 4–6 µm in diameter and producing ovoid secretory cells 6–8 µm in diameter; older segments with denser medullary filaments, filling the segment near the thallus base. Cortex 2–3 cells thick above, 3–5 cells thick below, the inner cortex with an outer layer of ovoid to isodiametric cells 12–30 µm across, a mid layer of more elongate cells, and an inner layer of elongate cells connected to the medullary filaments, with a sparse outer cortex of small ovoid cells, 5–10 µm in diameter, cut off around the larger cells, dividing to form very slight rosettes on older branches. Hairs common. Branch constrictions (Fig. 58C) solid, pseudoparenchymatous. Rhodoplasts discoid, in chains in most cells.

Reproduction. Gametangial thalli dioecious. Carpogonial and auxiliary cell branches not observed. Carposporophyte (Fig. 58D) erect with a massive basal fusion cell producing slender gonimoblast filaments with all upper cells forming ovoid to clavate carposporangia 15–30 µm in diameter; basal nutritive tissue present, erect filaments disintegrating. Cystocarps scattered on lesser branches or surface of compressed branches, external, often near branch bases, globular to slightly urceolate and beaked, basally constricted, 600–900 µm in diameter, ostiolate; pericarp 35–60 µm and 4–8 cells thick, inner cells stellate.

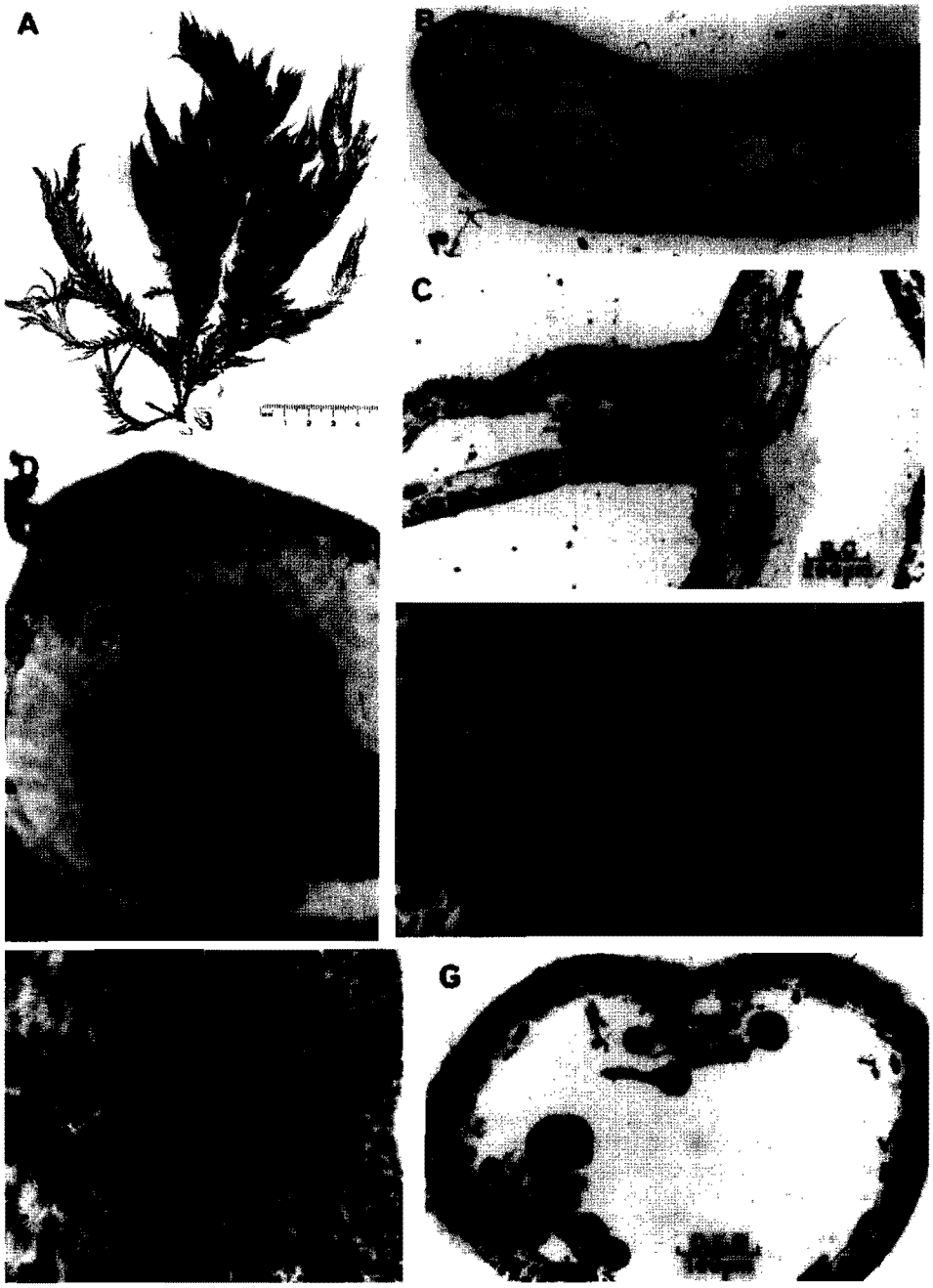


Fig. 58. *Lomentaria pyramidalis* (**A–C, E–G,** AD, A18983; **D,** AD, A29273). **A.** Habit. **B.** Transverse section of compressed branch. **C.** Longitudinal section with a constriction. **D.** Section of cystocarp showing basal fusion cell and carposporangia. **E.** Surface view of spermatangial sorus. **F.** Surface view of tetrasporangial sori. **G.** Transverse section of branch with tetrasporangial sori.

Spermatangia (Fig. 58E) cut off via initials from cells of the rosettes, ovoid, 2–3 µm in diameter.

Tetrasporangia in irregular to elongate, depressed sori (Fig. 58F) 200–500 µm across, numerous per sorus, cut off inwardly (Fig. 58G) from small cells lining the depression, subspherical, 50–75 µm in diameter, tetrahedrally divided.

Thallus erectus, pyramidalis (2-) 5–20 (-45) cm altus, 3–4-pinnatus, cum ramulis dispersis ex superficie ramorum maiorum ortis, axes percurrentes. Rami maiores compressi, basin constricti, contracti, (2-) 3–4 (-5) mm lati, 300–500 µm crassi, in ramulis subteretibus, 300–600 µm latis angustati. Haptera discoidea, 1–3 mm diametro; vel in Posidoniam vel Amphibolem vel Acrocarpiam epiphytica, vel fortasse epilithica. Structura multiaxialis, cellulis apicalibus reticulum laxum medullare filamentorum 4–6 µm diametro cum cellulis ovoideis secretoriis producentibus. Cortex insuper 2–3-cellulas crassus, 3–5-cellulas infra, cum cortice exteriore sparso cellulorum ovoidearum, parvarum circum cellulas interiores maiores, rosulas exiguas in ramis senioribus formantes. Constrictiones ramorum solidae pseudoparenchymatae.

Dioica. Rami carpogoniferi atque cellularum auxiliarium haud visi. Carposporophytum erectum, cellula coniunctionis basalis magna, omnes cellulae supernae carposporangia 15–30 µm diametro formantes; contextus basalis nutricius praesens, filamenta erecta fatiscentia. Cystocarpia in minoribus compressisve ramulis dispersa, plerumque prope bases ramorum, globosa ad urceolata et rostrata, 600–900 µm diametro, ostiolata; pericarpium 35–60 µm atque 4–8 cellulas crassum. Spermatangia per initias ex cellulis rosularum producta, ovoidea, 2–3 µm diametro. Tetrasporangia in soris irregularibus depressis 200–500 µm diametro, ex cellulis, 50–75 µm diametro, depressionem introrsum obtectis intrinsecus producta, tetraedice divisa.

Type from Port MacDonnell, S. Aust., drift (*Womersley*, 19.viii.1953); holotype and isotypes in AD, A18983).

Distribution: Point Peron, W. Aust., to Flinders, Vic.

Selected specimens: Point Peron, W. Aust., drift (*Womersley*, 18.viii.1979; AD, A51006). Marino, S. Aust., drift (*Womersley*, 26.x.1975; AD, A46642). Robe, S. Aust., drift on *Posidonia australis* (*Womersley*, 24.viii.1960; AD, A24438 and 15.v.1965; AD, A29273) and on jetty piles, 1–2 m deep (*Womersley & R. Lewis*, 14.v.1972; AD, A42199). Port MacDonnell, S. Aust., drift (*Womersley*, 18.ix.1993; AD, A63027, and *G. & R. Kraft, K9096*, 25.ix.1992; MELU and AD, A63400). Gardens Beach, Portland Bay, Vic., drift (*Beauglehole*, 11.viii.1951; AD, A21654). Queenscliff, Vic., 4–5 m deep near jetty, on *Amphibolis* (*Kraft & Saunders*, 9.ix.1993; MELU, K9591). Flinders, Vic., drift (*Womersley*, 25.x.1986; AD, A57839 and *Kraft & Hommersand*, 4.viii.1995; MELU).

L. pyramidalis is a distinctive, large, species of pyramidal form, with a single discoid holdfast and most commonly epiphytic on *Posidonia* on the SE coast of South Australia.

3. **Lomentaria monochlamydea** (J. Agardh)Kylin 1931: 27, pl. 13 fig. 30. May 1965: 361.
Chylocladia monochlamydea J. Agardh 1890: 22; 1896: 87. De Toni 1900b: 576. Tisdall 1898: 506. Wilson 1892: 180.

FIG. 59

Thallus (Fig. 59A) dark red-brown, forming entangled clumps 2–5 cm high and across, with basal stolons producing erect, mostly simple, compressed blades 0.5–2 cm high and 0.5–2 mm broad, basally constricted and tapering to a rounded apex. Stolons branched, often curved, with erect blades 1–3 (-5) mm apart, terete and 300–800 µm in diameter, attached by small haptera to the substrate or other branches; epilithic or on solid substrates. *Structure* multiaxial, with apical cells producing an interconnected network of medullary filaments 4–6 µm in diameter and bearing ovoid secretory cells 5–8 µm in diameter. Cortex (Fig. 59B) 3–4 cells thick, the inner cortex of 2–3 cells with an outer layer of ovoid or isodiametric cells 10–22 µm across, a mid layer of slightly larger cells and an inner layer of elongate cells connected to the medullary filaments and also bearing occasional secretory cells, and a sparse outer cortex of small cells, scarcely forming rosettes. Older parts and stolons hollow but cortex 4–6 cells thick. Branch constrictions (Fig. 59C) solid, pseudoparenchymatous. Rhodoplasts discoid, often in chains.

Reproduction. Gametangial thalli unknown.

Tetrasporangia in irregular, depressed, sori (Fig. 59D) 200–500 μm across, cut off inwardly from small cells lining the depression, subspherical to pyriform, 30–50 μm in diameter, tetrahedrally divided.

Type from Port Phillip Heads, Vic. (*Wilson 19*, 21.i.1886); holotype in Herb. Agardh, LD, 25818.

Distribution: Port Stanvac, S. Aust., to Port Phillip Heads, Vic., and Coffs Harbour, N.S.W. (Millar 1990, p. 375).

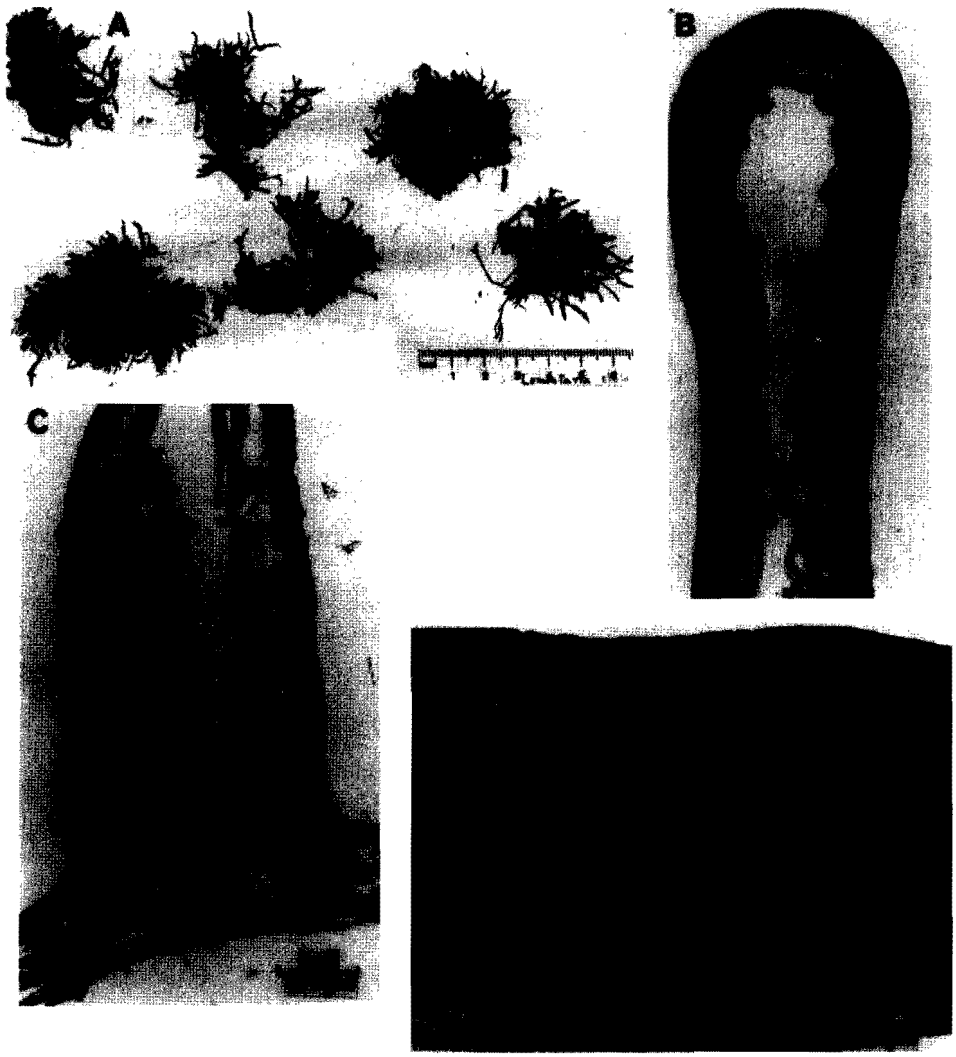


Fig. 59. *Lomentaria monochlamydea* (AD, A39524). **A.** Habit. **B.** Transverse section of thallus. **C.** Longitudinal section through a constriction. **D.** Surface view of tetrasporangial thallus.

Selected specimens: Port Stanvac, S. Aust., 3–12 m deep on jetty piles (*Clarke & Engler*, 14.iv.1979; AD, A50342). Robe, S. Aust., 3 m deep on jetty piles (*Kildea & Collings*, 26.ix.1992; AD, A62822). Apollo Bay, Vic., 0–1 m deep on pipeline in harbour (*Kraft 3719 & Owen*, 2.ix.1971; MELU and AD, A39524). Gloucester Reserve, Williamstown, Vic., 2–4 m deep (*Kraft* 9466 & *Williams*, 27.x.1992; MELU, 42062; AD, A63399).

This comparatively rare species was recorded from N.S.W. by Millar (1990, p. 375, fig. 31A–D) and Millar & Kraft (1993, p. 30). It is characterised by its stoloniferous base and small size with mainly irregular branching. Some more erect branches are subpinnate and resemble small branches of *L. pyramidalis*, but the latter has a single discoid holdfast, is a much larger species, and is usually epiphytic on *Posidonia* or *Amphibolis*.

Genus SEMNOCARPA Huisman, Foard & Kraft 1993: 145

Thallus erect, usually with percurrent axes bearing irregularly radial branches for 1–3 orders; branches terete to slightly compressed, hollow, basally constricted with solid partitions; holdfast discoid. *Structure* multiaxial, with a cluster of apical cells, developing a cortex of a single layer of larger cells and an outer cortex 1–2 cells thick of small cells and a medulla of irregular slender filaments bearing secretory cells; constrictions pseudoparenchymatous.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 3-celled, borne on inner cortical (supporting) cells together with a 2-celled auxiliary cell branch. Carposporophytes with partially fused basal cells and all gonimoblast cells forming carposporangia. Cystocarp immersed, with the carposporophyte surrounded by an involucre of erect filaments derived from inner cortical cells, and the outer cortical cells branching to surround the ostiole. Spermatangia in sori near branch apices, cut off via initials from outer cortical cells.

Tetrasporangia in depressed sori, cut off laterally from outer cortical cells, tetrahedrally divided.

Type species: *S. corynephora* (J. Agardh)Huisman, Foard & Kraft 1993: 146.

A genus of two species, the type and *S. minuta* Huisman, Foard & Kraft, both from southern Australia and south-western Western Australia.

Semnocarpa differs from *Lomentaria* in having immersed carposporophytes surrounded by an involucre of erect filaments, compared to the protruding cystocarps with a cortical pericarp in the latter.

KEY TO SPECIES OF *SEMNOCARPA*

1. Thallus 4–20 cm high, much branched with percurrent axes and irregular laterals of 2–3 orders ..... 1. *S. corynephora*
1. Thallus 0.1–3 cm high, simple to branched with axes bearing short clavate laterals ..... 2. *S. minuta*

1. **Semnocarpa corynephora** (J. Agardh)Huisman, Foard & Kraft 1993: 146, figs 1–17.
Chylocladia corynephora J. Agardh 1890: 23; 1896: 87. De Toni 1900b: 577. Wilson 1892: 180.
Lomentaria corynephora (J. Agardh)Kylin 1931: 27, pl. 15 fig. 34. May 1965: 361.

FIGS 60, 61A, B

Thallus (Fig. 60A) medium red to grey-red, mucilaginous, (3-) 6–10 (-20) cm high, pyramidal in outline, with one or a few percurrent axes bearing irregularly radially laterals for 2–3 orders. Main axes terete to slightly compressed, 1–3 mm broad, laterals terete, 1–2 mm broad, ultimate branchlets clavate, 0.5–1 mm broad, apices rounded, bases constricted. Holdfast discoid, 1–3 mm across, with several fronds; epiphytic on various algae or epilithic. *Structure* multiaxial, with a cluster of apical cells producing a cortex of a single layer of

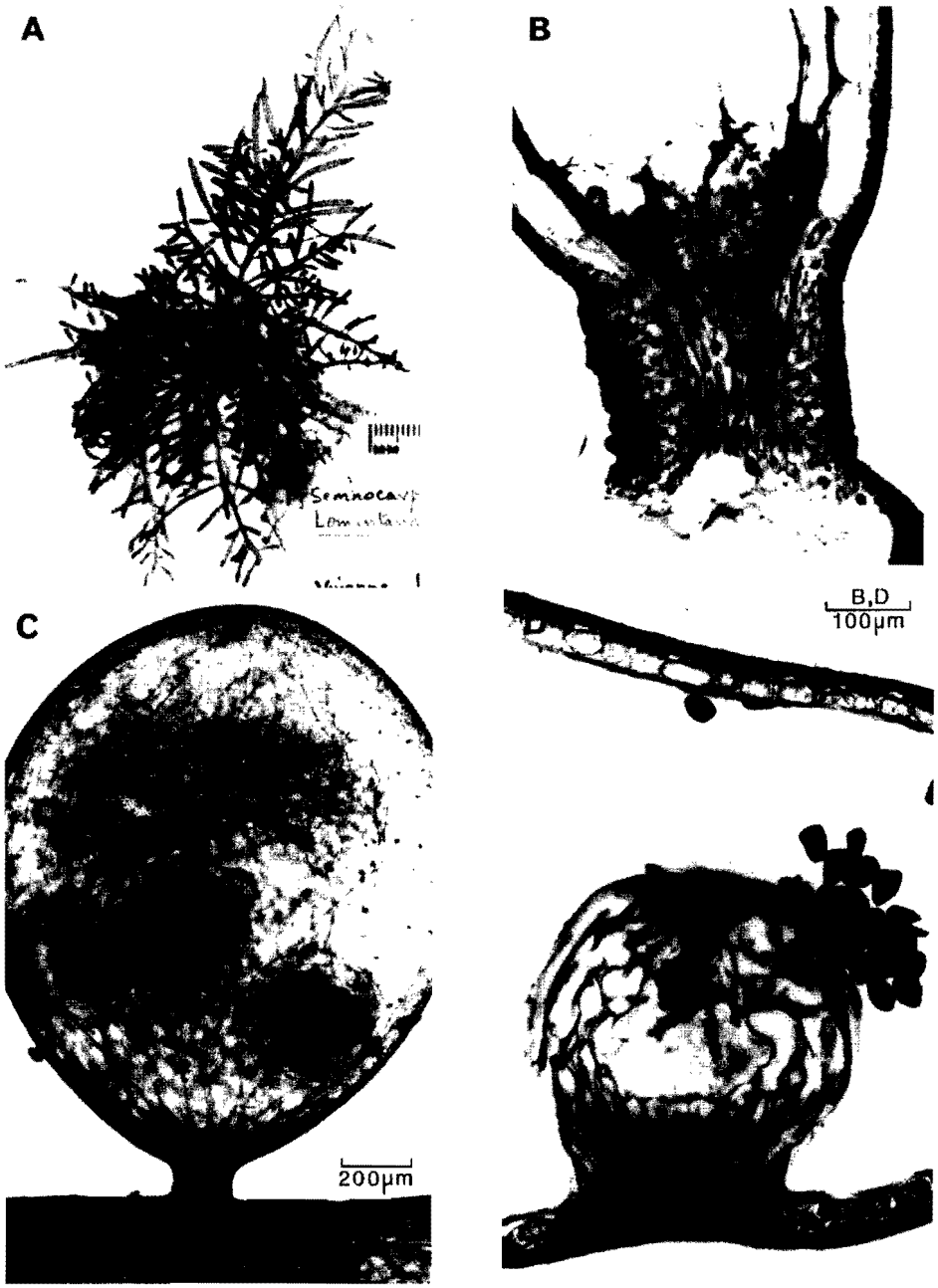


Fig. 60. *Semnocarpa corynephora* (AD, A33693). **A.** Habit. **B.** Longitudinal section through a constriction. **C.** Branch with three cystocarps. **D.** Longitudinal section of thallus with a cystocarp, showing basal fusion cell, prominent erect filaments, and displaced carposporangia.

large inner cells 30–80 μm across and an outer cortex 1–2 cells thick, outer cells ovoid and 5–10 μm in diameter, with a medulla of a network of branched filaments (5–10 μm broad) adjacent to the cortex, with some cells bearing ovoid secretory cells 10–20 μm in diameter. Constrictions (Fig. 60B) pseudoparenchymatous, 220–320 μm long, with filaments on each side. Rhodoplasts discoid, in chains in inner cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 3-celled, borne on inner cortical cells near branch apices, with 2-celled auxiliary cell branches. Carposporophyte (Fig. 60D) with basal partly fused cells and all upper cells forming lobes of ovoid carposporangia 40–60 μm in diameter, surrounded by an involucre (Fig. 60D) of lax erect filaments from the auxiliary cell initial; cystocarps (Fig. 60C) immersed in the branchlet, 500–650 μm in diameter, with a small ostiole formed by cortical proliferation. Spermatangia unknown.

Tetrasporangia in scattered, depressed, sori (Fig. 61A, B) 120–180 μm across, and 180–200 μm deep, cut off laterally from cells lining the depression, (50-) 75–110 μm in diameter, tetrahedrally divided.

Type from Western Port, Vic. (*Wilson*, 24.i.1885); holotype in Herb. Agardh, LD, 25827.

Distribution: Yanchep, W. Aust., to Western Port, Vic.

Selected specimens: Yanchep, W. Aust., drift on *Amphibolis antarctica* (*Kraft & Herrington*, 29.ix.1990; MELU, A40012). Pearson Is, S. Aust., 30–32 m deep on *Codium galeatum* (*Shepherd*, 7.i.1969; AD, A33693). Point Avoid, S. Aust., drift (*Womersley*, 2.xii.1975; AD, A46891). Investigator Strait, S. Aust., 33 m deep (*Watson*, 4.i.1971; AD, A41068). Vivonne Bay, Kangaroo I., S. Aust., drift (*Womersley*, 14.i.1948; AD, A6850). Stinky Bay, Nora Creina, S. Aust., drift (*Womersley*, 7.xi.1965; AD, A29644). Warrnambool, Vic., drift (*Kraft & Herrington*, 28.x.1988; MELU, A40014). Port Phillip Heads, Vic. (*Wilson*, 14.i.1885; MEL, 612087).

2. **Semnocarpa minuta** Huisman, Foard & Kraft 1993: 148, figs 18–30

FIG. 61C–E

Thallus 1–10 (-30) mm high, with one to several simple or branched terete axes, elongate-clavate and saccate, branches ovoid to clavate, basally constricted, apices rounded; axes and branches 0.5–1 mm in diameter. Holdfast (Fig. 61C) monostromatic, 0.3–0.8 mm across; epiphytic on various algae. *Structure* multiaxial, with a group of short apical filaments producing the network of medullary filaments bearing secretory cells and cutting off outwardly the layer of large, ovoid, inner medullary cells 20–35 μm in diameter and an outer cortex 1–2 cells thick of small ovoid cells 4–6 μm in diameter. Holdfast cells ovoid, 8–12 μm in diameter. Rhodoplasts discoid, in chains in inner cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 3-celled, borne on inner cortical cells together with a 2-celled auxiliary cell branch, auxiliary cell with a proteinaceous globule. Carposporophyte (Fig. 61D) developing within the branch cavity, producing several lobes with all cells forming ovoid carposporangia 8–12 μm in diameter, surrounded by an involucre of relatively coarse filaments connected to the auxiliary cell initial and adjacent cortical filaments. Cystocarps completely immersed, projecting into the cavity, with a small cortical ostiole. Spermatangia in sori near the branch apices, cut off from initials on the outer cortical cells, elongate-ovoid, 3–6 μm in diameter.

Tetrasporangia (Fig. 61E) in depressed sori, cut off thallus inwardly from cortical cells lining the depression, subspherical to ovoid, 120–135 μm in diameter, tetrahedrally divided.

Type from Green I., Rottnest I., W. Aust., epiphytic on *Rhodopeltis borealis* (*Kraft & Huisman*, 3.x.1990); holotype in MELU, A40100.

Distribution: Port Denison, W. Aust., to Margaret Brock Reef, Cape Jaffa, S. Aust., and Eaglehawk Neck, Tas. Probably more widely distributed but easily overlooked.

Selected specimens: Seamount off Cannan Reefs, S. Aust., 22–30 m deep on *Dictyota prolifera* (*Branden*, 22.i.1991; AD, A61202). Vivonne Bay, Kangaroo I., S. Aust., on *Rhodymenia australis*, 1–4 m deep on jetty piles (*Kraft*, 6.iv.1972; AD, A42379). Margaret Brock Reef, Cape Jaffa, S. Aust.,

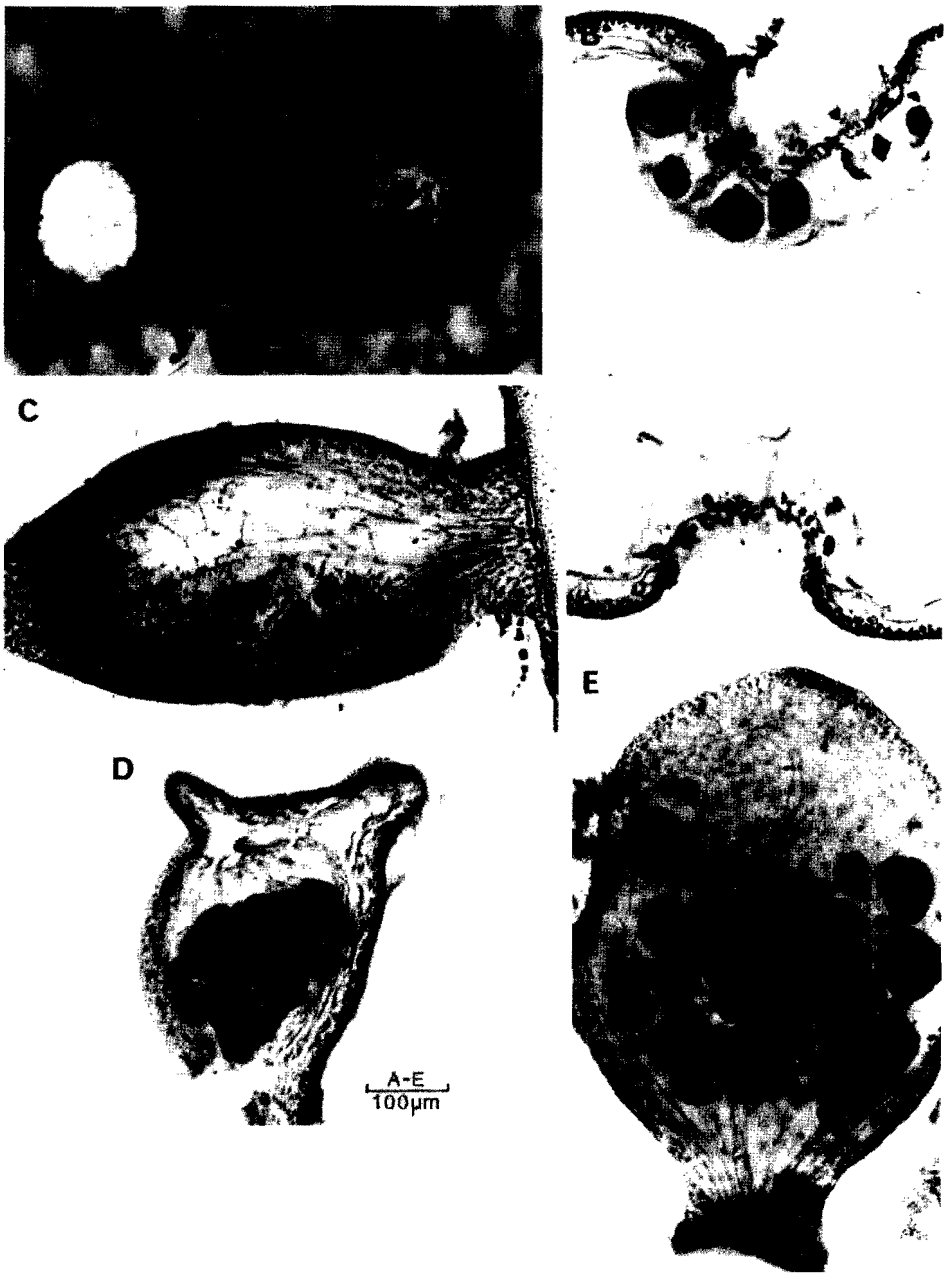


Fig. 61. A, B. *Semnocarpa corynephora* (AD, A33693). **A.** Surface view of tetrasporangial sori. **B.** Section of branch with tetrasporangial sori, the lower one without tetrasporangia. **C–E.** *Semnocarpa minuta* (**C,** AD, A42379; **D,** AD, A42927; **E,** AD, A61202). **C.** Longitudinal section of thallus on *Rhodymenia*. **D.** Section of a cystocarp, with basal fusion cell, erect filaments and carposporangia. **E.** Thallus with tetrasporangia.

on *Craspedocarpus venosus*, 3–5 m deep (*R.K. Lewis*, 29.xi.1972; AD, A42927). Eaglehawk Neck, Tas., on *Carpopeltis phyllophora*, 12–21 m deep (*Kraft* 9655, 12.xii.1993; AD, A63397 and MELU).

S. minuta was described from the west coast of Western Australia, but isolated collections are known from southern Australia and it may be more plentiful than presently indicated. It was described as epiphytic on *Rhodopeltis, Amphibolis, Halimeda* and *Hennedya*, and apparently occurs on several firm-surfaced red algae.

Thalli only 1 mm long are usually reproductive.

ORDER **CORALLINALES*** Silva & Johansen 1986: 250

Thallus mostly calcified, growing on rock, plants, animals or other hard substrates, or partly to almost entirely endophytic; partly to completely affixed by cell adhesion, envelopment of host axes or a crustose or rhizoidal holdfast, or growing unattached and free-living as rhodoliths; in geniculate taxa, branches composed of alternating uncalcified genicula and calcified intergenicula. *Structure* pseudoparenchymatous or more rarely partly to largely composed of unconsolidated filaments; organisation usually dorsiventral and/or radial or isobilateral. Construction in non-geniculate taxa monomerous and/or dimerous or diffuse; monomerous portions consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; dimerous portions consisting of two distinct groups of laterally cohering filaments or cells: a unistratose ventral or internal layer in which each filament is composed of palisade cells, non-palisade cells or both, and secondly epithallial cells or multicellular filaments arising more or less perpendicularly from cells of the ventral or internal layer of filaments; diffuse portions consisting of branched endophytic or epigenous filaments that are partially or largely non-cohering but usually become partially consolidated in areas of conceptacle production; structure of geniculate taxa usually regarded as multiaxial and differentiated into cortex and medulla; walls of most vegetative cells other than genicula usually impregnated with calcite; cells of adjacent filaments joined by cell-fusions or secondary pit-connections or rarely both, or not interconnected; epithallial cells terminating most filaments at thallus surface, distal walls commonly uncalcified; rhodoplasts discoid and without pyrenoids; pit-plugs with two cap layers including an outer dome-like cap layer. Growth of filaments usually from apical or subapical initials.

Life history triphasic with more or less isomorphic gametangial and tetrasporangial generations and a heteromorphic carposporangial generation.

Reproduction. Vegetative reproduction by thallus fragmentation, apomeiotic bispores or propagules.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate uniporate conceptacles or rarely in the same conceptacle. Carpogonial filaments mostly 1- to 4-celled, arising from the conceptacle chamber floor or rarely also from the chamber walls. Carposporophytes developing within female conceptacles after karyogamy; carposporangia commonly terminating short gonimoblast filaments that usually arise from a conspicuous or inconspicuous fusion cell, or developing more or less directly from the fertilized carpogonium. Spermatangial filaments unbranched or branched, restricted to the conceptacle chamber floor, or borne on the floor, walls and sometimes the roof.

Tetrasporangia formed within uniporate or multiporate conceptacles or within calcified compartments that may be solitary or more commonly aggregated into sori in non-geniculate taxa; each mature sporangium containing four zonately or (in Sporolithaceae) cruciately arranged spores and in some genera producing apical plugs that individually block a pore of a multiporate conceptacle or a calcified compartment, or collectively block the pore of a uniporate conceptacle prior to spore release; meiotic bisporangia sometimes replacing tetrasporangia; 3-celled sporangia present in *Jania minuta*.

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* The order description was compiled by W.J.W. with input from H.B.S.W. and H.W.J. The comments which follow on non-geniculate taxa are by W.J.W.

The Corallinales includes two families, both represented in southern Australia. Discussions of characters used to delimit the Corallinales as an order are provided by Silva & Johansen (1986) and Woelkerling (1988, pp. 83–85), and further comments on relationships to other orders are given by Garbary & Gabrielson (1990, pp. 490–491).

The above ordinal circumscription and those for families, subfamilies, and genera reflect current knowledge of these groups. Information on various features, especially relating to reproduction, remain incompletely known or unknown for many species, and as further data become available, modifications to present circumscriptions will become necessary. A comparison of the classification system used here with that used by Woelkerling (1988) testifies to the extent change has been required in the last eight years as a consequence of new research. Similarly, species distribution records for Australia and elsewhere will require updating as new data become available.

Colour may be more or less constant within a species or vary considerably from light to dark pink to purplish, greyish, yellowish, brownish or reddish pink, to red-brown, etc. depending on the interactions of age, habit, light availability, depth of collection, sun-induced bleaching, degree of calcification, and other factors (also note comments of Chamberlain & Keats 1995, p. 138). Senescent or severely stressed specimens sometimes become orangish, greenish or whitish. The colour of partly to largely endophytic species cannot be determined readily. In this account, the colour of many species is described simply as pinkish (*sensu* Stearn 1983, p. 483); colour is not a reliable diagnostic character for species occurring in southern Australia and cannot be used as a sole basis for identifying specimens.

Notes on the identification of specimens lacking genicula

The calcified nature of the thallus and the occurrence of reproductive structures in conceptacles (or sori) readily identifies most members of the Corallinales. Determination to genus and species, however, traditionally has presented formidable problems. Most non-geniculate species cannot be identified from appearance and growth form, and their anatomical features have necessitated the use of specialised terminology.

The internal anatomy of most species can look quite different in different planes of view (Fig. 62B). Except for cell connections, most vegetative features are best seen or can only be seen in sections cut or fractured parallel to the direction of filament growth (i.e. along a group of filaments); such longitudinal views are essential in determining whether the thallus construction is monomerous or dimerous. To determine whether cell-fusions or secondary pit-connections are present, however, it is necessary to examine sections cut or fractured more or less perpendicularly to the direction of filament growth (i.e. across a group of filaments) because such connections occur largely or entirely between cells of different filaments rather than between successive cells of the same filament. When examining conceptacles, it is essential to use sections cut vertically through pore canals and conceptacle chambers; glancing sections through pore canals often show only the peripheral parts of conceptacle chambers and can give a false impression of the structure of reproductive bodies and carposporophytes. Further information on the planes of sectioning is provided by Woelkerling (1988, p. 31).

To facilitate identification of southern Australian specimens lacking genicula, most keys include references to figures showing relevant characters and character states. In addition, a photographic guide to general morphological and anatomical features not explicitly illustrated in the species figures is provided in Figs 62–64. Important characters and character states found in taxa lacking genicula, with references to figures, may be summarised as follows:

GROWTH FORMS: unconsolidated (Fig. 62F, G); encrusting (Figs 69A, B; 80A, 82A); warty (Figs 80B, 88B); lumpy (Fig. 65B); fruticose (Figs 65C, 75A, 88C, 102D, 104D); discoid (Fig. 90A); layered (Figs 86B, 98B, 100B; 108C, D); foliose (Fig. 84B); arborescent (Figs 73A, 113). Woelkerling *et al.* (1993) provide a detailed account of growth forms in non-

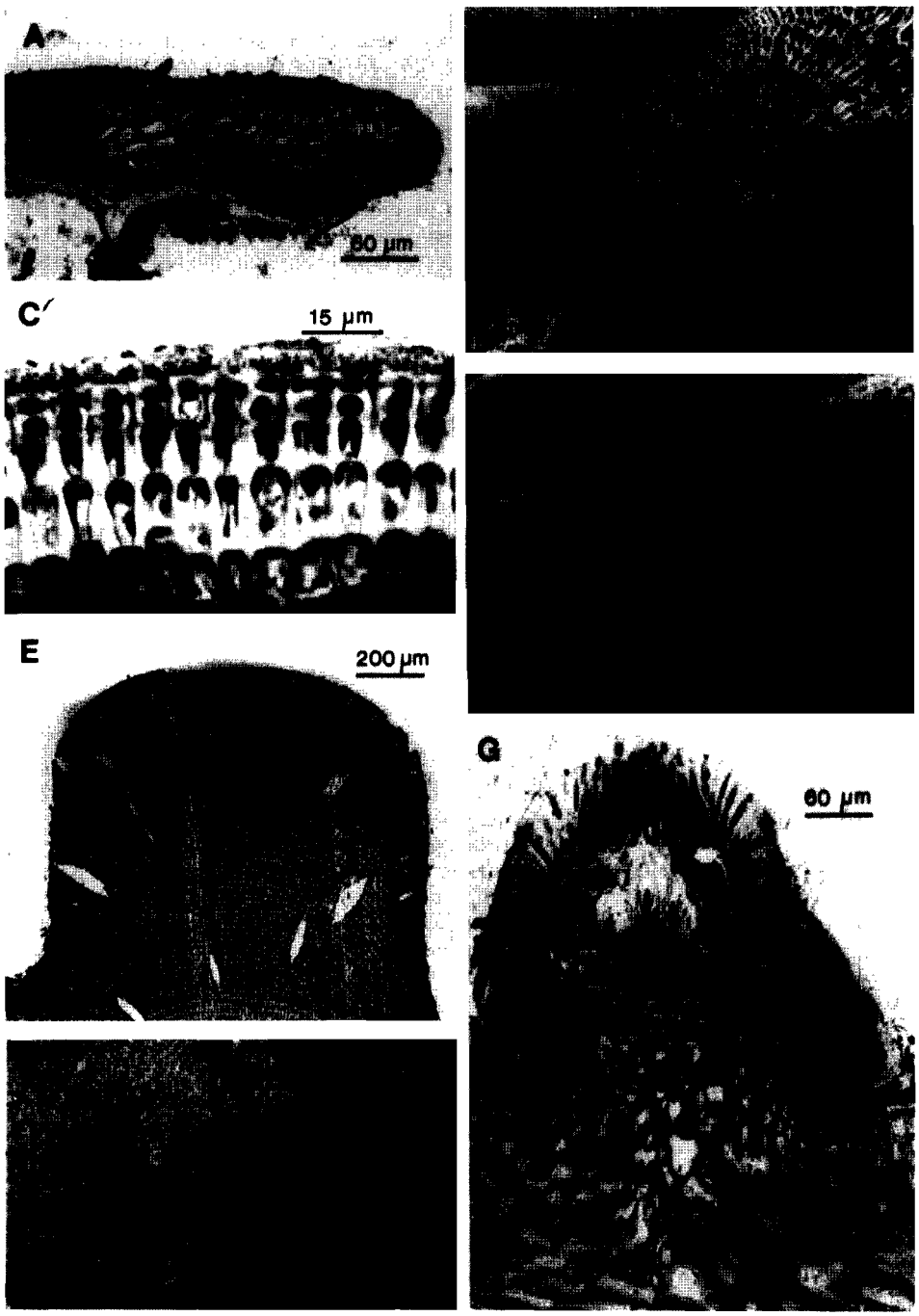


Fig. 62. Thallus construction in non-geniculate Corallinales (**A,** LTB, 12831; **B,** LTB, 11719; **C,** LTB, 13268; **D,** LTB, 13188; **E,** LTB, 13703; **F,** LTB, 12937; **G,** LTB, 10851). **A.** Monomerous construction in a longitudinal section of an encrusting plant of *Mesophyllum macroblastum*. **B.** Monomerous construction in both longitudinal (L) and transverse (T) views in a fracture of an encrusting plant of *Mesophyllum incisum*. Note difference in appearance in thallus construction in the two planes of view. **C.** Dimerous construction in a longitudinal section of *Melobesia rosanoffii*.

geniculate Corallinales and emphasise that the growth form of many individuals is intermediate between two focal points [e.g. encrusting to fruticose (Fig. 90C), discoid to layered (Fig. 84D), etc.].

BRANCHES: protuberant branch (Figs 62C, 80C, 84C); lamellate branch (Figs 84B, 84D, 98B); ribbon like branch (Fig. 73A); struts (Fig. 78C).

THALLUS ORGANISATION: dorsiventral (Figs 62A–D); radial (Fig. 62E).

THALLUS CONSTRUCTION: monomerous (Fig. 62A, B); dimerous (Fig. 62C, D); diffuse (Fig. 62F, G).

CELLS AND CELL CONNECTIONS: flattened epithallial cells (Fig. 63A); rounded epithallial cells (Fig. 63B); flared epithallial cells (Fig. 63C); palisade cells (Fig. 63D, G); cell fusions (Fig. 63D, F); primary pit-connections (Figs 63E, 63G); secondary pit-connections (Fig. 63E).

RELATIVE LENGTH OF SUBEPITHALLIAL INITIALS: as short as or shorter than the cells immediately subtending them (Fig. 63A); as long as or longer than the cells immediately subtending them (Fig. 63B).

TRICHOCYTES: solitary (Fig. 64A); vertical rows (Fig. 64B); horizontal fields (Fig. 64C); horizontal rows (Fig. 64D).

HAUSTORIA (Fig. 101C).

REPRODUCTIVE STRUCTURES: multiporate conceptacles (Figs 76E, 85A); uniporate conceptacles (Figs 96C, 104E, 114A, B); sori (Fig. 65D); calcified compartments (Fig. 66A).

GAMETANGIA AND CARPOSPOROPHYTES: carpogonial filaments (Figs 68B, 91A, 105A, 109A); trichogynes (Figs 68B, 91A, 105A, 109A); unbranched spermatangial filaments (Figs 83D, 101C, 109C, 112B); branched spermatangial filaments (Figs 66D, 91C); carposporophytes (Figs 83C, 96B, 103C, 107C, 112A); conspicuous central fusion cell (Figs 101B, 112A); irregularly shaped fusion cell that looks discontinuous in section (Figs 83C, 91B); gonimoblast filaments (Figs 83C, 103C, 107C, 112A); carposporangia (Figs 83C, 103C, 107C, 112A).

TETRASPORANGIA AND BISPORANGIA: tetrasporangia with apical plugs (Figs 67E, 76D, E, 93A); tetrasporangia without apical plugs (Figs 100D, F, 108E); bisporangia (Fig. 94D); columella (Fig. 100E, F); tetrasporangia with cruciately arranged spores (Fig. 65E); tetrasporangia with zonately arranged spores (Figs 76E, 84E); conceptacles arising at thallus surface from a group of subepithallial initials (Figs 86C, 89A); conceptacles arising adventitiously from a group of vegetative cells within the thallus (Figs 78E, 80E).

Of the 40 or so southern Australian species of Corallinales lacking genicula, 11 or 12 may sometimes be identifiable in the field or with a hand lens or stereomicroscope. The following guide is provided to facilitate preliminary identification; such identifications always require confirmation, however.

Note how multicellular filaments are arising dorsally from cells of the unistratose ventral layer. **D.** Dimerous construction in a longitudinal fracture of *Lithophyllum frondosum*. **E.** Monomerous construction in a median longitudinal section of a protuberant branch of *Lithophyllum corallinae*. **F.** Diffuse construction (arrows) in an unidentified epiphytic species of Mastophoroideae. **G.** Diffuse construction (arrows) in a plant of *Lesueuria minderiana*.

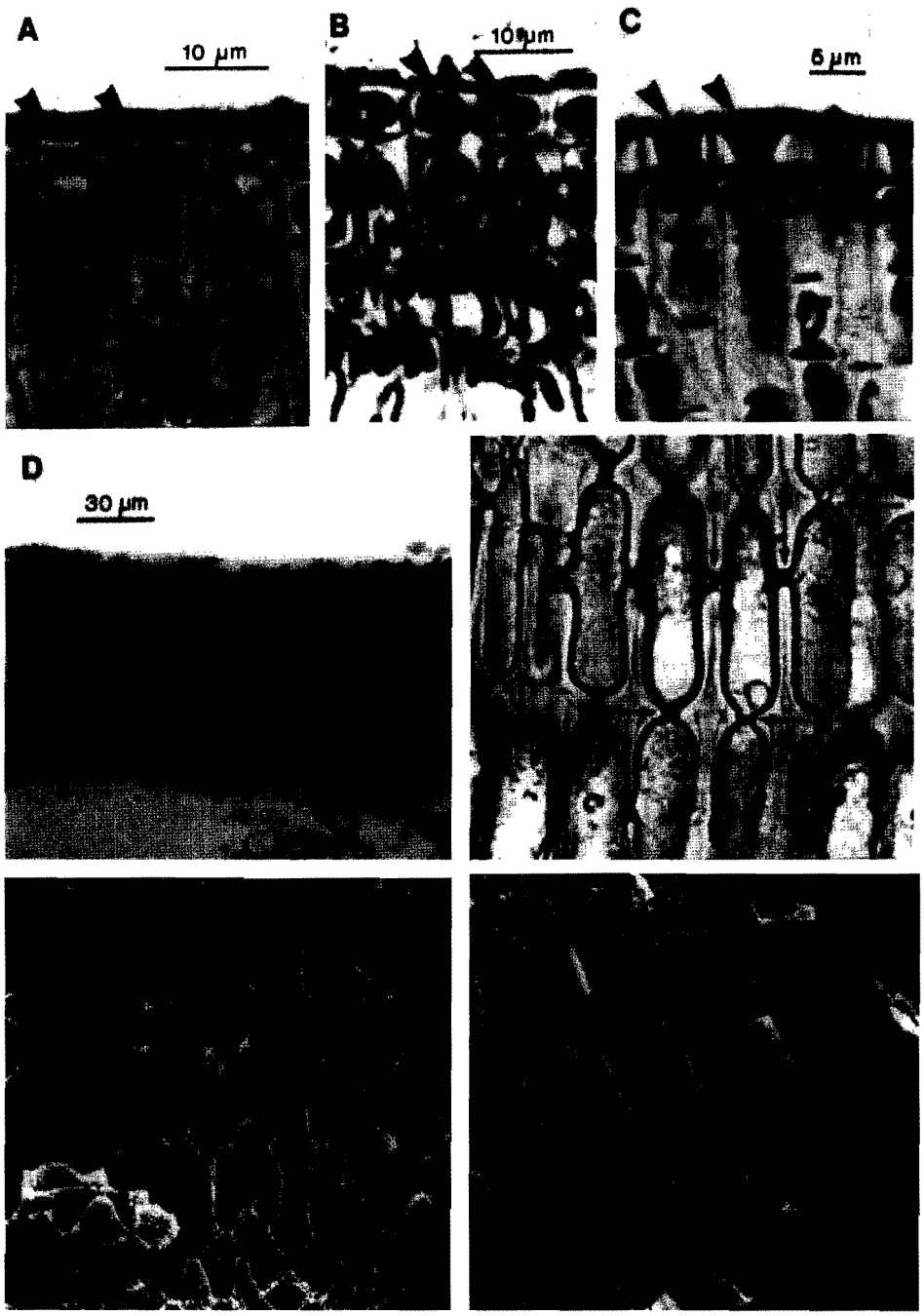


Fig. 63. Cell morphology and anatomy in non-geniculate Corallinales (**A**, LTB, 12787; **B**, LTB, 15249; **C**, LTB, 14171; **D**, LTB, 15688; **E**, TRH, Howe no. 199; **F**, LTB, 14493; **G**, LTB, 15578). **A.** Section of *Phymatolithon masonianum* showing compressed epithallial cells (arrowheads) and vegetative initials (arrows) that are shorter than the cells immediately subtending them. **B.** Section of *Mesophyllum printzianum* showing rounded epithallial cells (arrowheads) and vegetative initials (arrows) that are as long as or longer than the cells immediately subtending them. **C.** Section of

GUIDE FOR THE PRELIMINARY IDENTIFICATION OF NON-GENICULATE SPECIES WITH DISTINCTIVE CHARACTERS OBSERVABLE IN THE FIELD OR WITH A HAND LENS

I. Endophytic taxa growing in branches of geniculate corallines

- A. Conceptacles of endophyte external on genicula of *Metagoniolithon*; no evident deformities of host: *Lesueuria minderiana* (Fig. 101A).
- B. Conceptacles of endophyte external on geniculate branches of *Haliptilon* or *Jania*; no evident deformities of host: *Choreonema thuretii* (Fig. 92A, B).
- C. Conceptacles of endophyte largely buried within gall like deformities of geniculate branches of *Haliptilon*: *Austrolithon intumescens* (Fig. 67A, B).

II. Epigenous taxa with distinctive growth forms

- A. Thallus arborescent; tetrasporangial conceptacles multiporate: *Mastophoropsis canaliculata* (Fig. 73A, B). Caution: male and female/carposporangial conceptacles are uniporate.
- B. Thallus arborescent; tetrasporangial conceptacles uniporate: *Metamastophora flabellata* (Figs 113A, 114C). Male and female/carposporangial conceptacles also are uniporate.
- C. Thallus forming small, relatively thin discs affixed at one point to branches of the red algae *Ballia* or *Camontagnea*: *Synarthrophyton patena* (Fig. 90A). Other growth forms of *S. patena* (Fig. 90B–D) cannot be distinguished from thalli of other species using external features.
- D. Thallus forming epilithic plate-like discs commonly 20–150 mm across and 1–3 mm thick that are loosely attached and commonly produce ventral struts: *Phymatolithon masonianum* (Fig. 78A–C).
- E. Thallus producing tightly appressed layers of lamellate branches that look terraced in surface view and commonly are swirled: *Lithophyllum prototypum* (Fig. 98B).

III. Epigenous taxa with distinctive reproductive structures

- A. Reproductive structures (tetrasporangia) aggregated into surface sori: *Sporolithon durum* (Fig. 65D).
- B. Multiporate conceptacles composed of a peripheral rim and a central somewhat sunken pore-plate:
  1. Thallus forming very thin encrusting thalli, often occurring in large numbers: *Melobesia membranacea* (Fig. 69A, B).
  2. Thallus more massive, encrusting to warty, somewhat lumpy or layered or fruticose: *Mesophyllum macroblastum* (Figs 86D, 87A); *Mesophyllum printzianum* (Figs 88D, 89B). These two species cannot be distinguished from one another without anatomical examination of tetrasporangial conceptacle roofs.

Sporolithon durum showing epithallial cells (arrow heads) with flared outer walls **D.** Palisade cells of contiguous filaments of *Metamastophora flabellata* showing cell-fusions (F). **E.** Columnar cells of *Lithophyllum frondosum* showing primary (arrow - p) and secondary (arrow - s) pit connections. **F.** Fracture of *Sporolithon durum* showing fusions (F) between cells of contiguous filaments. **G.** Fracture of *Lithophyllum corallinae* showing pit connections in surface (arrowhead) and sectional (arrow) views.

KEY TO FAMILIES OF CORALLINALES

1. Tetrasporangia containing cruciately arranged spores, produced within calcified compartments (Fig. 66A) that may be solitary or grouped into sori and are derived from the walls of tetrasporangial initials ..... SPOROLITHACEAE
1. Tetrasporangia containing zonately arranged spores, produced within conceptacles (Figs 76E, 100F) ..... CORALLINACEAE

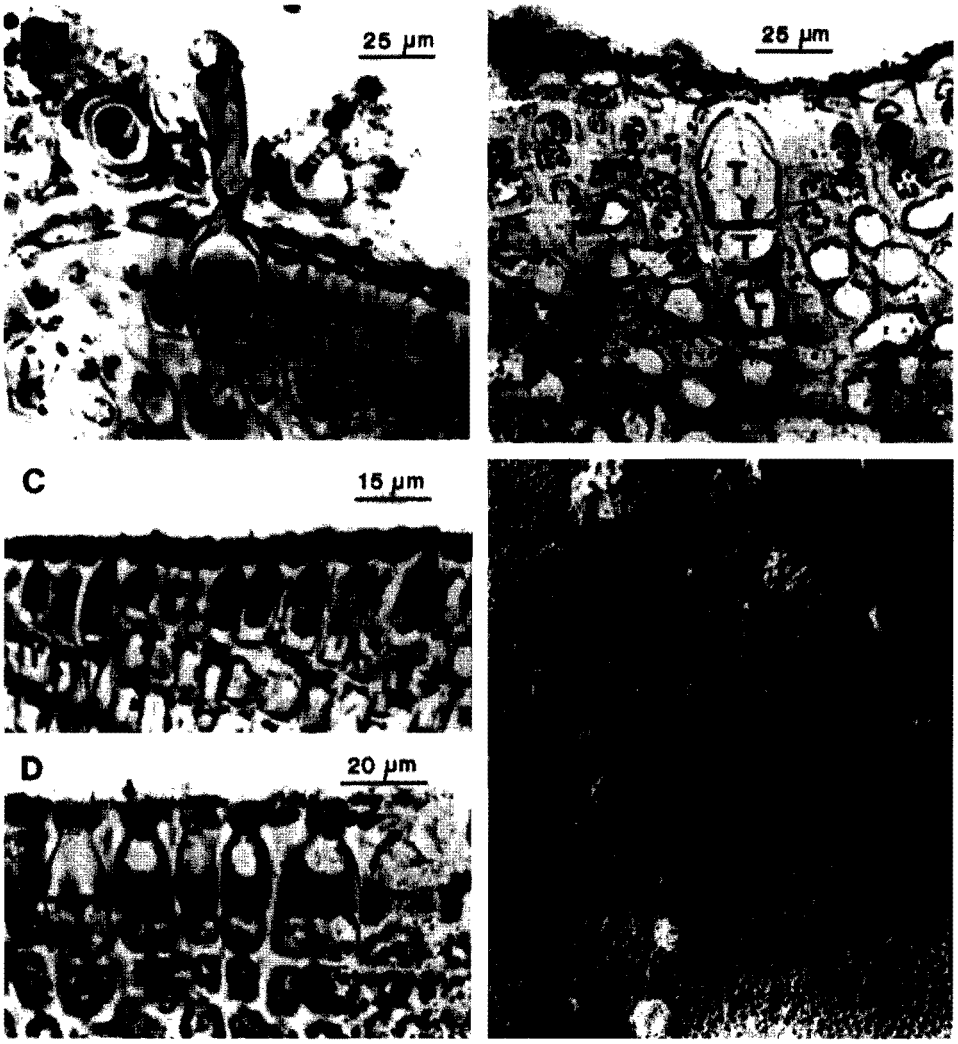


Fig. 64. Trichocytes in non-geniculate Corallinales (**A, B,** LTB, 13506; **C,** LTB, 15249; **D,** LTB, 14388; **E,** LTB, 11646). **A.** Solitary trichocyte with intact hair in *Neogoniolithon brassica-floridum*. **B.** Vertical row of trichocytes (T) in *Neogoniolithon brassica-floridum*. **C.** Horizontal field of trichocytes in *Mesophyllum printzianum*. **D.** Horizontal row of trichocytes in *Hydrolithon cymodoceae*. **E.** Surface view of clusters of trichocytes (arrows) in *Hydrolithon cymodoceae*.

FAMILY SPOROLITHACEAE Verheij 1993a: 195

by W.J. Woelkerling

Thallus mostly calcified, encrusting to warty, lumpy or fruticose; epigenous and partially to completely affixed by cell adhesion, or growing unattached and free-living as rhodoliths; non-geniculate. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; walls of most vegetative cells impregnated with calcite; cells of adjacent filaments joined laterally by both fusions and secondary pit-connections but proportions varying within and between species; epithallial cells terminating most filaments at thallus surface, distal walls commonly uncalcified; haustoria unknown.

Life history triphasic with isomorphic gametangial and tetrasporangial generations and a heteromorphic carposporangial generation.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia and carposporangia borne in uniporate conceptacles; tetrasporangia borne in calcified compartments that may be solitary or aggregated into sori and are derived from the walls of tetrasporangial initials; gametangia and carposporangia normally formed on separate thalli from tetrasporangia. Reports of bisporangia unconfirmed.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles or rarely in the same conceptacle. Carpogonial filaments usually 1 to 4-celled, arising from the female conceptacle chamber floor and in some species also from the walls. Carposporophytes developing within female conceptacles after karyogamy, carposporangia either developing more or less directly from the fertilized carpogonium or terminating short gonimoblast filaments that usually arise from an inconspicuous fusion cell. Spermatangial filaments branched, restricted to the male conceptacle chamber floor or borne on the floor, walls and roof.

Tetrasporangia formed within calcified compartments that may be solitary or more usually aggregated into sori of irregular shape and indefinite size, compartments interspersed amongst vegetative filaments or enclosed in sporangial complexes; each mature sporangium containing four cruciately arranged tetraspores and possessing an apical plug that blocks the compartmental pore prior to spore release.

Type genus: *Sporolithon* Heydrich 1897a: 66.

The Sporolithaceae includes a single subfamily, the Sporolithoideae Setchell (1943, p. 134, as 'Sporolitheae'), with two genera. *Heydrichia* (see Townsend *et al.* 1995) is known only from southern Africa, while *Sporolithon* is known from various tropical and temperate regions, including southern Australia. Additional information on the Sporolithaceae is provided by Verheij (1993a) and Townsend *et al.* (1995).

Genus **SPOROLITHON** Heydrich 1897a: 66

Thallus encrusting to warty, lumpy or fruticose, epigenous and partially to completely affixed by cell adhesion or unattached and completely free-living as rhodoliths; genicula absent. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; cell elongation characteristics uncertain in most species; cells of adjacent filaments usually joined by both fusions and secondary pit-connections but proportions varying within and between species; epithallial cells terminating most filaments at thallus surface, distal walls usually flattened and flared; trichocytes occasional in some species; haustoria unknown.

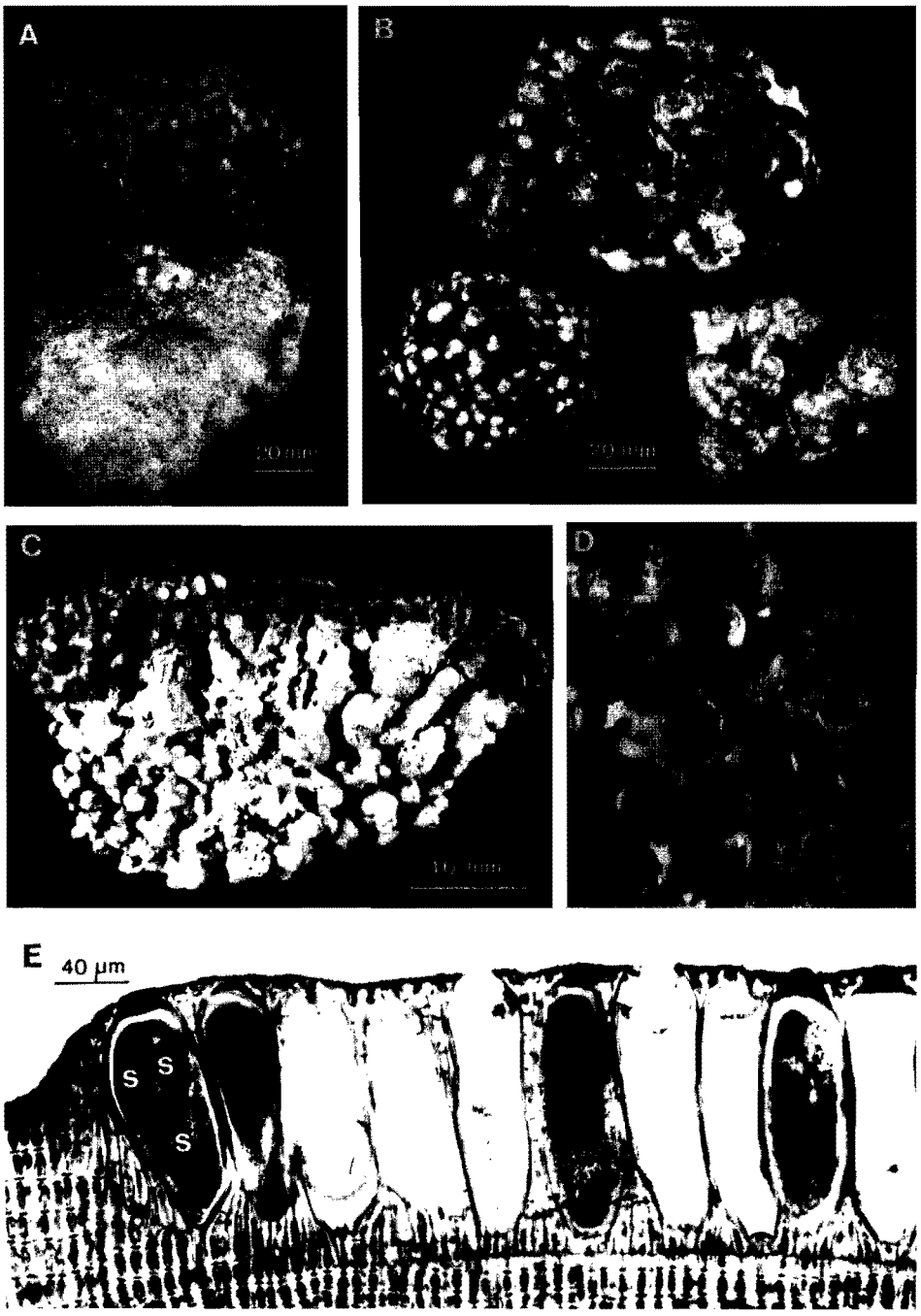


Fig. 65. *Sporolithon durum* (**A**, LTB, 14493; **B**, LTB, 15546; **C**, LTB, 14200; **D**, LTB, 11402; **E**, LTB, 16705). **A.** Encrusting to fruticose thallus attached to rock. **B.** Encrusting (lower right), lumpy (top) and fruticose (lower left) thalli forming rhodoliths. **C.** Portion of a large fruticose thallus. **D.** Surface view of tetrasporangial sori. **E.** Section of part of a tetrasporangial sorus with tetrasporangia containing cruciately arranged spores (S) and empty calcified compartments.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia and carposporangia borne in uniporate conceptacles; tetrasporangia borne in calcified compartments that may be solitary or aggregated into sori; gametangia and carposporangia formed on separate thalli from tetrasporangia. Reports of bisporangia unconfirmed.

Gametangial thalli monoecious or dioecious, carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 2–4-celled filaments arising from the female conceptacle chamber floor and in some species also from the walls. Mature carposporophytes with carposporangia either developing more or less directly from the fertilized carpogonium or terminating short gonimoblast filaments that arise from the dorsal surface of an inconspicuous fusion cell. Spermatangial filaments branched, borne on the male conceptacle chamber floor, walls and roof.

Tetrasporangia formed within calcified compartments that may be solitary or more usually aggregated into sori of irregular shape and indefinite size, compartments interspersed amongst vegetative filaments; each mature sporangium containing cruciately arranged tetraspores and possessing an apical plug that blocks the compartmental pore prior to spore release; older sori sloughed off or becoming buried within the thallus.

Type species: *S. ptychoides* Heydrich 1897a: 67.

At least 12 species have at some stage been referred to *Sporolithon*, and over 125 additional specific and infraspecific taxa have been recognised under the names *Archaeolithothamnion* and *Archaeolithothamnium* (Woelkerling 1988, p. 207), here considered as heterotypic synonyms of *Sporolithon* (see also Moussavian & Kuss 1990). Most species are poorly known (Dawson 1960a, p. 40, Woelkerling 1988, pp. 207–209, Keats & Chamberlain 1993, p. 541). Information on male, female and carposporangial stages is available only for several species (Verheij 1992, 1993a; Townsend *et al.* 1995), and reports of bisporangia and zonate tetrasporangia are probably incorrect (Woelkerling 1988, p. 209; Verheij 1993, p. 186). Recent accounts of the type species are provided by Verheij (1993a) and Keats & Chamberlain (1993), and additional information on the lectotype collection of *S. ptychoides* is given by Woelkerling (1993, p. 183). Details relating to generic etymology, nomenclature, synonymy, *etc.* are provided by Woelkerling (1988, pp. 203–207). *Sporolithon* is represented in southern Australia by one species; this account follows Townsend *et al.* (1995).

Sporolithon durum (Foslie)Townsend & Woelkerling *in* Townsend *et al.* 1995: 86, figs 1–17.

Archaeolithothamnion durum Foslie 1907a: 11. Adey 1970: 18. Adey & Lebednik 1967: 84. Dawson 1960a: 41. De Toni 1924: 606. Johnson 1963: 206, pl. 30 fig. 9. Woelkerling 1993: 80.

Sporolithon erythraeum sensu Woelkerling 1988: 207.

FIGS 63C, F, 65, 66

Thallus normally pinkish to grey-pink, encrusting to warty, lumpy or fruticose, mostly 30–195 mm across and 1–115 mm thick or tall, epigenous and completely affixed by cell adhesion or unattached and forming rhodoliths mostly 16–114 mm in greatest dimension; protuberant branches simple or branched, free from one another or fused to varying degrees, mostly 5–26 mm in diameter and 5–23 mm long. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions and radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 5–12 µm in diameter and 6–23 µm long; epithallial cells 2–5 µm in diameter and 7–10 µm long, terminating most filaments at the thallus surface, with distal walls flattened and flared; cell elongation occurring mainly behind actively dividing subepithallial initials that are most commonly as short as or shorter than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions, secondary pit-connections apparently uncommon and not observed in most (southern Australian) thalli; haustoria absent; one trichocyte recorded.

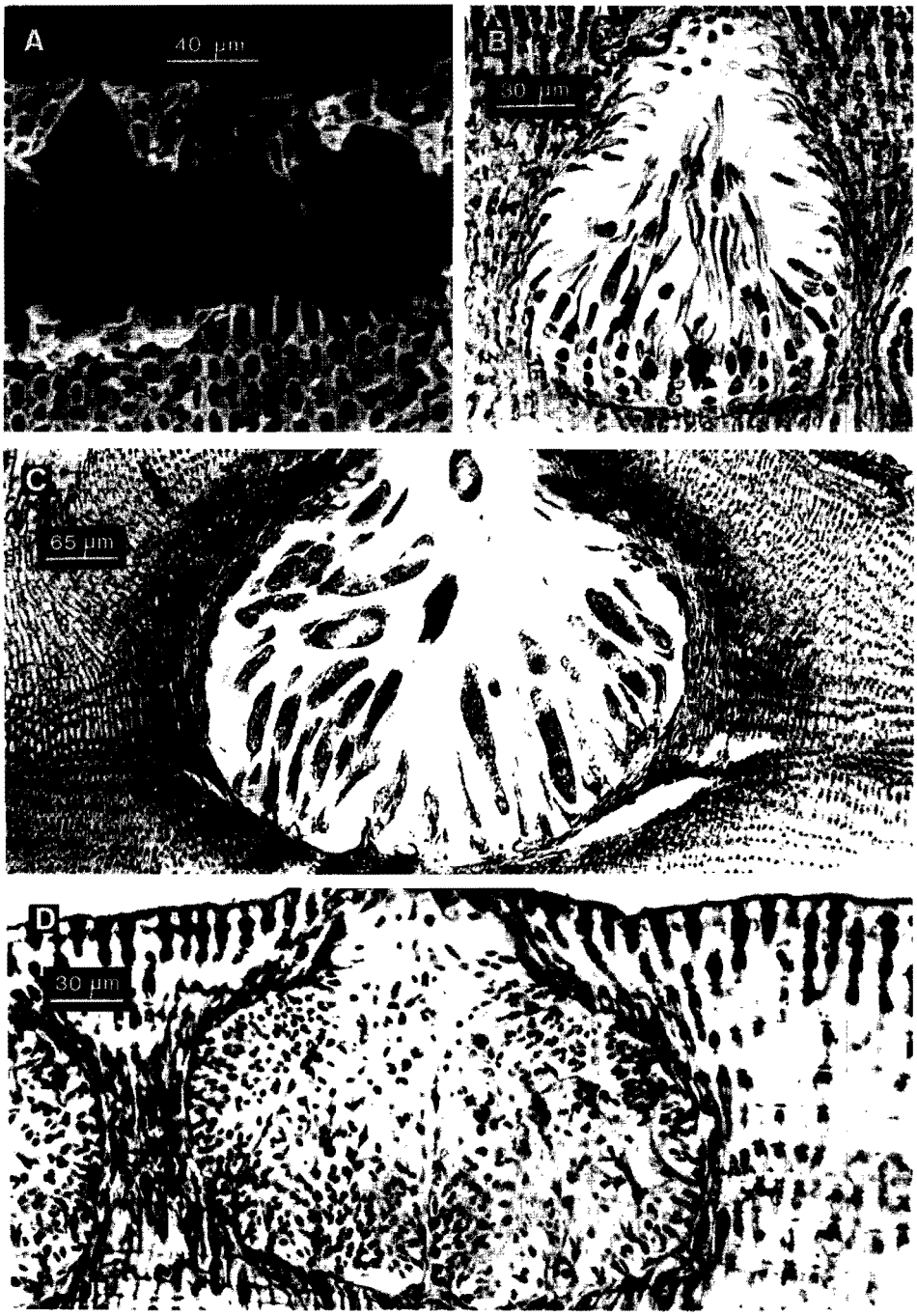


Fig. 66. *Sporolithon durum* (**A**, LTB, 14493; **B**, LTB, 15595; **C**, LTB, 15683; **D**, LTB, 17280). **A.** Fracture of a sorus showing calcified compartments in surface view. **B.** Section of female-carposporangial conceptacle with mature carpogonial filaments. **C.** Section of female-carposporangial conceptacle with mature carposporophyte. **D.** Section of male conceptacle with mature, branched spermatangial filaments arising from chamber floor, walls and roof.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia and carposporophytes produced in uniporate conceptacles; tetrasporangia produced on separate thalli in calcified compartments that are aggregated into sori and are derived from the walls of tetrasporangial initials. Bisporangia unknown.

Gametangial thalli probably dioecious. Carpogonia terminating 2–4-celled filaments arising from the female conceptacle chamber floor and sometimes from the chamber walls. Mature female-carposporangial conceptacle roofs flush with or slightly protruding above the surrounding thallus surface, 13–215 μm thick, composed of 3–18 layers of cells above the chamber, conceptacle chambers 80–445 μm in diameter and 70–370 μm high. Carposporophytes apparently consisting only of carposporangia 16–30 μm in diameter and 105–119 μm long, developing directly from fertilized carpogonia and subtended by one- or several-celled stalks that presumably are the remains of carpogonial filaments; fusion cells and gonimoblast filaments unknown. Spermatangial filaments branched, arising from the floor and roof of male conceptacle chambers, mature conceptacle roofs flush with or slightly sunken below surrounding thallus surface, 13–81 μm thick, composed of 3–11 layers of cells above the chamber, conceptacle chambers 67–245 μm in diameter and 67–122 μm high.

Tetrasporangial sori irregularly shaped, (<1-) 5–15 (-40) mm in greatest dimension and very slightly raised above surrounding thallus surface, composed of sterile filaments and calcified compartments, each compartment with a tetrasporangium; each mature sporangium 38–60 μm in diameter and 80–110 μm long, containing cruciately arranged tetraspores and possessing an apical plug that blocks the compartmental pore prior to spore release; older sori almost always sloughed off.

Type from Cape Jaffa, South Australia; lectotype in TRH (unnumbered; includes two slides both numbered 355); designated by Adey in Adey & Lebednik (1967, p. 84); depicted in Printz (1929, pl. 43, figs 1–3, as *Archaeolithothamnion*) and in Townsend *et al.* (1994, fig. 1A); additional data provided by Woelkerling (1993, pp. 80–81).

Distribution: Rottnest I., W. Aust., to Bowen I., Jervis Bay, N.S.W.

The species has not been reported from Tasmania.

Selected specimens: Jeannies Lookout, Rottnest I., W. Aust., 1–3 m deep on dead shell (*Woelkerling*, 12.ii.1978; LTB, 10624). Observatory Point, Esperance, W. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 5.ii.1984; LTB, 14160, 14171). Point Malcolm, SW of Israelite Bay, W. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 7.ii.1984; LTB, 14200). 'Nine Mile Reef', 15 km W of Eyre, W. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 1.ii.1984; LTB, 13948). Point Sinclair, S. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 15.ii.1984; LTB, 14493). Pearson I., (on causeway between South and Middle I.), S. Aust., upper sublittoral (*Specht*, 17.ii.1960; AD, A24548 = LTB, 16693). Boston I. (reef near Homestead landing), Port Lincoln, S. Aust., upper sublittoral, shaded (*Womersley*, 14.v.1968; AD, A32622 = LTB, 16692). Nuyts Reef, S. Aust., 30 m deep (*Shepherd*, 26.iii.1980; AD, A52210 = LTB, 16696). Port Willunga, S. Aust., 5 m deep (*P. Gordon*, 21.iii.1964; AD, A27685). Aldinga Beach, S. Aust. (*Woelkerling*, 3.i.1977; LTB, 11402). The Bluff (W side of Yorke Pen.), S. Aust., 1–2 m deep (*Womersley*, 15.ii.1981; AD, A52003). Port Elliot, S. Aust., 3–4 m deep (*Littler*, 31.xii.1975; AD, A47022 = LTB, 14680). Cape Willoughby, Kangaroo I., S. Aust., 0–2 m deep (*Campbell & Penrose*, 6.iv.1988; LTB, 15595). Cape Jaffa (Margaret Brock Reef), S. Aust., 10 m deep (*Lewis*, 15.ii.1974; AD, A45023 = LTB, 13631). Beachport, S. Aust., 3–6 m deep (*Campbell & Penrose*, 26.ii.1988; LTB, 15683). Cape Northumberland, S. Aust., 0–1 m deep (*Campbell & Penrose*, 2.xii.1986; LTB, 15546; *Harvey & Mascini*, 29.xi.1993; LTB, 16705; *Harvey & Daume*, 27.i.1994; LTB, 17280 and *Woelkerling*, 6.i.1977; LTB, 11401). Koonya Beach, Mornington Pen., Vic., rock pool (*Townsend*, 9.vii.1978; LTB, 17303 and 21.iv.1979; LTB, 17313). Sorrento (Back Beach), Vic., 0–1 m deep (*Townsend*, 11.vi.1978; LTB, 17314). Bowen I., Jervis Bay, N.S.W., 0–10 m deep (*Townsend*, 28.vii.1979; LTB, 17315).

Sporolithon durum occurs in intertidal reef pools and subtidally to depths of 30 m attached to rock or unattached and free-living as rhodoliths. At some localities, populations of rhodoliths are abundant and occur intermixed with attached thalli. Male and female-carposporangial thalli appear uncommon but can occur intermixed with tetrasporangial thalli, and several collections contain rhodoliths composed of male and tetrasporangial thalli. Because tetrasporangial sori are shed, most populations contain a high proportion of sterile thalli throughout the year.

Notes on other taxa reported from southern Australia

Townsend *et al.* (1995) provide information on 3 additional species that at some stage were ascribed to *Sporolithon* or *Archaeolithothamnion* and reported from southern Australia. One (*Sporolithon erythraeum*) involves an incorrect record; one (*Archaeolithothamnion australasicum*) involves a species of uncertain status; and one (*A. mirabile*) involves a heterotypic synonym of *Lithothamnion muelleri*, the type species of *Lithothamnion*.

FAMILY CORALLINACEAE Lamouroux 1812: 185 (as 'Corallineae')

Non-geniculate taxa by W.J. Woelkerling (with contributions by A.S Harvey & D.L. Penrose).

Geniculate taxa by H.B.S. Womersley & H.W. Johansen.

Thallus mostly calcified, of varying growth form; partly to almost entirely endophytic, or growing on various substrates (epigenous) and partially to completely affixed by cell adhesion, envelopment of host axes or a crustose or rhizoidal holdfast, or growing unattached and free-living as rhodoliths; branches with alternating, uncalcified genicula and calcified intergenicula, or without genicula. *Structure* pseudoparenchymatous or partly to largely composed of unconsolidated or contiguous filaments; organisation usually dorsiventral and/or radial or isobilateral; construction monomerous and/or dimerous or diffuse; monomerous portions consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; dimerous portions consisting of two distinct groups of filaments/cells: a unistratose ventral or internal layer in which each filament is composed of palisade cells, non-palisade cells or both, and secondly epithallial cells or multicellular filaments arising more or less perpendicularly from cells of ventral or internal layer filaments; diffuse portions consisting of branched endophytic or epigenous filaments that usually become partially consolidated in areas of conceptacle production; walls of most vegetative cells other than genicula usually completely impregnated with calcite; cells of adjacent filaments joined by cell-fusions or secondary pit-connections or rarely both, or not interconnected; epithallial cells present in most genera, terminating most filaments at thallus surface, distal walls commonly uncalcified; haustoria present in some genera.

Life history triphasic with isomorphic gametangial and tetrasporangial generations and a heteromorphic carposporangial generation.

Reproduction. Vegetative reproduction by thallus fragmentation, apomeiotic bispores or propagules. Gametangia and carposporangia borne in uniporate conceptacles; tetrasporangia and bisporangia borne in uniporate or multiporate conceptacles; gametangia and carposporangia normally formed on separate thalli from tetrasporangia and bisporangia.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles or rarely in the same conceptacle. Carpogonia terminating 1–4-celled filaments arising from the female conceptacle chamber floor. Carposporophytes with carposporangia arising directly from the fusion cell or terminating short gonimoblast filaments that usually arise from a conspicuous or inconspicuous fusion cell. Spermatangial filaments unbranched or branched, restricted to the male conceptacle chamber floor, or borne on the floor, walls and sometimes the roof.

Tetrasporangia arising from the conceptacle chamber floor; each mature sporangium usually containing four zonately arranged spores and in some non-geniculate genera producing apical plugs that individually block a pore of a multiporate conceptacle or collectively block the pore of a uniporate conceptacle prior to spore release; meiotic or apomeiotic bisporangia sometimes present.

Type genus: *Corallina* Linnaeus 1759: 805.

The Corallinaceae includes eight subfamilies, all represented in southern Australia, and it contains the most diverse array of growth forms and thallus structure of any family in the Rhodophyta. While some species are more or less constant in form and structure, other

species can vary greatly. Geniculate taxa are clearly multiaxial, and nongeniculate thalli or portions of thalli with monomerous construction can be interpreted as being multiaxial, and those with diffuse construction as being uniaxial. It is difficult, however, to interpret dimerous construction as being either multiaxial or uniaxial, and as a consequence, the terms uniaxial and multiaxial are not used here in describing the internal structure of non-geniculate corallines. Similarly, the terms cortex and medulla have not been used for the non-geniculate corallines (see Woelkerling & Irvine 1988, pp. 17, 18), but are for the geniculate taxa.

Macroscopically, the Corallinaceae are readily separated into geniculate and non-geniculate taxa, and although the presence or absence of genicula may not be of greater fundamental phylogenetic importance than various other characters (Cabioch 1972; Harvey & Woelkerling 1995, pp. 380, 381), it traditionally has been used as the first character in keys to subfamilies and genera (see below).

Most non-geniculate species cannot be identified solely from external features , and it is almost always necessary to examine tetrasporangial conceptacles cut vertically through the pore canal(s) to effect unequivocal determination. Most species possessing genicula, in contrast, can be identified from external features.

Nomenclatural information relating to the Corallinaceae and a summary of data on all subfamilies and tribes involving non-geniculate genera are provided by Woelkerling (1988, pp. 85–88); nomenclatural data on the subfamilies and tribes involving geniculate genera are summarised by Lebednik (1977a, p. 381), with additional data provided by Johansen & Silva (1978) and Johansen (1981). Harvey & Woelkerling (1995, p. 381, Table 3) provide a comparative summary of the diagnostic features of subfamilies as delimited here.

KEY TO SUBFAMILIES OF CORALLINACEAE

1. Thalli non-geniculate, lacking branches composed of uncalcified genicula and calcified intergenicula 2
1. Thalli geniculate, producing branches composed of uncalcified genicula and calcified intergenicula 6

2. Tetrasporangial and bisporangial conceptacles multiporate (Figs 76E, 85A) 3
2. Tetrasporangial and bisporangial conceptacles uniporate (Figs 97E, 104E) 4

3. Cells of adjacent filaments not linked by cell-fusions (Fig. 63D, F) or secondary pit-connections (Fig. 63E) ..... AUSTROLITHOIDEAE
3. Cells of adjacent filaments linked by cell-fusions; secondary pit-connections unknown ..... MELOBESIOIDEAE

4. Tetrasporangia and bisporangia producing apical plugs (Fig. 93A) that collectively block the pore of each conceptacle prior to spore release; cells of adjacent filaments not linked by cell-fusions or secondary pit-connections ..... CHOREONEMATOIDEAE
4. Tetrasporangia and bisporangia lacking apical plugs (e.g. Fig. 98C); cells of adjacent filaments linked by secondary pit-connections and/or cell-fusions 5

5. Cells of adjacent filaments linked principally by secondary pit-connections (Fig. 63E); cell-fusions (Fig. 63D, F) absent or rare ..... LITHOPHYLLOIDEAE
5. Cells of adjacent filaments linked principally by cell-fusions; secondary pit-connections absent or rare ..... MASTOPHOROIDEAE

6. Genicula (1-) multitiered; cells of adjacent filaments linked by secondary pit-connections; cell-fusions absent or rare ..... AMPHIROIDEAE
6. Genicula with a single tier or non-tiered; cells of adjacent filaments linked by cell-fusions; secondary pit-connections absent or rare 7

7. Branches from the top of intergenicula, dichotomous, pinnate, irregularly radial or proliferous; genicula composed of a single tier of cells; mucilage on branch apices not prominent ..... CORALLINOIDEAE
7. Branches from the genicula, clustered or rarely dichotomous; genicula composed of untiered multicellular filaments; terminal intergenicula with a prominent mucilaginous cap ..... METAGONIOLITHOIDEAE

SUBFAMILY AUSTROLITHOIDEAE Harvey & Woelkerling 1995: 363

by W.J. Woelkerling & A.S. Harvey

Thallus largely unconsolidated or encrusting; endophytic or epigenous and affixed by cell adhesion; genicula absent. *Structure* filamentous, partly or entirely pseudoparenchymatous with diffuse or dimerous construction; cells of adjacent filaments not joined by cell-fusions or secondary pit-connections.

Reproduction. Vegetative reproduction unknown. Gametangia borne in uniporate conceptacles; tetrasporangia and bisporangia borne in multiporate conceptacles.

Gametangial thalli apparently dioecious. Carpogonial filaments usually 2-celled, arising from each female conceptacle chamber floor. Carposporophytes developing within female conceptacles after karyogamy, composed of carposporangia terminating short gonimoblast filaments that arise from a central fusion cell. Spermatangial filaments unbranched or branched, produced from the floor, walls and roof of male conceptacle chambers.

Tetrasporangia and bisporangia borne on separate thalli from gametangia and carposporangia, with apical plugs each blocking a roof pore prior to spore release; tetrasporangia each containing zonately arranged spores; bisporangia each containing two bispores. Conceptacle roofs formed from filaments interspersed amongst and peripheral to developing sporangia.

Type genus: *Austrolithon* A. Harvey & Woelkerling 1995: 363.

The Austrolithoideae includes two genera: *Austrolithon*, known only from southern Australia, and *Boreolithon*, known only from the British Isles and France (A. Harvey & Woelkerling 1995). *Chaetolithon*, long interpreted as a corallinacean endophyte with multiporate tetrasporangial conceptacles, is now known to prossess uniporate tetrasporangial conceptacles and is considered a heterotypic synonym of *Choreonema*; a full account is provided by Woelkerling (1987b).

Genus AUSTROLITHON A. Harvey & Woelkerling 1995: 363

Thallus largely unconsolidated except in areas of conceptacle production, almost entirely endophytic including conceptacles; genicula absent. *Structure* partly filamentous and partly pseudoparenchymatous, without apparent dorsiventral, radial or isobilateral organisation; construction diffuse, consisting of branched endophytic filaments that usually become partially consolidated in areas of conceptacle production but collectively lack any regularised internal structure; epithallial cells absent from vegetative portions of thallus but terminating most conceptacle roof filaments, with distal walls rounded or flattened but not flared; cell elongation characteristics uncertain; cell-fusions, secondary pit-connections, haustoria and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporangia borne in largely endophytic uniporate conceptacles; tetrasporangia borne in largely endophytic multiporate conceptacles. Bisporangia unknown.

Gametangial thalli dioecious. Carpogonia terminating 2-celled filaments arising from the female conceptacle chamber floor. Carposporophytes each composed of a central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments both unbranched and branched, borne on the floor, walls and roof of each male conceptacle chamber.

Tetrasporangia scattered across the conceptacle chamber floor, roofs formed by filaments interspersed amongst and peripheral to sporangial initials; each mature sporangium

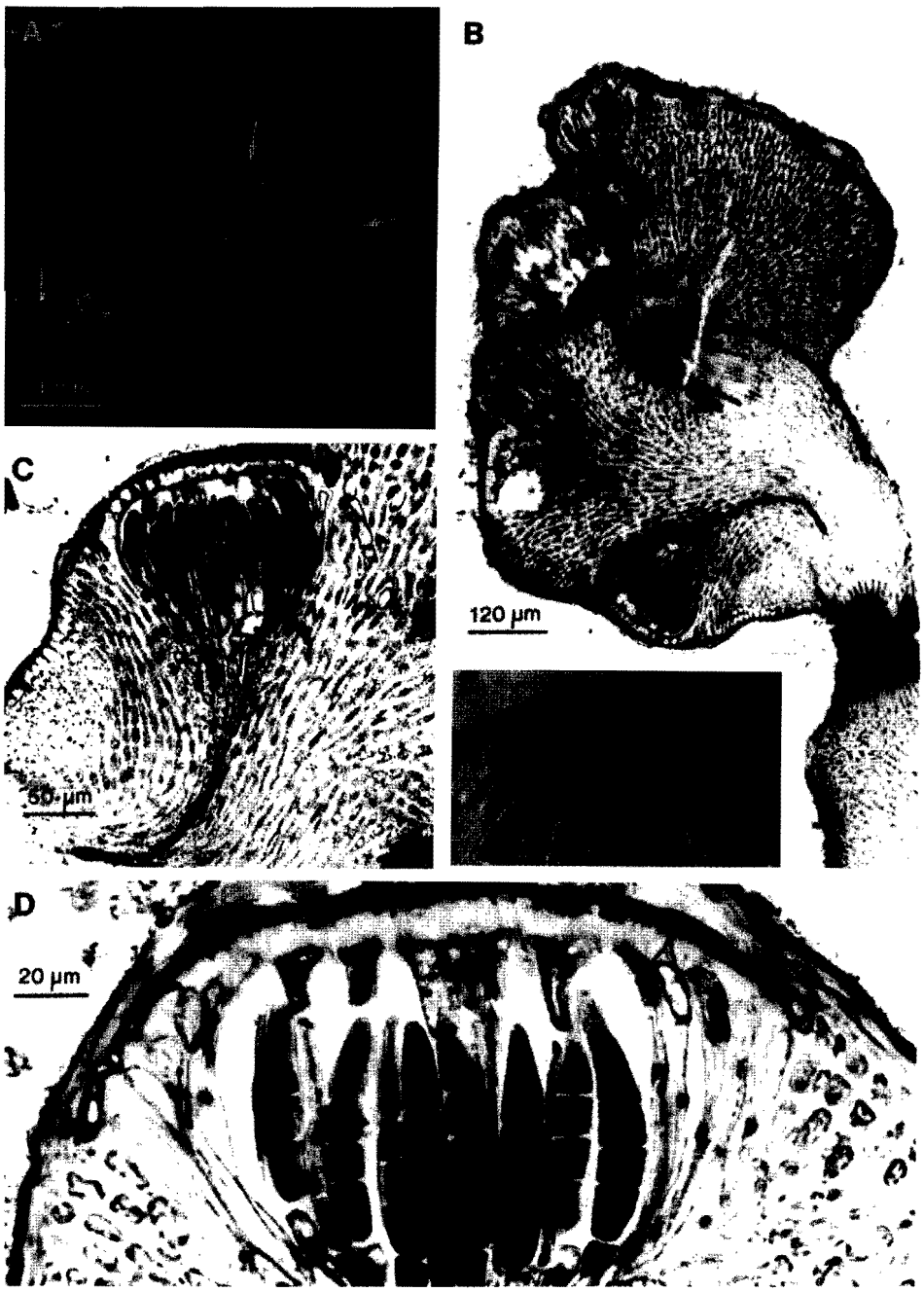


Fig. 67. *Austrolithon intumescens* (**A**, LTB, 15299; **B–E**, LTB, 15232). **A.** Portion of host (*Haliptilon roseum*) with swollen, gall-like deformed branch tips (arrows) containing *Austrolithon intumescens*. **B.** Section of a gall-like deformity with thalli of *Austrolithon intumescens*. **C.** Thallus of *Austrolithon intumescens* embedded within the host. **D.** Section of mature tetrasporangial conceptacle (pore plugs not evident with permanganate staining). **E.** Portion of tetrasporangial conceptacle roof with darkly stained pore plugs blocking the pore canals (stained with toluidine blue).

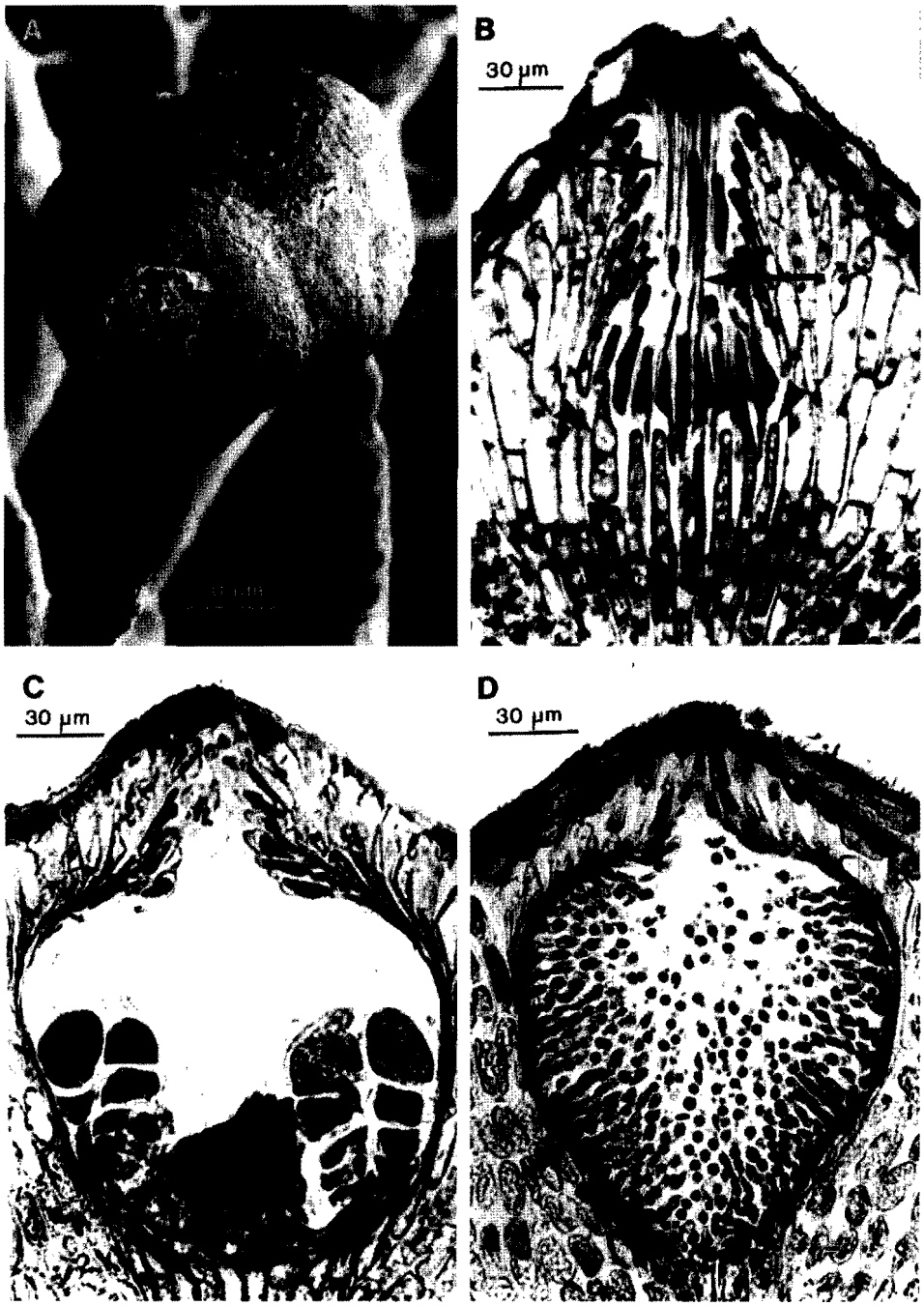


Fig. 68. *Austrolithon intumescens* (**A, B, D,** LTB, 15232; **C,** LTB, 14764). **A.** Surface view of multiporate tetrasporangial conceptacle largely embedded within gall-like deformity of host. **B.** Section of female-carposporangial conceptacle with mature carpogonial filaments (arrowheads) and trichogynes (arrows). **C.** Section of female-carposporangial conceptacle with mature carposporophyte. **D.** Section of male conceptacle with spermatangial filaments arising from chamber floor and walls.

containing four zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release.

Type species: *A. intumescens* A. Harvey & Woelkerling 1995: 363.

Austrolithon includes a single known species. This account is based on data in A. Harvey & Woelkerling (1995).

Austrolithon intumescens A. Harvey & Woelkerling 1995: 363, figs 1–41.

FIGS 67, 68

Thallus largely unconsolidated, mostly 0.2–3.0 mm in greatest extent, endophytic except for conceptacle roofs and formed within gall-like deformities of host branches mostly less than 1 mm in greatest dimension. *Structure* partly filamentous and partly pseudoparenchymatous; construction diffuse, consisting of branched filaments with cells mostly 6–12 μm in diameter and 16–49 μm long; epithallial cells mostly 5–12 μm in diameter and 12–14 μm long, terminating most conceptacle roof filaments but absent from vegetative thallus, with outermost walls rounded or flattened but not flared; cell elongation characteristics uncertain; cell-fusions and secondary pit-connections absent; haustoria and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporophytes produced in largely endophytic uniporate conceptacles; tetrasporangia produced in largely endophytic multiporate conceptacles. Bisporangia unknown.

Gametangial thalli probably dioecious. Carpogonia terminating 2-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs flush with or protruding above the host gall surface, 32–68 μm thick, composed of 2–5 layers of cells above the chamber, conceptacle chambers 59–145 μm in diameter and 67–115 μm high. Mature carposporophytes composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia 13–24 μm in diameter. Both unbranched and branched spermatangial filaments present, arising from the floor, walls and roof of male conceptacle chambers, mature male conceptacle roofs flush with or protruding above the host gall surface, 19–49 μm thick, composed of 2–5 layers of cells above the chamber, conceptacle chambers 54–125 μm in diameter and 54–140 μm high.

Tetrasporangial conceptacle roofs flush with or protruding slightly above the host gall surface, 17–23 μm thick above the chamber and composed of two cell layers, conceptacle chambers 81–140 μm in diameter and 62–108 μm high; tetrasporangia scattered across the conceptacle chamber floor, each mature sporangium 12–19 μm in diameter and 57–65 μm long, containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release.

Type from Kitty Miller Bay, Phillip I., Vic., (*Woelkerling, Campbell & Penrose*, 2.xii.1985); holotype in LTB (15232); depicted in A. Harvey & Woelkerling (1995, p. 364, figs 1–4).

Distribution: St Francis I., Isles of St Francis, S. Aust., to Kitty Miller Bay, Phillip I., Vic., and from Hunter I., Bass Strait, Tasmania.

Selected specimens: St Francis I., Isles of St Francis, S. Aust., 0–2 m deep (*Shepherd*, 6.i.1971; AD, A63422 = LTB, 15300). Cape du Couedic, Kangaroo I., S. Aust., lower eulittoral (*Womersley*, 12.i.1948; AD, A63423 = LTB, 17295). Cape Willoughby, Kangaroo I., S. Aust., drift (*Womersley*, 12.i.1947; AD, A63425 = LTB, 15301). Lawrence Rocks, Portland, Vic., 22 m deep (*Watson*, 20.xii.1982; AD, A63420 = LTB, 15298). Dinghy Cove, Lady Julia Percy I., Vic., 3–6 m deep (*Shepherd*, 4.i.1968; AD, A63424 = LTB, 15299). Kitty Miller Bay, Phillip I., Vic., on *Haliptilon* (*Turner*, 24.i.1979; LTB, 14764). Hunter I., Tas., in pools (*Bennett*, 14.i.1954; AD, A63421 = LTB, 15303).

Austrolithon intumescens has been found only in the geniculate coralline *Haliptilon roseum;* host thalli containing the endophyte have been collected from intertidal pools and subtidally to depths of 22 m. *A. intumescens* causes irregularly shaped, swollen, gall-like deformities of host branches; galls can be readily detected on host specimens using a stereomicroscope. Apical plugs on tetrasporangia stain well with toluidine blue but not with potassium permanganate.

SUBFAMILY MELOBESIOIDEAE Bizzozero 1885: 109 (as 'Melobesieae')

by W.J. Woelkerling

Thallus encrusting to warty, lumpy, fruticose, discoid, layered, foliose or arborescent, prostrate to erect; partially endophytic, epigenous or unattached and free-living as rhodoliths; genicula absent. *Structure* pseudoparenchymatous with monomerous or dimerous construction; cells of adjacent filaments joined by cell-fusions, secondary pit-connections unknown.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia borne in uniporate conceptacles; tetrasporangia and bisporangia borne in multiporate conceptacles.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles or rarely in the same conceptacle. Carpogonial filaments mostly 2–4-celled, arising from the female conceptacle chamber floor. Carposporophytes developing within female conceptacles after karyogamy, composed of carposporangia terminating short gonimoblast filaments that arise from a central fusion cell or more commonly from an irregularly shaped fusion cell that may look discontinuous in section, or from a several-celled fusion cell complex, or without an evident fusion cell. Spermatangial filaments unbranched or branched, confined to the male conceptacle chamber floor or more commonly produced from both floor and roof.

Tetrasporangia and bisporangia borne on thalli separate from gametangia and carposporangia, with apical plugs each blocking a roof pore prior to spore release; tetrasporangia each containing four zonately arranged spores; bisporangia each containing two bispores. Conceptacle roofs formed from filaments interspersed amongst and peripheral to developing sporangia.

Type genus: *Melobesia* Lamouroux 1812: 186.

The Melobesioideae includes nine genera, six of which (*Lithothamnion, Mastophoropsis, Melobesia, Mesophyllum, Phymatolithon, Synarthrophyton*) are represented in southern Australia. *Clathromorphum* (see Lebednik 1977b; Shepherd & Turner 1985, p. 288; Woelkerling 1988) is reported from various parts of the world but is not known from Australia (Woelkerling & Harvey 1993, p. 600); *Exilicrusta* (see Chamberlain 1992; Chamberlain & Irvine 1994c) is known only from the British Isles, and *Kvaleya* (see Adey & Sperapani 1971; South & Tittley 1986; Woelkerling 1988) is known from various localities in the boreal Atlantic and Arctic. *Sporolithon*, formerly placed by many authors (see Woelkerling & Townsend 1988, p. 203) in the Melobesioideae, is now referred to a separate family, the Sporolithaceae. *Leptophytum*, recognised by some authors, is considered in need of further evaluation (Woelkerling 1988, p. 217; Wilks & Woelkerling 1994, pp. 199–201). The Lithothamnioideae Foslie (1908: 19) is a heterotypic synonym of the Melobesioideae, while the Nulliporoideae Harvey (1849: 94) is an illegitimate older name (see Woelkerling 1988, p. 158).

KEY TO GENERA OF MELOBESIOIDEAE

1. Thallus construction dimerous (Figs 69C, 71C); consisting of two distinct groups of laterally cohering filaments/cells: a ventral unistratose layer of filaments each composed of palisade or non-palisade cells and secondly epithallial cells or multicellular filaments arising more or less perpendicularly from cells of the ventral-most layer....MELOBESIA
1. Thallus construction monomerous (Fig. 62A, B); consisting of a single system of branched, laterally cohering, filaments that contribute to a ventrally or centrally situated core and a peripheral region where portions of filaments curve outwards towards the thallus surface.....2

    2. Thalli arborescent (Fig. 73A), composed of flattened, branched, flexible, ribbon like ascending or erect axes that arise from a distinct holdfast and a compressed to flattened stipe.....MASTOPHOROPSIS
    2. Thalli encrusting, warty, lumpy, fruticose, discoid, layered and/or foliose; not producing ribbon like branches, stipes and holdfasts 3

3. Distal walls of terminal epithallial cells flattened and flared (Fig. 63C) ..... LITHOTHAMNION
3. Distal walls of terminal epithallial cells rounded or flattened but not flared (Fig. 63A, B) 4

4. Subepithallial initials as short as or shorter than the cells immediately subtending them (Fig. 63A); tetrasporangial and bisporangial conceptacles arising adventitiously from groups of vegetative cells within the thallus (Figs 78E, 80E) ..... PHYMATOLITHON
4. Subepithallial initials as long or longer than the cells immediately subtending them (Fig. 63B); tetrasporangial and bisporangial conceptacles arising directly from groups of subepithallial initials (Figs 86C, 89A) 5

5. Male conceptacles with only unbranched spermatangial filaments (Figs 83D, 85D) ..... MESOPHYLLUM
5. Male conceptacles with mostly branched spermatangial filaments (Fig. 91C) ..... SYNARTHROPHYTON

Note on key: The use of spermatangial characters to delimit *Synarthrophyton* from *Mesophyllum* is discussed by Harvey *et al.* (1994, pp. 340–341). Because tetrasporangial or bisporangial plants are more commonly found than male plants in southern Australia, the following supplementary tabular key is provided for the identification of the five southern representatives of these genera (4 species of *Mesophyllum*; one of *Synarthrophyton*). Further comments on identifying *Mesophyllum engelhartii* and *Synarthrophyton patena* are provided in the accounts of those species.

Supplementary tabular key to southern Australian species of *Mesophyllum* and *Synarthrophyton*. T/B = tetrasporangial/bisporangial. Characters are depicted in figures accompanying each species account.

	T/B CONCEPTACLE ROOF	T/B CONCEPTACLE PORE CANALS	SPERMATANGIAL FILAMENTS
Mesophyllum engelhartii (Figs 82, 83)	not differentiated into a peripheral rim and a central sunken pore-plate	pore canals bordered by cells similar in size and shape to other roof cells above chamber	simple
Mesophyllum incisum (Figs 84, 85)	not differentiated into a peripheral rim and a central sunken pore-plate	pore canals bordered by cells that are narrower and more elongate than adjacent roof cells	simple
Mesophyllum macroblastum (Figs 86, 87)	differentiated into a peripheral rim and a central sunken pore-plate	pore canals bordered by cells similar in size and shape to other roof cells above chamber	simple
Mesophyllum printzianum (Figs 88, 89)	differentiated into a peripheral rim and a central sunken pore-plate	pore canals bordered by cells that are narrower and more elongate than adjacent roof cells	simple
Synarthrophyton patena (Figs 90, 91)	not differentiated into a peripheral rim and a central sunken pore-plate	pore canals bordered by cells similar in size and shape to other roof cells above chamber	branched

Genus MELOBESIA Lamouroux 1812: 186

Thallus encrusting, epigenous and completely affixed by cell adhesion; genicula absent. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, consisting of two distinct groups of cohering filaments/cells: a single ventral layer in which each filament is composed of palisade and/or non-palisade cells, and secondly epithallial cells or multicellular filaments arising dorsally and more or less perpendicularly from cells of ventral layer filaments; cell elongation characteristics uncertain; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; epithallial cells terminating most filaments at thallus surface, distal walls rounded or flattened but not flared; haustoria and trichocytes unknown.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia and carposporangia borne in uniporate conceptacles; tetrasporangia and bisporangia borne in multiporate conceptacles that apparently arise from groups of subepithallial initials; gametangia and carposporangia formed on separate thalli from tetrasporangia and bisporangia.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Carposporophytes when mature apparently composed of one (or several?) inconspicuous fusion cell (or lacking an evident fusion cell) and several-celled gonimoblast filaments with terminal carposporangia. Spermatangial filaments unbranched, borne on the floor, walls and roof of male conceptacle chambers.

Tetrasporangia and bisporangia scattered across the conceptacle chamber floor, roofs formed by filaments interspersed amongst and peripheral to sporangial initials; each mature sporangium containing zonately arranged tetraspores or two bispores and possessing an apical plug that blocks a roof pore prior to spore release.

Type species: *M. membranacea* (Esper)Lamouroux 1812: 186. Basionym: *Corallina membranacea* Esper 1806: Corallina Tab. XII.

Over 160 species and infraspecific taxa have at some stage been ascribed to *Melobesia* (Woelkerling 1988, p. 190). Many of these, including 13 species recorded from southern Australia (Wilks & Woelkerling 1991, pp. 527–529), are now known to belong to other genera. The number of true species of *Melobesia* remains uncertain, and reliable concepts for most species scarcely exist. Details relating to generic etymology, nomenclature, synonymy, infrageneric classification, *etc.* are provided by Woelkerling (1988, p. 186–191). This account of southern Australian species, including the type species, follows Wilks & Woelkerling (1991).

KEY TO SPECIES OF *MELOBESIA*

1. Mature tetrasporangial conceptacle roofs raised above or flush with surrounding thallus surface; pore-plate (Fig. 69E) composed of cells that are similar in size and shape to other roof cells; tetrasporangial initials situated one cell layer below the thallus surface; mature male and female-carposporangial conceptacle roofs (Fig. 70C, D) composed of short, squat cells ..... 1. *M. membranacea*
1. Mature tetrasporangial conceptacle roofs flush with or slightly sunken below surrounding thallus surface; pore-plate (Fig. 71D) sharply differentiated from the remainder of roof, composed of cells that differ in size and shape from other roof cells; tetrasporangial initials situated five or more cell layers below the thallus surface; mature male and female-carposporangial conceptacle roofs (Fig. 72C, D) containing at least one layer of longer cells overlying layers of small, densely packed cells ..... 2. *M. rosanoffii*

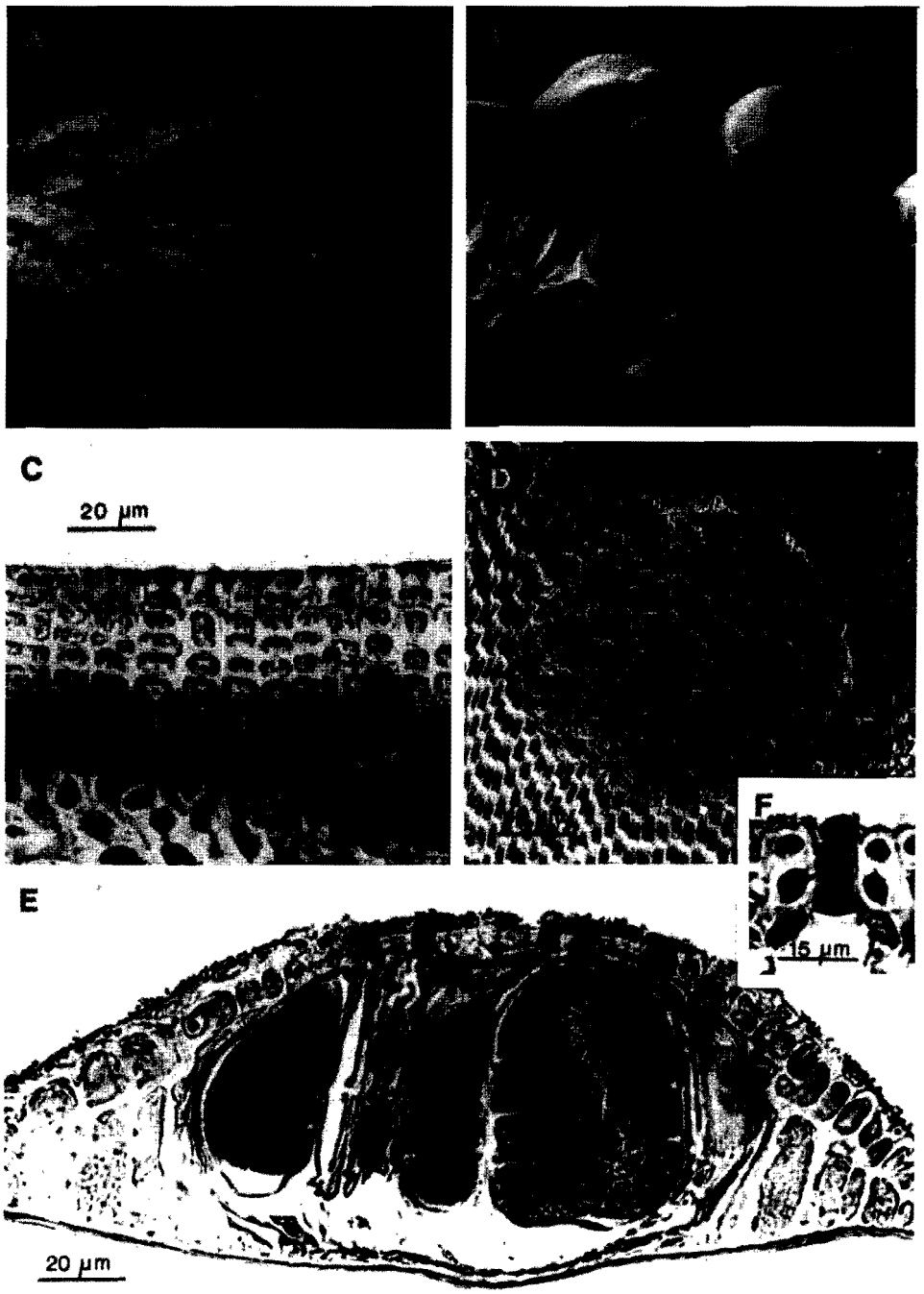


Fig. 69. *Melobesia membranacea* (**A,** LTB, 16101; **B, E,** LTB, 15801; **C,** LTB, 16034; **D,** LTB, 16121; **F,** LTB, 15913). **A.** Population of encrusting thalli growing on *Laurencia*. **B.** Encrusting thalli with tetrasporangial conceptacles growing on *Caulerpa papillosa*. **C.** Section of vegetative thallus showing dimerous construction. Note ventral layer of filaments (arrows) from which new filaments arise dorsally. **D.** Surface view of multiporate tetrasporangial conceptacle. **E.** Section of mature tetrasporangial conceptacle. **F.** Portion of tetrasporangial conceptacle roof with a pore canal and bordering filaments.

1. **Melobesia membranacea** (Esper)Lamouroux 1812: 186. Chamberlain 1985: 673, figs 1–4. Chamberlain & Irvine 1994c: 196, figs 7B, 39A, 75, 93, 94. Harvey 1863, synop.: xxx. Rosanoff 1866: 66, pl. II figs 13–16, pl. III fig. 1. Wilks & Woelkerling 1991: 522, figs 1–22. Woelkerling 1988: 197, figs 214–216.
Corallina membranacea Esper 1806: Corallina Tab. XII.
Epilithon membranaceum (Esper)Heydrich 1897a: 408. Kylin 1928: 7, figs 19–21. Suneson 1937: 59, fig. 36.
Lithothamnion membranaceum (Esper)Foslie 1898b: 7. Lucas 1912: 162; 1931b: 57.
Melobesia corticiformis Kützing 1849: 696. Barton 1893: 202.

Additional references involving these binomials, previous southern Australian records and known heterotypic synonyms are given by Wilks & Woelkerling (1991).

FIGS 69, 70

Thallus normally pinkish, encrusting, mostly 0.4–15 mm across and 10–75 μm thick, epigenous and completely affixed by cell adhesion. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, consisting of a single ventral layer of branched, laterally cohering, filaments each composed of palisade or non-palisade cells 2–13 μm long and 2–30 μm high, and additionally of epithallial cells or multicellular simple or branched, laterally cohering, filaments that arise dorsally and more or less perpendicularly from most cells of ventral layer filaments and are each composed only of an epithallial cell 2–10 μm in diameter and 2–8 μm long or with additional subtending cells 2–15 μm in diameter and 2–15 μm long; distal walls of epithallial cells rounded or flattened but not flared; cell elongation characteristics uncertain; cells of adjacent filaments joined by cell-fusions; secondary pit-connections, haustoria, and trichocytes not observed.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporophytes produced in uniporate conceptacles; tetrasporangia produced in multiporate conceptacles; bisporangia not observed.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above or flush with surrounding thallus surface, 5–25 (-40) μm thick, composed of 2–8 layers of short, squat cells, conceptacle chambers 50–250 μm in diameter and 25–80 μm high. Carposporophytes when mature apparently consisting of one (or several?) inconspicuous fusion cells bearing several-celled gonimoblast filaments with terminal carposporangia 18–60 μm in diameter. Spermatangial filaments unbranched, arising from the floor, walls and roof of male conceptacle chambers, mature male conceptacle roofs protruding above or flush with surrounding thallus surface, 7–20 μm thick, composed of 2–7 layers of more or less squat cells, conceptacle chambers 57–130 μm in diameter and 25–40 μm high.

Tetrasporangial conceptacle roofs protruding above or flush with surrounding surface, commonly but not always differentiated into a peripheral rim and a central sunken pore-plate, pore-plate composed of cells that are similar in size and shape to other roof cells, roof 2–5 cells thick above the chamber, conceptacle chambers (35-) 50–252 μm in diameter and 15–83 μm high; tetrasporangial initials situated one cell layer below the thallus surface, scattered across the conceptacle chamber floor, each mature sporangium 10–53 μm in diameter and 22–65 μm long, containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release; bisporangia not observed.

Type from an unspecified locality in France; neotype in CN (unnumbered); designated by Chamberlain (1985, p. 677); depicted in Chamberlain (1985, p. 675 fig. 2) and Wilks & Woelkerling (1991, p. 509, fig. 1).

Distribution: Widespread, but many records require confirmation (Wilks & Woelkerling 1991, p. 524; Chamberlain & Irvine 1994c, p. 199). In Australia, Flat Rock (30 km N of Dongara), W. Aust., to Gabo I., Vic., and around Tasmania.

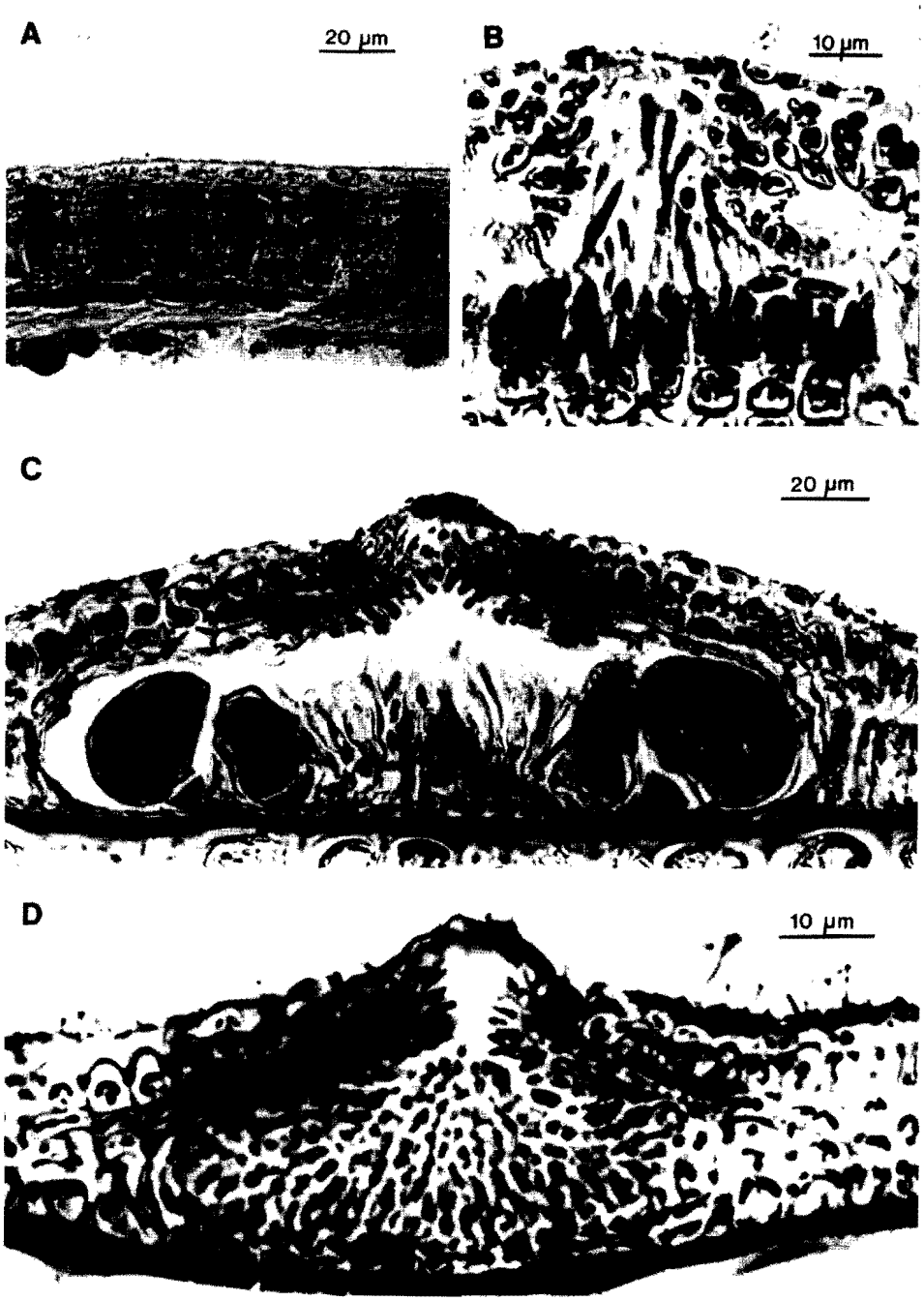


Fig. 70. *Melobesia membranacea* (**A,** LTB, 16030; **B,** LTB, 16020; **C,** LTB, 15981; **D,** LTB, 15983). **A.** Section of very young tetrasporangial conceptacle with initials one cell layer below the thallus surface (compare with Fig. 72A of *M. rosanoffii*). **B.** Section of female-carposporangial conceptacle with mature carpogonial filaments. **C.** Section of female-carposporangial conceptacle with mature carposporophyte. **D.** Section of male conceptacle with mature, unbranched spermatangial filaments arising from chamber floor and roof.

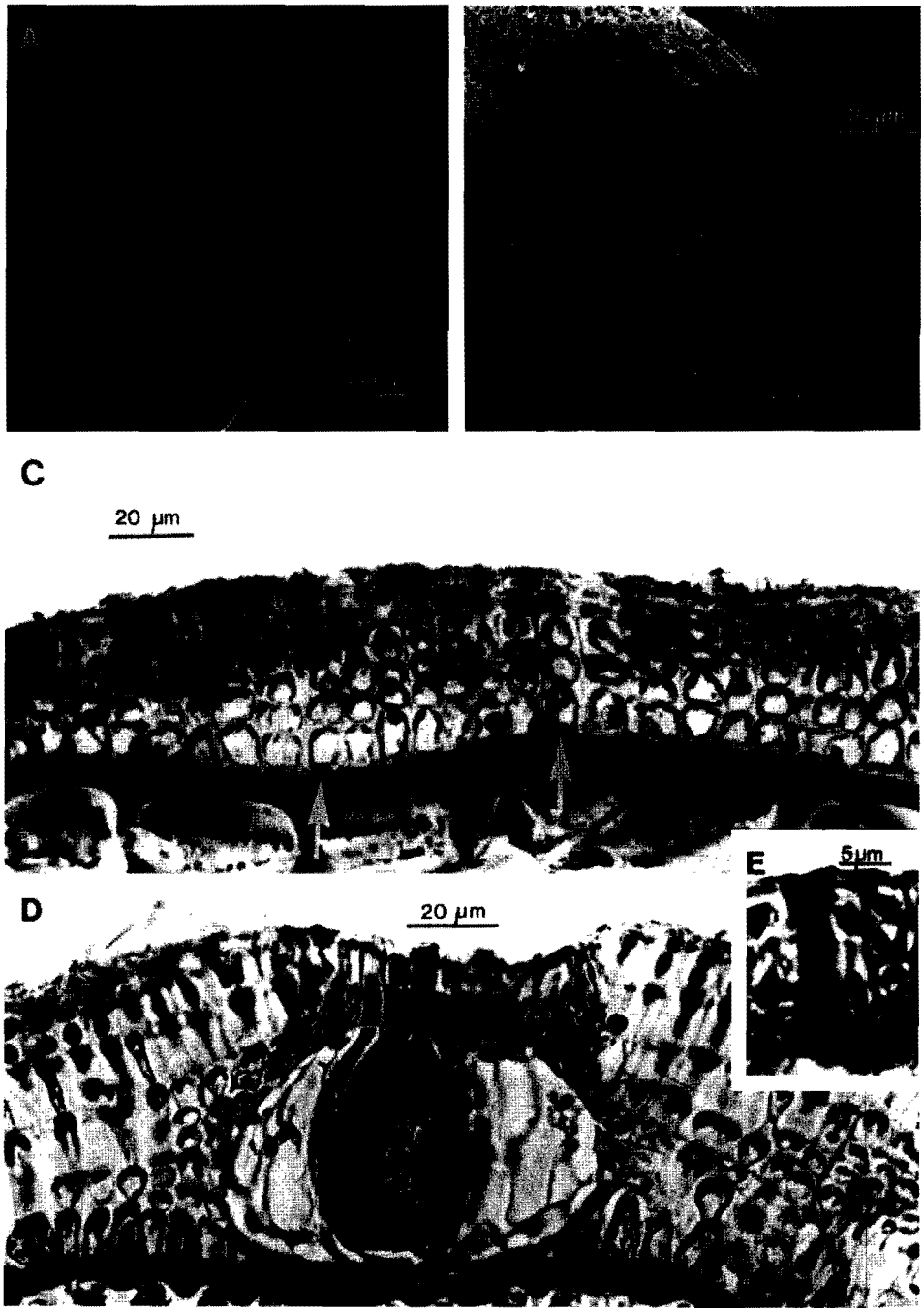


Fig. 71. *Melobesia rosanoffii* (**A, D,** LTB, 13268; **B, E,** TRH, unnumbered holotype; **C,** LTB, 17293). **A.** Population of encrusting thalli growing on *Acrocarpia paniculata*. **B.** Surface view of multiporate tetrasporangial conceptacle. **C.** Section of vegetative thallus showing dimerous construction. Note ventral layer of filaments (arrows) from which new filaments arise dorsally. **D.** Section of mature tetrasporangial conceptacle. **E.** Portion of tetrasporangial conceptacle roof with a pore canal and bordering filaments.

Selected specimens: Flat Rock (30 km N of Dongara), W. Aust. (*Woelkerling*, 26.ii.1979; LTB, 14849). Port Denison, W. Aust., outer reef pools (*Woelkerling*, 8.xi.1968; AD, A60520 = LTB, 16060). Esperance (Twilight Cove), W. Aust. (*Woelkerling*, 29.i.1978; LTB, 14881). Great Australian Bight (32¡24'S, 133¡30'E), S. Aust., 42 m deep (*Symond*, 5.v.1973; AD, A60353 = LTB, 16075). Elliston, S. Aust., 13 m deep (*Woelkerling*, 16.v.1968; AD, A60581 = LTB, 16121). Port Elliot, S. Aust., drift (*Womersley*, 17.x.1948; AD, A60578 = LTB, 16118). Cape du Couedic, Kangaroo I., S. Aust., shaded littoral pools (*Womersley*, 16.i.1965; AD, A60529 = LTB, 16069). Nora Creina, S. Aust., 0–3 m deep (*Campbell & Penrose*, 6.xi.1987; LTB, 15801). Beachport (Three Mile Rocks), S. Aust., on *Caulerpa cactoides* (*Wilks*, 17.ii.1990; LTB, 16030 and 20.ii.1990; LTB, 16034) and (*Woelkerling*, 26.ii.1988; LTB, 15981, 15983). Port MacDonnell, S. Aust. (*Woelkerling*, 12.ii.1989; LTB, 16020). Bridgewater Bay, Vic., drift (*Beauglehole*, 17.vii.1949; AD, A60548 = LTB, 16088). Rye (Number 16 reef, Ocean Beach), Vic., rock pool (*Platt & Woelkerling*, 21.xii.1982; LTB, 12612). Kitty Miller Bay, Phillip I., Vic., 0–2 m deep (*Wilks & Penrose*, 11.xii.1989; LTB, 15913). Gabo I., Vic., 13 m deep (*Shepherd*, 14.ii.1973; AD, A60538 = LTB, 16078). East Cove, Deal I., Tas., 1 m deep (*Shepherd & Lewis*, 5.v.1974; AD, A60561 = LTB, 16101). Fluted Cape, Bruny I., Tas., 16 m deep (*Shepherd*, 12.ii.1972; AD, A60543 = LTB, 16083). Clydes I., Eaglehawk Neck, Tas., 0–6 m deep (*Platt & Woelkerling*, 26.ii.1983; LTB, 13282).

Melobesia membranacea occurs epiphytically on a variety of green, brown and red algae in southern Australia and has been found intertidally on rocky reefs and in tide pools and subtidally to depths of 42 m. Dense populations involving vast numbers of thalli commonly occur and usually contain both gametangial and tetrasporangial individuals. Carposporophytes with conspicuous central fusion cells (Kylin 1928, p. 38; Suneson 1937, p. 60) were not found in southern Australian material, but fusion cell morphology in mature carposporophytes requires clarification (see Wilks & Woelkerling 1991, p. 525). Chamberlain & Irvine (1994c, pp. 197, 198, fig. 94D) suggest that gonimoblast filaments are borne peripherally from a central agglomeration of fusion cells, but this is not evident in their illustration. Chamberlain & Irvine (1994c, p. 198) also report that tetrasporangia very occasionally have cruciately arranged spores and that bisporangia occur; these have not been observed in southern Australian specimens.

2. **Melobesia rosanoffii** (Foslie)Lemoine 1912: LXIV. Wilks & Woelkerling 1991: 525, figs 23–37.
Lithothamnion rosanoffii Foslie 1908: 5. Woelkerling 1993: 191.
Epilithon rosanoffii (Foslie)Foslie 1909: 55.

Additional records are provided by Wilks & Woelkerling (1991).

FIGS 62C, 71, 72

Thallus normally pinkish, encrusting, mostly 1–10 mm across and 25–113 µm thick; epigenous and completely affixed by cell adhesion. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, consisting (in longitudinal view) of a single ventral layer of branched, laterally cohering, filaments each composed of palisade or non-palisade cells 5–10 µm long and 5–20 µm high, and additionally of epithallial cells or multicellular simple or branched, laterally cohering, filaments that arise dorsally and more or less perpendicularly from most cells of ventral layer filaments and are each composed only of an epithallial cell 2–5 µm in diameter and 2–5 µm long or with additional subtending cells 2–15 µm in diameter and 2–15 µm long; distal walls of epithallial cells rounded or flattened but not flared; cell elongation characteristics uncertain; cells of adjacent filaments joined by cell-fusions; secondary pit-connections, haustoria, and trichocytes not observed.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporophytes produced in uniporate conceptacles; tetrasporangia produced in multiporate conceptacles. Bisporangia unknown.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 2-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs more or less flush with surrounding thallus surface, 35–63 µm thick, composed of 5–14 layers of cells and commonly including at least one layer of longer cells overlying layers of small, densely packed cells; conceptacle chambers 100–193 µm in diameter and 30–55 µm high. Carposporophytes when mature apparently lacking an evident fusion cell and consisting of

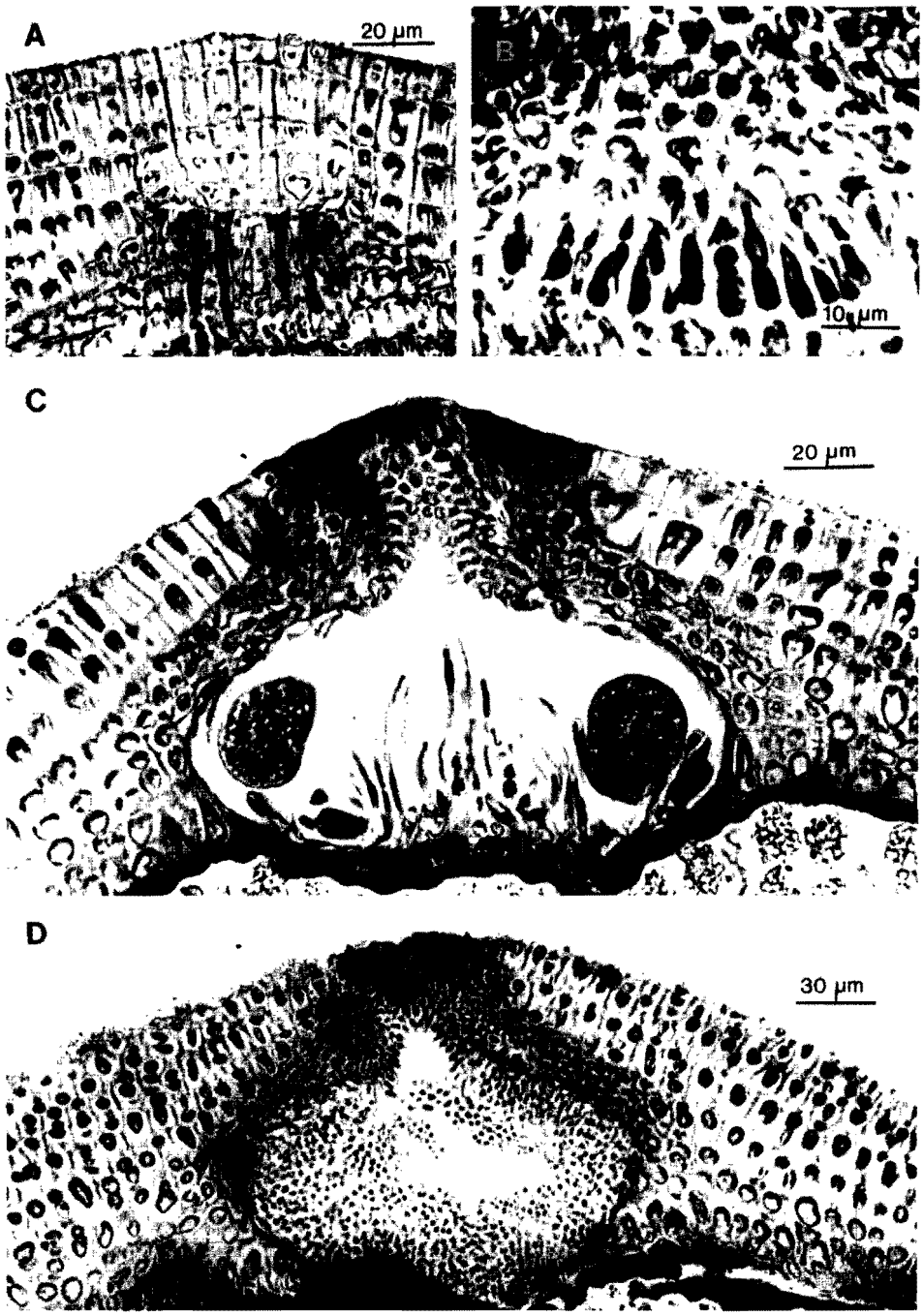


Fig. 72. *Melobesia rosanoffii* (**A,** LTB, 15757; **B,** LTB, 16021; **C, D,** LTB, 13268). **A.** Section of very young tetrasporangial conceptacle with initials more than five cell layers below the thallus surface (compare with Fig. 70A of *M. membranacea*). **B.** Section of female-carposporangial conceptacle with developing carpogonial filaments. **C.** Section of female-carposporangial conceptacle with mature carposporophyte. **D.** Section of male conceptacle with mature, unbranched spermatangial filaments arising from chamber floor and roof.

several-celled gonimoblast filaments bearing terminal carposporangia 25–30 μm in diameter. Spermatangial filaments unbranched, arising from the floor, walls and roof of male conceptacle chambers, mature male conceptacle roofs more or less flush with surrounding thallus surface, 25–43 μm thick, composed of 5–10 layers of cells including several layers of longer cells overlying layers of small, densely packed cells; conceptacle chambers 100–138 μm in diameter and 30–75 μm high.

Tetrasporangial conceptacle roofs more or less flush with or slightly sunken below surrounding surface, not normally differentiated into a peripheral rim and a central sunken pore-plate but pore-plate sharply differentiated anatomically from the remainder of roof and composed of cells that differ in size and shape from other roof cells, roof 2–7 cells thick above the chamber; conceptacle chambers 45–118 μm in diameter and 40–80 μm high; tetrasporangial initials situated five or more cell layers below the thallus surface, scattered across the conceptacle chamber floor, each mature sporangium 10–25 μm in diameter and 25–63 μm long, containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release.

Type from Port Phillip Bay, Vic.; holotype in TRH (unnumbered; includes slides 1342, 1641, and one unnumbered slide); depicted in Wilks & Woelkerling (1991, figs 23, 24), additional data provided by Woelkerling (1993, p. 191).

Distribution: Three Mile Rocks, Beachport, S. Aust., to Rye, Vic., and from Clydes I., Eaglehawk Neck, Tas.

Known specimens: Three Mile Rocks, Beachport, S. Aust. (*Woelkerling*, 26.ii.1988; LTB, 15989). Beachport (near Schnapper Point), S. Aust., drift on *Acrocarpia* (*Campbell & Penrose*, 26.ii.1988; LTB, 15757 and *Woelkerling*, 25.ii.1991; LTB, 16125). Port MacDonnell, S. Aust., on *Cystophora* (*Woelkerling*, 12.ii.1989; LTB, 16021).Rye (Number 16 reef, Ocean Beach), Vic., reef edge on *Laurencia elata* (*Morcom & Medhurst*, 2.iii.1994; LTB, 17293). Clydes I., Eaglehawk Neck, Tas., 0–6 m deep (*Platt & Woelkerling*, 26.ii.1983; LTB, 13268).

Melobesia rosanoffii has been found epiphytically on the brown algae *Acrocarpia* and *Cystophora* and on the red alga *Laurencia* in intertidal pools and subtidally to depths of 6 m. Most collections contain large populations of thalli and include both gametangial and tetrasporangial individuals.

Notes on other taxa reported from southern Australia

Wilks & Woelkerling (1991, pp. 527–529) provide information on 13 additional species and infraspecific taxa that at some stage were ascribed to *Melobesia* and reported from southern Australia. These include taxa whose status is uncertain, taxa now known to belong to other genera and taxa that are conspecific with species belonging to other genera.

Genus **MASTOPHOROPSIS** Woelkerling 1978: 210

Thallus arborescent, composed of a basal holdfast and erect stipes bearing branched, flexible, ribbon like branches; genicula absent. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; cell elongation occurring mainly behind actively dividing subepithallial initials that are usually as short as or shorter than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; epithallial cells terminating most filaments at thallus surface, distal walls rounded or flattened but not flared; haustoria and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporangia borne in uniporate conceptacles; tetrasporangia borne in multiporate conceptacles that apparently arise from groups of subepithallial initials; gametangia and carposporangia formed on separate thalli from tetrasporangia; conceptacle always borne only on dorsal surface of branches. Bisporangia unknown.

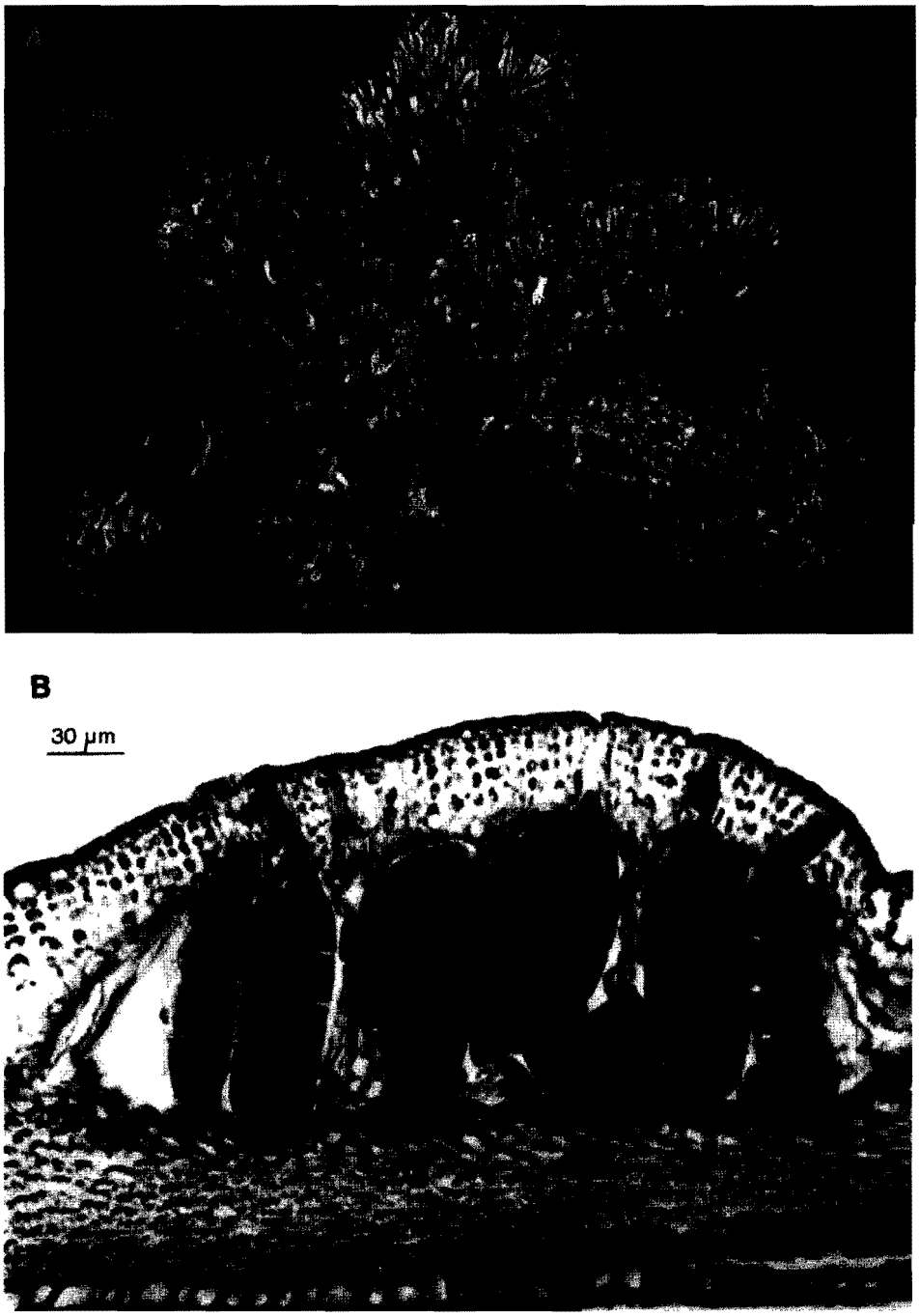


Fig. 73. *Mastophoropsis canaliculata* (**A,** LTB, 12731; **B,** LTB, 11579). **A.** Arborescent thallus detached from rock. **B.** Section of mature tetrasporangial conceptacle.

Gametangial thalli dioecious. Carpogonial filaments and young female conceptacles unknown. Mature carposporophytes composed of a inconspicuous central fusion cell and short gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, borne on the floor, walls and roof of male conceptacle chambers.

Tetrasporangia scattered across the conceptacle chamber floor; roofs formed by filaments interspersed amongst and peripheral to sporangial initials, each mature sporangium containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release.

Type species: *M. canaliculata* (Harvey)Woelkerling 1978: 210.

Mastophoropsis includes a single known species that appears restricted to southern Australia. This account is based on Woelkerling (1978) and Woelkerling (1988, pp. 180–185).

Mastophoropsis canaliculata (Harvey)Woelkerling 1978: 210, figs 1–19. Woelkerling 1988: 180, figs 201–213.

Mastophora canaliculata Harvey 1859: 310; 1863, synop.: xxx, pl. 263. Printz 1929: 47, pl. 73 figs 10–12.

Metamastophora canaliculata (Harvey)Setchell 1943: 132.

Additional references are provided by Woelkerling (1978, 1988).

PLATE 3 fig. 1; FIGS 73, 74

Thallus normally dark pink to dull red-brown, arborescent, mostly 5–15 cm tall, attached by a basal holdfast that produces 1–several erect stipes with flattened, branched, ribbon like branches that commonly have vein like thickenings in older portions; branching mostly in one plane, pseudodichotomous to pseudopolychotomous. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction monomerous, stipes and branches each consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 3–15 μm in diameter and 5–40 μm long; epithallial cells 5–15 μm in diameter and 4–15 μm long, terminating most filaments at the thallus surface, with distal walls rounded or flattened but not flared; cell elongation occurring mainly behind actively dividing subepithallial initials that are usually as short as or shorter than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions although sometimes difficult to detect; secondary pit-connections, haustoria, and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporophytes produced in uniporate conceptacles; tetrasporangia produced in multiporate conceptacles. Bisporangia unknown.

Gametangial thalli dioecious. Carpogonial stages unknown. Mature female-carposporangial conceptacle roofs protruding above surrounding thallus surface, 95–125 μm thick, usually composed of 13–17 layers of cells, conceptacle chambers 380–550 μm in diameter and 110–180 μm high. Mature carposporophytes apparently composed of an inconspicuous central fusion cell and short gonimoblast filaments bearing terminal carposporangia 30–80 μm in diameter. Spermatangial filaments unbranched, arising from the floor, walls and roof of male conceptacle chambers, mature male conceptacle roofs protruding above surrounding thallus surface, 45–100 μm thick, composed of 6–14 layers of cells; conceptacle chambers 340–450 μm in diameter and 30–75 μm high.

Tetrasporangial conceptacle roofs protruding above surrounding surface, 4–10 cells thick above the chamber, pore canals lined by cells that are similar in size and shape to other roof cells, conceptacle chambers 318–607 μm in diameter and 95–118 μm high; tetrasporangia scattered across the conceptacle chamber floor, each mature sporangium 40–63 μm in diameter and 70–135 μm long, containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release.

Type from Tasmania (locality not specified); lectotype in TCD (unnumbered); designated by Woelkerling (1978, p. 211); depicted in Woelkerling (1978, p. 212, fig. 1).

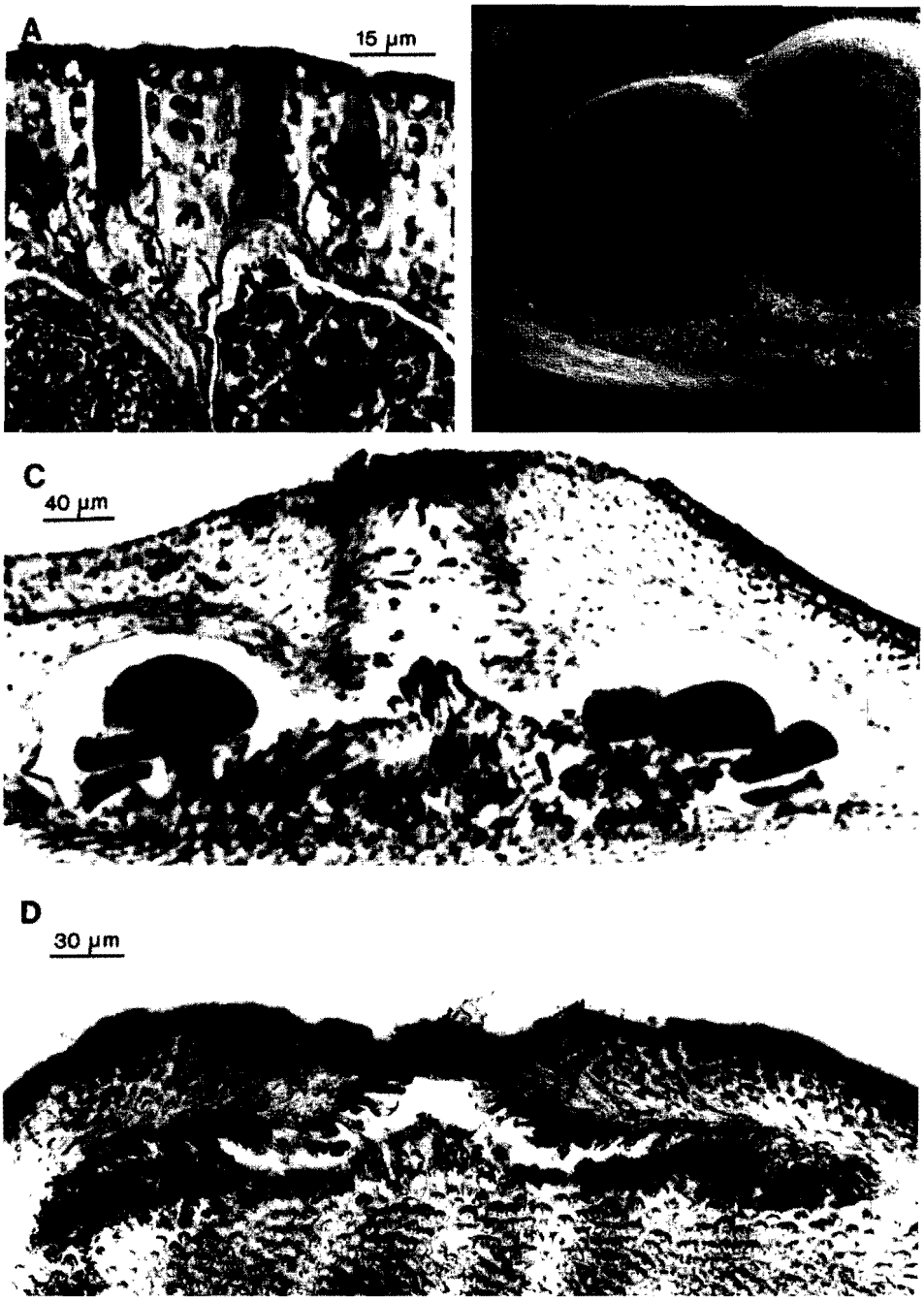


Fig. 74. *Mastophoropsis canaliculata* (**A,** LTB, 11579; **B,** LTB, 12731; **C,** LTB, 182; **D,** LTB, 17320). **A.** Portion of tetrasporangial conceptacle roof with pore canal and bordering filaments. **B.** Surface view of tetrasporangial conceptacle. **C.** Section of female-carposporangial conceptacle with mature carposporophyte. **D.** Section of male conceptacle with unbranched spermatangial filaments arising from chamber floor and roof.

Distribution: Encounter Bay, S. Aust., to Waterloo Bay, Wilsons Prom., Vic. and from Tasmania.

Selected specimens: Encounter Bay, S. Aust. (*Cleland*, 1932; NSW, A3337). Robe, S. Aust., drift (*Womersley*, 15.iv.1959; AD, A23001). Nora Creina, S. Aust., drift (*Woelkerling*, 20.viii.1966; LTB, 182). Three Mile Rocks, Beachport, S. Aust., drift (*Woelkerling*, 26.ii.1988; LTB, 15973 and 18.ii.1995; LTB, 17320). Cape Northumberland, S. Aust., 15 m deep (*Turnbull*, 30.ix.1975; AD, A46600). Dinghy Cove, Lady Julia Percy I. Vic., 4.5–7.5 m deep (*Shepherd*, 3.i.1968; AD, A32315). Warrnambool, Vic., drift (*Womersley*, 13.iv.1959; AD, A22916). Anglesea, Vic. (*Lucas*, Jan. 1900; NSW, A 3336). Waterloo Bay, Wilsons Prom., Vic., 10 m deep (*Leach & Anderson*, 21.x.1977; LTB, 10264) and 3–4 m deep (*Leach*, 3.iii.1979; LTB, 11579). Spike Bay, Clarke I., Bass Strait, Tas., 6 m deep (*Leach*, 28.ii.1979; LTB, 11602). Limestone Gully, S of Deep Glen Bay, Forestier Pen., Tas., 8–14 m deep (*Gowlett-Holmes*, 14.v.1995; AD, A64421). Ninepin Point, D'Entrecasteaux Channel, Tas., 6–7 m deep (*Woelkerling, Platt & Brown*, 18.ii.1983; LTB, 12731). Recherche Bay, SE Tas., 18 m deep (AIMS–NCI, Q66C, 14.ii.1991; AD, A61345). Lady Bay, Southport, Tas., 2–3 m deep (*Brown & Kenchington*, 14.x.1986; AD, A57655).

Mastophoropsis canaliculata is known mainly from drift specimens, but thalli attached to rock have been found in intertidal cave pools and at depths of 10 m in Victoria, 15 m in South Australia and 18 m in Tasmania. Thalli of *M. canaliculata* are usually easily recognised in the field from their arborescent growth form and multiporate tetrasporangial conceptacles. Only a few male thalli are known, and it is uncertain whether spermatangial filaments are simple or branched. Carposporangial thalli are uncommon, and the ontogeny of all reproductive structures requires further investigation.

Genus **LITHOTHAMNION** Heydrich 1897b: 412, *nom. cons.*

Thallus encrusting to warty, lumpy or fruticose, epigenous and partially to completely affixed by cell adhesion or envelopment of host axes, or unattached and free-living as rhodoliths; genicula absent. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; cell elongation occurring mainly within actively dividing subepithallial initials that are usually as long as or longer than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions; secondary pit-connections absent; epithallial cells terminating most filaments at thallus surface, distal walls usually flattened and flared; trichocytes occasional in some species; haustoria unknown.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia and carposporangia borne in uniporate conceptacles; tetrasporangia and bisporangia borne in multiporate conceptacles that apparently arise from groups of subepithallial initials; gametangia and carposporangia formed on separate thalli from tetrasporangia and bisporangia.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles or rarely within the same conceptacle. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature carposporophytes apparently lacking a conspicuous central fusion cell and composed of short gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments both unbranched and branched, borne on the male conceptacle chamber floor, walls and roof.

Tetrasporangia and bisporangia scattered across the conceptacle chamber floor, roofs formed by filaments interspersed amongst and peripheral to sporangial initials, each mature sporangium containing zonately arranged tetraspores or bispores and possessing an apical plug that blocks a roof pore prior to spore release.

Lectotype species: *L. muelleri* Lenormand *ex* Rosanoff 1866: 101; designated by Woelkerling (1983a: 193).

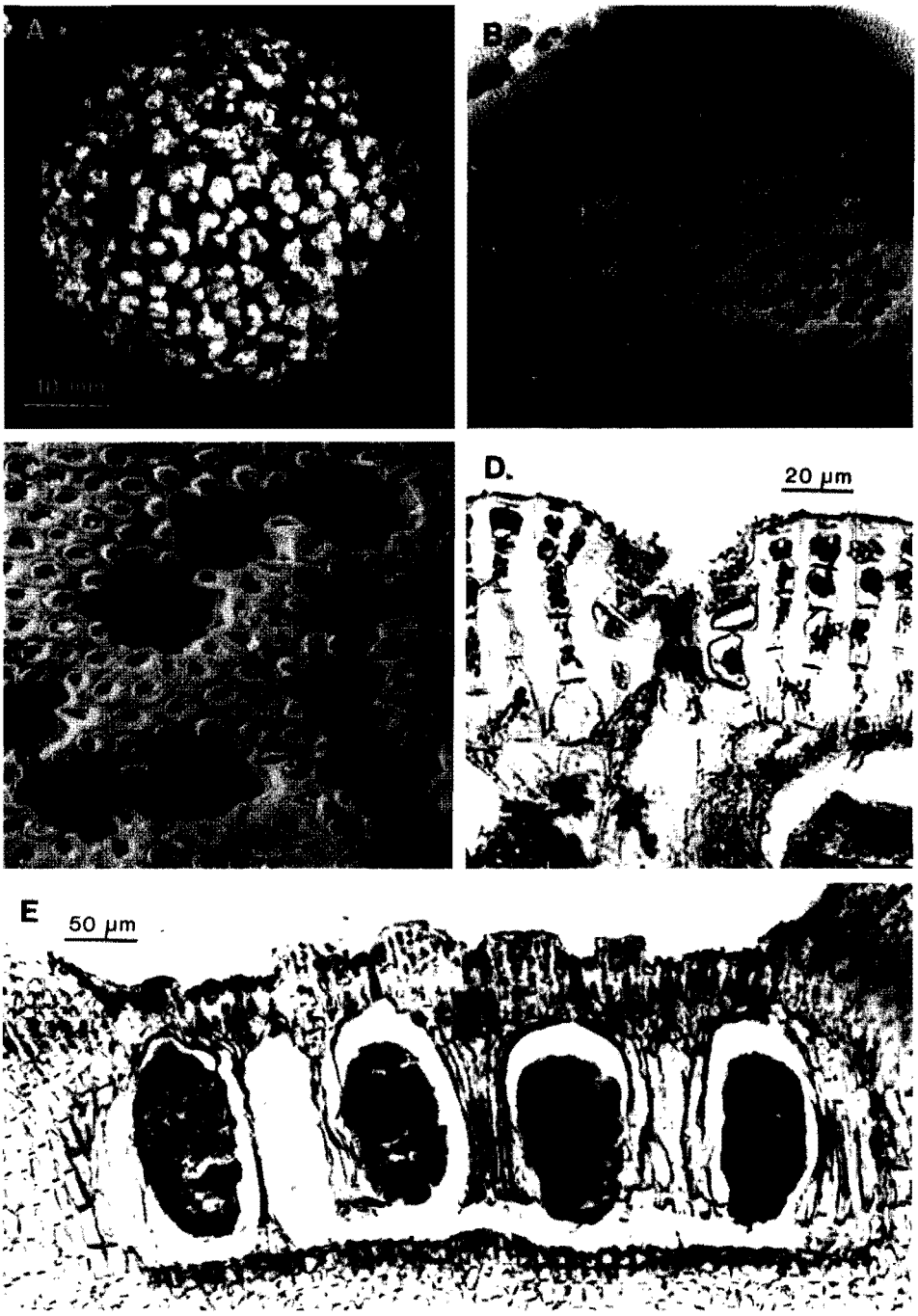


Fig. 75. *Lithothamnion indicum* (**A–E,** LTB, 12729). **A.** Fruticose thallus forming a rhodolith. **B.** Surface view of tetrasporangial conceptacles. **C.** Surface view of tetrasporangial conceptacle roof pitted with depressions around pore canals. **D.** Portion of tetrasporangial conceptacle roof with pore canals and bordering filaments whose cells differ somewhat in shape from other roof filaments. **E.** Section of mature tetrasporangial conceptacle.

Over 730 species and infraspecific taxa have been ascribed to *Lithothamnion* (Woelkerling 1988, p. 179). The number of true species of *Lithothamnion* is unclear, and reliable concepts for most species scarcely exist. Wilks & Woelkerling (1995) gave a detailed account of tetrasporangial thalli of the type species, but noted that gametangia and carposporophytes are poorly known. Thus, information on gametangia and carposporophytes provided in the generic description is based mainly on species other than the type and may require revision once new data on the type species become available. Early stages of carposporophyte development and gonimoblast filament ontogeny generally are poorly known. Details relating to generic etymology, nomenclature, synonymy, infrageneric classification, *etc.* are provided by Woelkerling (1988, pp. 169–180). This account of southern Australian species, including the lectotype, follows Wilks & Woelkerling (1995).

KEY TO SPECIES OF *LITHOTHAMNION*

1. Roofs of mature tetrasporangial conceptacles pitted with depressions, each of which overlies a pore (Fig. 75B); tetrasporangial conceptacle pore canals bordered by cells that usually differ in size and shape from cells in other roof filaments (Fig. 75D) ..... 1. *L. indicum*
1. Roofs of mature tetrasporangial conceptacles not pitted with depressions around pores (Fig. 76B); tetrasporangial conceptacle pore canals bordered by cells that do not differ in size and shape from cells in other roof filaments (Fig. 76D) ..... 2. *L. muelleri*

1. **Lithothamnion indicum** Foslie 1907a: 7. Adey & Lebednik 1967: 58. De Toni 1924: 640. Foslie 1907c: 99; 1907d: 183. Lemoine 1930: 42, pl. 3 fig. 1, text fig. 3. Printz 1929: 42, pl. 13 figs 20–25 (as f. *typica*). Wilks & Woelkerling 1995: 558, figs 7–12. Woelkerling 1993: 125.
Lithothamnion fruticulosum f. *confinis* Foslie 1904b: 4. Woelkerling 1993: 58.

FIG. 75

Thallus normally pinkish to gray-pink, warty to lumpy or fruticose, unattached and forming rhodoliths mostly 25–100 mm in greatest dimension; protuberant branches, simple or branched, free from one another or fused to varying degrees, mostly 2–12 mm in diameter and 2–10 mm long. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, filaments with cells 2–20 µm in diameter and 2–40 µm long; epithallial cells 2–5 µm in diameter and 2–10 µm long, terminating most filaments at the thallus surface, with distal walls flattened and flared; cell elongation occurring mainly within actively dividing subepithallial initials that are mostly as long as or longer than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions; secondary pit-connections, haustoria and trichocytes unknown.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia and carposporophytes unknown; tetrasporangia produced in multiporate conceptacles. Bisporangia unknown.

Tetrasporangial conceptacle roofs flush with or protruding above surrounding surface, 3–8 cells thick above the chamber, pitted with surface depressions resulting from the degeneration of the uppermost cells of filaments surrounding the pore canals; pore canals normally lined by filaments that differ in appearance from other roof filaments and are each composed of a squat to flattened cell subtended by 1–2 more elongate cells; conceptacle chambers 450–600 µm in diameter and 150–170 µm high; tetrasporangia scattered across the conceptacle chamber floor, each mature sporangium 40–80 µm in diameter and 80–100 µm long, containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release.

Type from Corner Inlet, Victoria; lectotype in TRH (unnumbered, includes slides 444 and 445); designated by Woelkerling (1993, p. 125); depicted in Foslie (1904c, pl. 1 fig. 7, as *Lithothamnion fruticulosum* f. *crassiuscula*), Printz (1929, pl. 13 fig. 20) and Wilks & Woelkerling (1995, fig. 7).

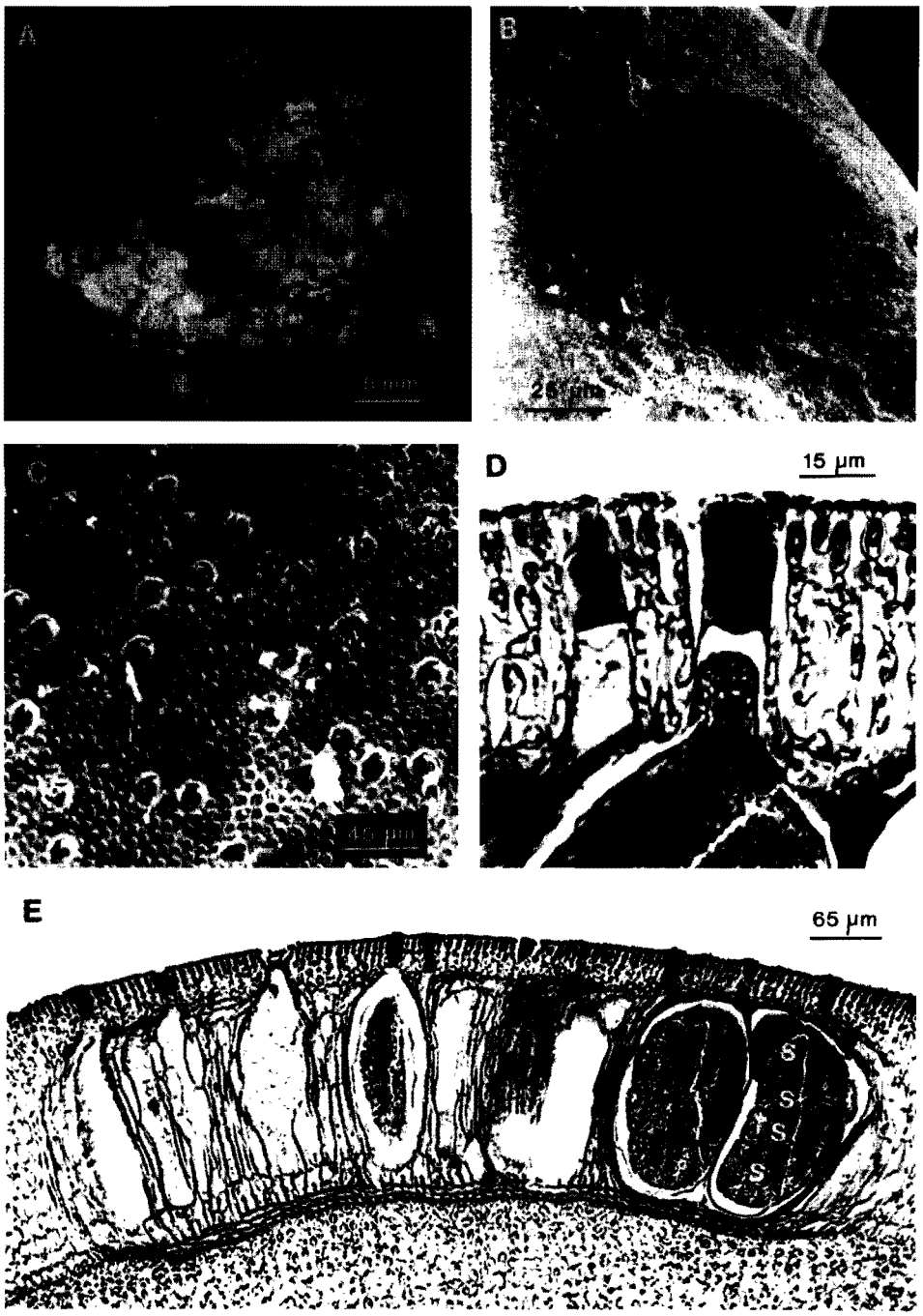


Fig. 76. *Lithothamnion muelleri* (**A, E,** LTB, 14121; **B,** LTB, 15364; **C, D,** LTB, 15719). **A.** Encrusting to warty thallus on rock. **B.** Surface view of tetrasporangial conceptacle. **C.** Surface view of tetrasporangial conceptacle roof showing pore canals flush with the surface. **D.** Portion of tetrasporangial conceptacle roof with pore canals and bordering filaments whose cells usually do not differ in size and shape from cells in other roof filaments. **E.** Section of mature tetrasporangial conceptacle showing sporangia with zonately arranged spores (s).

Distribution: Port Phillip Heads, Western Port and Corner Inlet, Victoria.

Records of this species from Mexico (Taylor 1945, p. 173) are unconfirmed and may be incorrect. Dawson (1960b, pp. 13–15) treated *L. indicum* as a synonym of '*Lithothamnion fruticulosum* (Foslie)Kützing', but the type of Kützing's taxon belongs to *Spongites*, and the correct name for the taxon to which Kützing's epithet *fruticulosum* has been misapplied has not been determined (Woelkerling 1985, pp. 135–139). Except for the type, the identities of specimens in TRH listed as *Lithothamnion indicum* (Adey & Lebednik 1967, p. 58) also require confirmation.

Known specimens: Port Phillip Heads, Vic., 16–20 m deep (1 km off Queenscliff lighthouse) (*Beanland*, 30.i.1983; LTB, 12729). Western Port, Vic (*Gabriel*, 1899; TRH, unnumbered, lectotype of *Lithothamnion fruticulosum* f. *confinis*). Corner Inlet, Vic. (*Gabriel*, 1897; TRH, unnumbered, lectotype; AD, A18856, isolectotype).

Lithothamnion indicum has been found at depths of 5–20 m as unattached and completely free-living rhodoliths. The presence of flattened and flared epithallial cells and multiporate tetrasporangial conceptacles clearly ally this species with *Lithothamnion*, but epigenous thalli are not known, gametangial and carposporangial thalli have not been observed, and further studies obviously are needed when additional material becomes available.

2. **Lithothamnion muelleri** Lenormand *ex* Rosanoff 1866: 101, pl. 6 figs 8–11. De Toni 1905: 1750. Lucas & Perrin 1947: 390. Wilks & Woelkerling 1995: 553, figs 1–6. Woelkerling 1983a: 190, figs 29–33.
Lithothamnion muelleri f. *cingens* Foslie 1900b: 69. Woelkerling 1993: 51.
Archaeolithothamnion mirabile Foslie 1899: 3. Woelkerling 1993: 151.
Lithothamnion mirabile (Foslie)Foslie 1909: 4.
Lithothamnion gabrieli Foslie 1905b: 3. Woelkerling 1993: 101.
Mesophyllum gabrieli (Foslie)Adey 1970: 24.

Additional references involving these binomials and further information on synonymy are provided by Wilks & Woelkerling (1995). Most published records of *L. muelleri* require confirmation as the name has been misapplied to thalli now known to belong to *Synarthrophyton patena* (see Harvey *et al.* 1994, p. 340; Wilks & Woelkerling 1995, p. 554).

FIGS 76, 77

Thallus normally dull pinkish, encrusting to warty, mostly 15–40 mm across and 0.1–4 mm thick or tall, epigenous and completely affixed by cell adhesion; protuberant branches simple or branched, mostly 1–4 mm in diameter and 1–6 mm long. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally situated core in crustose portions or centrally situated core in protuberant branches and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 2–15 µm in diameter and 2–30 µm long; epithallial cells 2–8 µm in diameter and 1–8 µm long, terminating most filaments at the thallus surface, with distal walls flattened and flared; cell elongation occurring mainly within actively dividing subepithallial initials that are mostly as long as or longer than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions; secondary pit-connections, haustoria, and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporophytes produced in uniporate conceptacles; tetrasporangia produced in multiporate conceptacles. Bisporangia unknown.

Gametangial thalli dioecious. Carpogonia and young female conceptacles unknown. Mature female-carposporangial conceptacle roofs protruding above or flush with surrounding thallus surface, 50–170 µm thick, composed of 5–25 layers of cells above the chamber, conceptacle chambers 240–600 µm in diameter and 100–200 µm high. Mature carposporophytes apparently lacking a conspicuous central fusion cell and consisting of

several-celled gonimoblast filaments bearing terminal carposporangia 50–80 μm in diameter. Spermatangial filaments arising from the floor, walls and roof of male conceptacle chambers; nature of spermatangial branching not observed; mature male conceptacle roofs protruding above or flush with surrounding thallus surface, 125–140 μm thick, composed of 12–16 layers of cells above the chamber, conceptacle chambers 200–275 μm in diameter and 60–75 μm high.

Tetrasporangial conceptacle roofs protruding above or flush with surrounding surface, 5–9 cells thick above the chamber, not pitted with surface depressions around pore canals, pore canals lined by cells that are similar in size and shape to other roof cells, conceptacle chambers 280–750 μm in diameter and 150–200 μm high; tetrasporangia scattered across the conceptacle chamber floor, each mature sporangium 30–140 μm in diameter and 100–175 μm long, containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release.

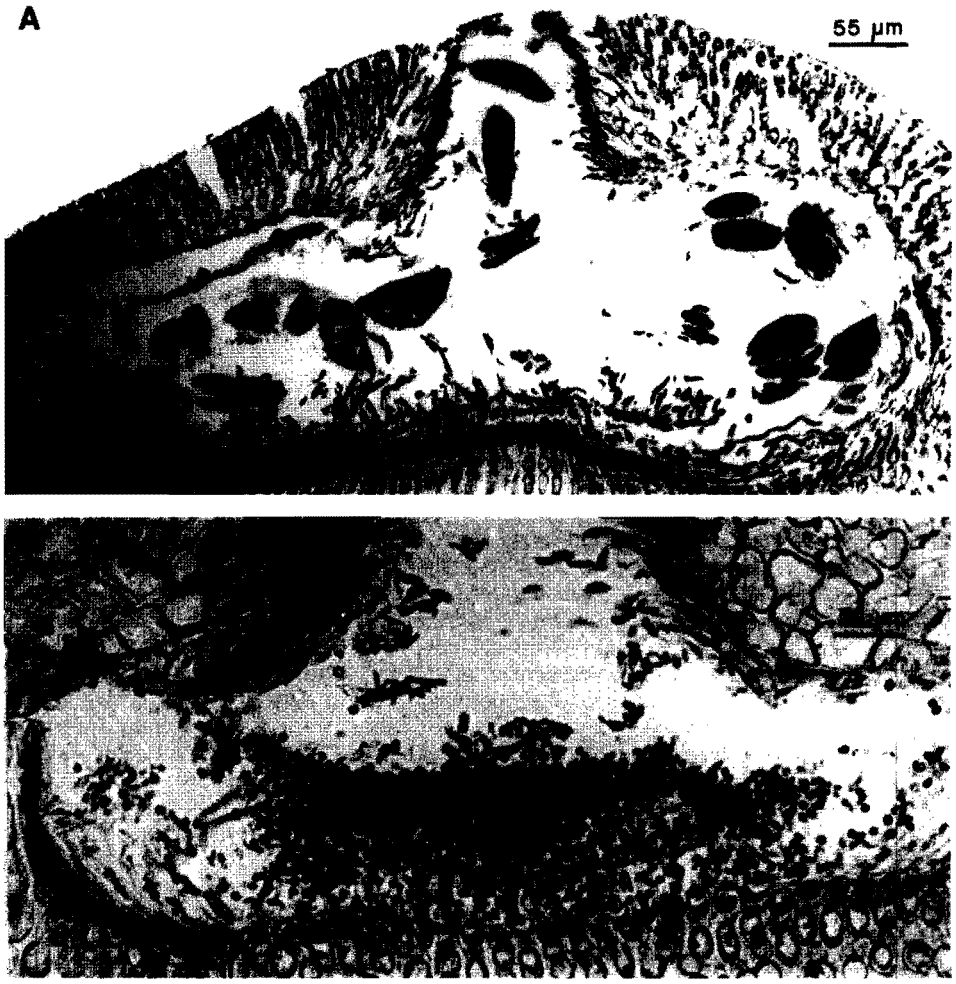


Fig. 77. *Lithothamnion muelleri* (**A, B,** L, 941.149–249, isolectotype). **A.** Section of old dried female-carposporangial conceptacle with mature carposporophyte. **B.** Section of old dried male conceptacle with remnants of spermatangial filaments on chamber floor and roof.

Type from Western Port, Vic.; lectotype in CN (Herb. Lenormand, unnumbered); designated by Woelkerling (1983a, p. 190); depicted in Woelkerling (1983a, fig. 29) and Wilks & Woelkerling (1995, fig. 1A).

Distribution: Point Valiant, Two People Bay, W. Aust., to Corner Inlet, Vic., and from Bruny I., Tas.

Records from Tierra del Fuego (Hariot 1895, p. 99; Lemoine 1913, p. 24; Papenfuss 1964, p. 31; Skottsberg 1941, p. 79) require confirmation and may involve misidentifications (see A. Harvey *et al.* 1994, p. 340).

Selected specimens: Point Valiant, Two People Bay, W. Aust., 0–5 m deep (*Woelkerling*, 2.ii.1978; LTB, 10727). Reef 10.4 km E of Eyre, W. Aust., 0–1 m deep (*Woelkerling, Platt & Jones*, 3.ii.1984; LTB, 14121). Point Malcolm, SW of Israelite Bay, W. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 7.ii.1984; LTB, 14218). Elliston, S. Aust., 6 or 11 m deep (*Turner*, 28–29.x.1981; LTB, 15364, 15365, 15369). Vivonne Bay, Kangaroo I., S. Aust., 0–0.5 m deep (*Campbell & Penrose*, 8.iv.1988; LTB, 15719). Cape Willoughby (60 nautical miles S), Kangaroo I., S. Aust., 85 m deep (*Bone*, 14.iii.1989; AD, A59823 = LTB, 15927). Cape Willoughby (16 nautical miles SW), Kangaroo I., S. Aust., 65 m deep (*Bone*, 13.iii.1989; AD, A59825 = LTB, 15962). Cape Jarvis, S. Aust., 6–12 m deep (*Turner*, 16.ix.1981; LTB, 15439). Potato Patch Reef, Anglesea, Vic., 8–9 m deep (*Beanland*, 31.viii.1982; LTB, 12715). Western Port Bay, Vic. (*Harvey* 1851; CN, unnumbered, lectotype; L 941.149–249, isolectotype; MEL, 588439, isolectotype). Ocean Beach, Phillip I., Vic. (*Gabriel*, April 1905; TRH unnumbered, holotype of *Lithothamnion gabrieli*). Corner Inlet, Vic., 14–18 m deep (*Gabriel*, i–ii.1897; TRH unnumbered, holotype of *Lithothamnion mirabile*). South Shore, Variety Bay, Bruny I., Tas., 2–4 m deep (*Platt, Woelkerling & Brown*, 17.ii.1983; LTB, 12988).

Lithothamnion muelleri occurs intertidally on reefs and in pools and is known subtidally to depths of 85 m. Thalli have been found growing on rock and on algae. Spermatangial thalli and carposporophytes are known with certainty only from two isolectotype collections (L, 941.149–249; MEL, 588439), and the nature of spermatangial branching has not been determined, thus leaving some uncertainty over whether *Lithothamnion*, which is typified by *L. muelleri*, is characterised by the presence of branched spermatangial filaments.

Notes on other taxa reported from southern Australia

Wilks & Woelkerling (1995) provide information on 23 additional species and infraspecific taxa that at some stage were ascribed to *Lithothamnion* and reported from southern Australia. These include taxa whose status is uncertain, incorrect records, heterotypic synonyms of other species of *Lithothamnion* and taxa now known to belong to other genera or conspecific with taxa belonging to other genera.

The type of *Goniolithon elatocarpum* f. *australasica* Foslie (1901a, p. 19) (also see Woelkerling 1993, p. 33), collected in Western Port, Victoria, also belongs to *Lithothamnion* but is considered of uncertain status because the poor condition of the material does not allow for unequivocal determination at species level.

Genus **PHYMATOLITHON** Foslie 1898a: 4, *nom. cons.*

Thallus encrusting to warty, lumpy, fruticose, discoid, layered or foliose, epigenous and partially to completely affixed by cell adhesion, or unattached and free-living as rhodoliths; genicula absent. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; cell elongation occurring mainly behind actively dividing subepithallial initials that are usually as short as or shorter than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions; secondary pit-connections absent; epithallial cells terminating most filaments at thallus surface, distal walls rounded or flattened but not flared; trichocytes occasional in some species; haustoria unknown.

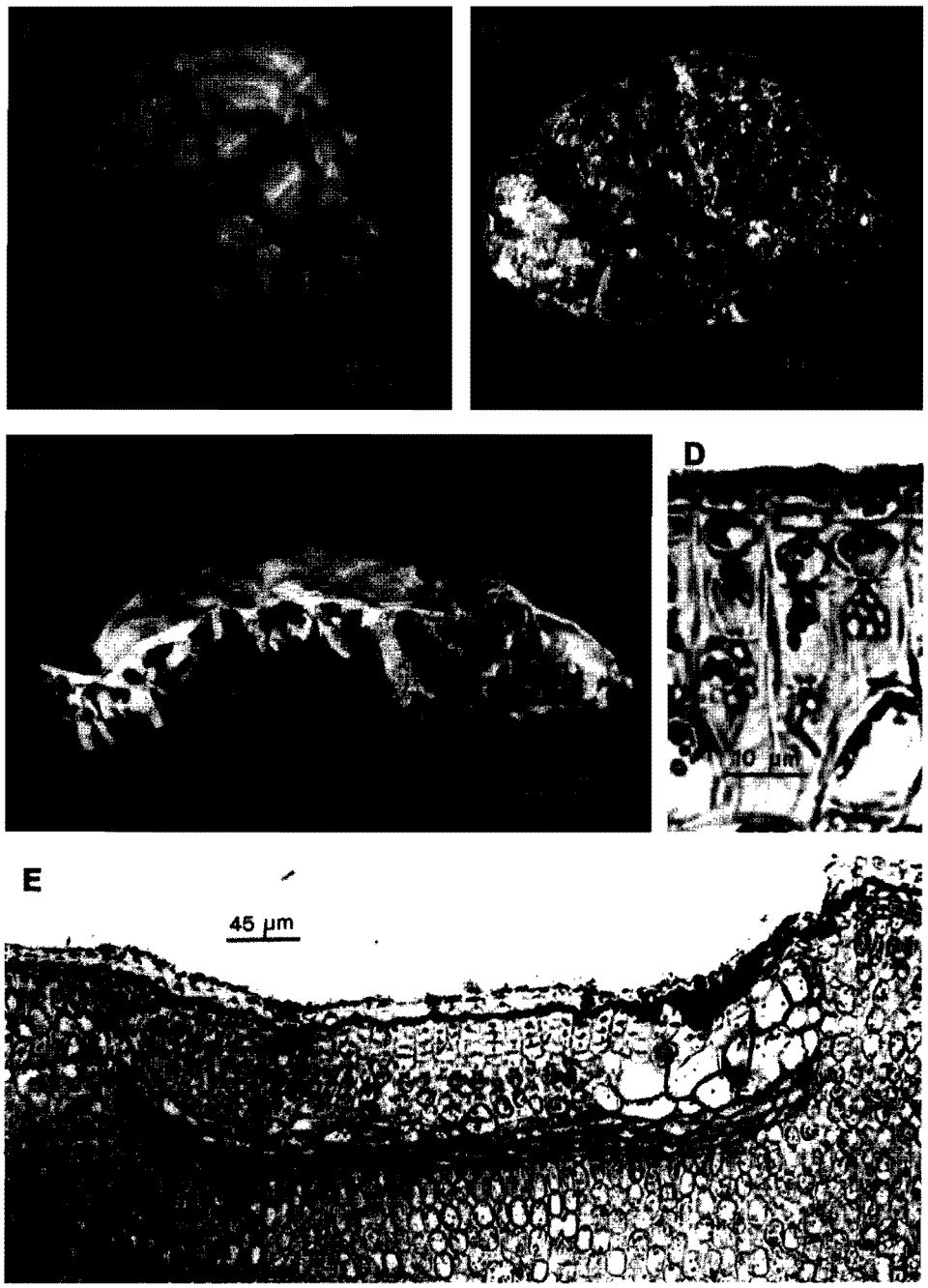


Fig. 78. *Phymatolithon masonianum* (**A, C,** AD, A60388; **B,** AD, A30645; **D,** LTB, 12787; **E,** LTB, 11601). **A.** The only known male thallus. **B.** Discoid tetrasporangial thallus. **C.** Edge view of a thallus showing strut-like branches arising from ventral surface. **D.** Section of thallus showing rounded epithallial cells and subepithallial initials that are shorter than the cells subtending them. **E.** Section of very young tetrasporangial conceptacle arising adventitiously from a group of vegetative cells within the thallus.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia and carposporangia borne in uniporate conceptacles; tetrasporangia and bisporangia borne in multiporate conceptacles that arise adventitiously from groups of vegetative cells within the thallus; gametangia and carposporangia formed on separate thalli from tetrasporangia and bisporangia.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia usually produced in separate conceptacles. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature carposporophytes apparently lacking a conspicuous central fusion cell and composed of short gonimoblast filaments bearing terminal carposporangia. Both unbranched and branched spermatangial filaments present, borne on the male conceptacle chamber floor, walls and roof.

Tetrasporangia and bisporangia scattered across the conceptacle chamber floor, roofs formed by filaments interspersed amongst and peripheral to sporangial initials; each mature sporangium containing zonately arranged tetraspores or bispores and possessing an apical plug that blocks a roof pore prior to spore release.

Type species: *P. polymorphum* (Linneaus)Foslie 1898a: 4. Basionym: *Millepora polymorpha* Linnaeus 1767: 1285. *M. polymorphum* Linnaeus is a superfluous substitute name for *M. calcarea* Pallas (1766, p. 265), and thus, as noted by Woelkerling & Irvine (1986a), the correct name of the type species of *Phymatolithon* is *P. calcareum* (Pallas)Adey & McKibbin (1970, p. 100).

Phymatolithon, as delimited here, incorporates the conclusions of Wilks & Woelkerling (1994) who found that characters proposed by Chamberlain (1990) and by Chamberlain & Keats (1994) to delimit *Leptophytum* from *Phymatolithon* were unsatisfactory and that *Leptophytum* is a genus in need of further evaluation. At least 40 species and infraspecific taxa have been ascribed to *Phymatolithon;* most are poorly known. Woelkerling & Irvine (1986a) gave a detailed account of tetrasporangial thalli of the type species, but noted that gametangia and carposporophytes are not known with certainty and have yet to be studied in a modern context. Moreover, early stages of carposporophyte development and gonimoblast filament ontogeny are poorly known in most species ascribed to the genus. Thus, information on gametangia and carposporophytes provided in the generic description is incomplete and will require revision once new data on the type and other species become available. Details relating to generic etymology, nomenclature, synonymy, *etc.* are provided by Woelkerling (1988, pp. 197–203). The proposal (Irvine & Woelkerling 1986) to conserve *Phymatolithon* Foslie (1898a) against *Apora* Gunnerus (1768) was approved by the Fifteenth International Botanical Congress in Tokyo in August 1993. This account of southern Australian species follows Wilks & Woelkerling (1994).

KEY TO SPECIES OF *PHYMATOLITHON*

1. Thallus discoid to foliose; tetrasporangial conceptacle chambers (Fig. 79A) filled with large, sterile, irregularly-shaped cells ..... 1. *P. masonianum*
1. Thallus encrusting to warty or fruticose; tetrasporangial conceptacle chambers (Fig. 80F) not filled with large, sterile cells ..... 2. *P. repandum*

1. **Phymatolithon masonianum** Wilks & Woelkerling 1994: 195, figs 11–15.

PLATE 3 fig. 2; FIGS 63A, 78, 79

Thallus normally pinkish to gray-pink, discoid to foliose, mostly 20–150 mm across and 1–3 mm thick, epigenous and usually loosely affixed, commonly with lamellate branches or perpendicularly orientated struts 1–30 mm long arising from the ventral surface, dorsal surface more or less smooth, often somewhat shiny when dried and without branching. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a centrally situated core and dorsal and ventral peripheral regions where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 5–15 μm in diameter and 5–30 μm long; epithallial

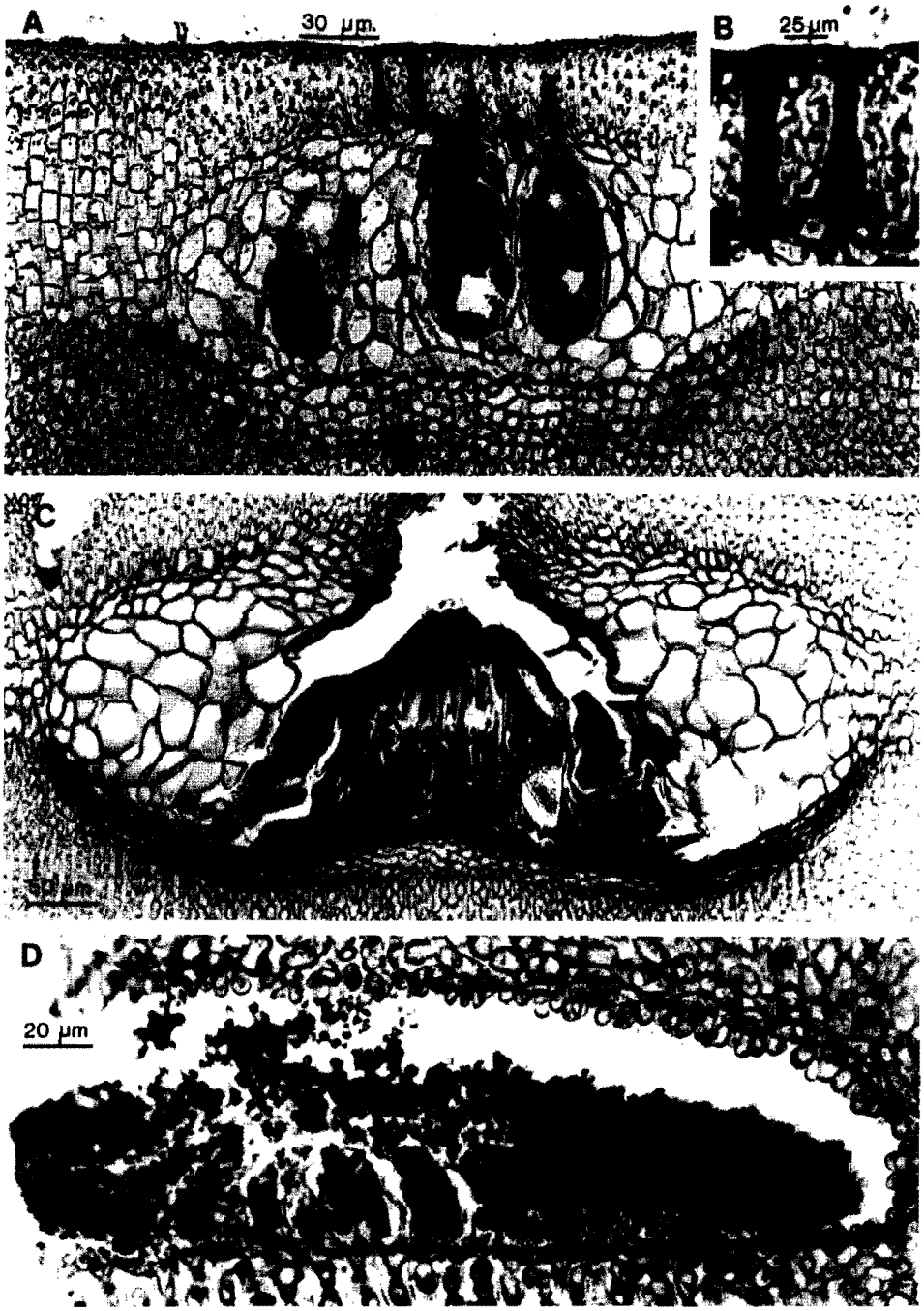


Fig. 79. *Phymatolithon masonianum* (**A, B,** LTB, 12787; **C,** AD, A61382; **D,** AD, A60388). **A.** Section of mature tetrasporangial conceptacle filled with enlarged vegetative cells interspersed amongst tetrasporangia. **B.** Portion of tetrasporangial conceptacle roof showing pore canals and bordering filaments whose cells do not differ in size and shape from other roof cells. **C.** Section of old dried female-carposporangial conceptacle with mature carposporophyte and enlarged vegetative cells in peripheral parts of the chamber. **D.** Section of old dried male conceptacle with spermatangial filaments on chamber floor and basal cells of old spermatangial filaments on roof.

cells 4–13 μm in diameter and 2–5 μm long, terminating most filaments at the thallus surface, with distal walls rounded or flattened but not flared; cell elongation occurring mainly behind actively dividing subepithallial initials that are usually as short as or shorter than their immediate inward derivatives; fusions between cells of adjacent filaments present; secondary pit-connections, haustoria, and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangial thalli and carposporophytes borne in uniporate conceptacles. Tetrasporangia produced in multiporate conceptacles. Bisporangia unknown.

Gametangial thalli apparently dioecious; carpogonial filaments not seen. Mature female-carposporangial conceptacle roofs protruding slightly above or flush with surrounding thallus surface, 50–75 μm thick, composed of 6–10 layers of cells above the chamber, conceptacle chambers 510–600 μm in diameter and 150–200 μm high. Mature carposporophytes apparently lacking a conspicuous central fusion cell and consisting of several-celled gonimoblast filaments bearing terminal carposporangia. Both unbranched and branched spermatangial filaments present, arising from the floor, walls and roof of male conceptacle chambers, mature male conceptacle roofs protruding slightly above or flush with surrounding thallus surface, 35–40 μm thick, composed of 5–7 layers of cells above the chamber, conceptacle chambers 220–520 μm in diameter and 50–80 μm high.

Tetrasporangial conceptacle roofs protruding above or flush with surrounding surface, 5–7 cells thick above the chamber, pore canals lined by cells that are similar in size and shape to other roof cells; conceptacle chambers 220–500 μm in diameter and 95–175 μm high, usually filled with enlarged sterile irregularly shaped vegetative cells interspersed amongst the sporangia and possessing distinct layers of darkly staining cells beneath the chamber floor, tetrasporangia scattered across the conceptacle chamber floor, each mature sporangium 30–60 μm in diameter and 70–125 μm long, containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release.

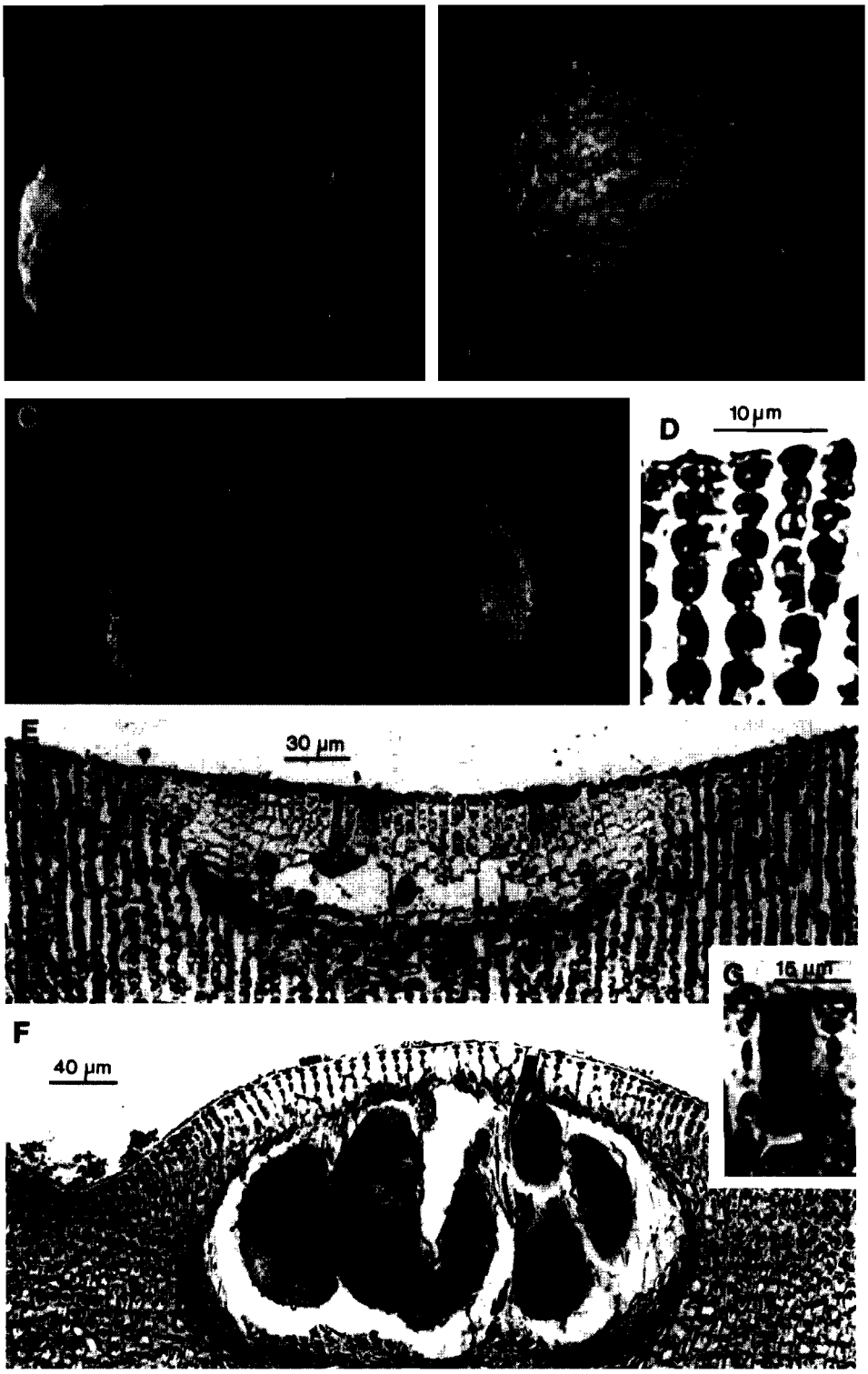
Type from Ninepin Point, D'Entrecasteaux Channel, Tas., 6–12 m deep (*Kraft*, 4.i.1993); holotype in LTB (16679); depicted in part in Wilks & Woelkerling (1994, p. 216, fig. 11A).

Distribution: Cape Buffon, S. Aust., to Walkerville, Vic., and around Tasmania.

Selected specimens: Cape Buffon, S. Aust., 5 m deep (*Kildea & Collings*, 27.ix.1992; AD, A61770 = LTB, 16582). 1.3 km off Middle Point, Cape Northumberland, S. Aust., 15 m deep (*Shepherd*, 14.xi.1975; AD, A46708). The Gap, Cunningham Bay, Phillip I., Vic., 2 m deep (*Kemp*, iv.1982; LTB, 12854). Walkerville, Vic., 2–3 m deep (*Platt et al.*, 30.xi.1983; LTB, 13912). Spike I., Bass Strait, Tas., 6 m deep (*Leach*, 28.ii.1979; LTB, 11601). North West Islet, Killiekranke Bay, Flinders I., Tas., 15 m deep (AIMS-NCI, Q66C 3574-Z, 21.ii.1990; AD, A60388 = LTB, 16678). Three Hummock I., NW Tas., 15 m deep (AIMS-NCI, Q66C 4952-Y, 9.ii.1991; AD A61382). Stapleton Point, Prosser Bay, Tas., 10 m deep (*Olsen*, 28.vii.1966; AD, A30645). Deep Glen Bay, Forestier Pen., Tas., 8–10 m deep (*Gowlett-Holmes*, 15.ix.1995; AD, A64476). Ninepin Point, D'Entrecasteaux Channel, Tas., 4–6 m deep (*Platt & Brown*, 18.ii.1983; LTB, 12760 and *Platt*, 18.ii.1983; LTB, 12787). Southport (Convict Burial Ground, S of Sister Bay), Tas., 3–4 m deep (*Platt*, 16.ii.1983; LTB, 12896). Lady Bay, Southport, Tas., 7 m deep (*Brown & Kenchington*, 14.x.1986; AD, A57695).

Phymatolithon masonianum has been found at depths of 2–15 m on sponges and on rock. Thalli of *P. masonianum* are usually easily recognised in the field from their distinctive discoid to foliose growth form and large thalli with smooth dorsal surfaces that often look somewhat shiny, with struts on the ventral surface; no other known southern Australian non-geniculate coralline shows this combination of features. Only one dried male thallus and two dried carposporangial thalli are known; carpogonial filaments have yet to be found, meaningful measurements of carposporangia could not be obtained, and the ontogeny of all reproductive structures requires further investigation.

2. **Phymatolithon repandum** (Foslie)Wilks & Woelkerling 1994: 190, figs 1–10.
Lithothamnion repandum Foslie 1904b: 4. Woelkerling 1993: 189.
Leptophytum repandum (Foslie)Adey 1970: 30.
Lithothamnion lenormandii f. *australis* Foslie 1901a: 8. Woelkerling 1993: 36.
Lithothamnion absonum Foslie 1907b: 6–7. Woelkerling 1993: 14.
Leptophytum absonum (Foslie)Adey 1970: 29.


D
10 µm
E
30 µm
F
40 µm
G
15 µm

Lithothamnion repandum f. *asperula* Foslie 1906: 5. Woelkerling 1993: 31.
Lithothamnion asperulum (Foslie)Foslie 1907b: 6.
Leptophytum asperulum (Foslie)Adey 1970: 29.

Additional references involving these binomials and information on synonymy are provided by Wilks & Woelkerling (1994).

PLATE 3 fig. 4; FIGS 80, 81

Thallus normally dull pinkish, encrusting to warty to fruticose, mostly 4–80 mm across and 0.1–4.0 mm thick or tall, epigenous and completely affixed by cell adhesion; protuberant branches, simple or branched, mostly 1–6 mm in diameter and 1–4 mm long. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally situated core in crustose portions or centrally situated core in protuberant branches and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 2–12 μm in diameter and 2–27 μm long; epithallial cells 2–8 μm in diameter and 1–8 μm long, terminating most filaments at the thallus surface, with distal walls rounded or flattened but not flared; cell elongation occurring mainly behind actively dividing subepithallial initials that are usually as short as or shorter than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions; secondary pit-connections, haustoria, and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporophytes produced in uniporate conceptacles; tetrasporangia and bisporangia produced in multiporate conceptacles.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles or occasionally in the same conceptacle. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above or flush with surrounding thallus surface, 22–100 μm thick, composed of 5–10 layers of cells above the chamber, conceptacle chambers 112–300 μm in diameter and 50–125 μm high. Mature carposporophytes apparently lacking a conspicuous central fusion cell and consisting of several-celled gonimoblast filaments bearing terminal carposporangia 12–75 μm in diameter. Both unbranched and branched spermatangial filaments present, arising from the floor, walls and roof of male conceptacle chambers, mature male conceptacle roofs protruding above surrounding thallus surface, 25–75 μm thick, composed of 4–9 layers of cells above the chamber, conceptacle chambers 100–250 μm in diameter and 45–150 μm high.

Tetrasporangial/bisporangial conceptacle roofs protruding above surrounding surface, 3–5 cells thick above the chamber, pore canals lined by cells that are similar in size and shape to other roof cells; conceptacle chambers 96–300 μm in diameter and 50–150 μm high, not filled with enlarged irregularly shaped vegetative cells interspersed amongst the sporangia and lacking distinct layers of darkly staining cells beneath the chamber floor; tetrasporangia scattered across the conceptacle chamber floor, each mature sporangium 15–80 μm in diameter and 32–125 μm long, containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release; bisporangia occasional, 15–80 μm in diameter and 32–125 μm long.

Type from Half Moon Bay, Port Phillip Bay, Vic. (*Gabriel*, 14.i.1899); lectotype in TRH (unnumbered; includes slides 358 and 516); designated by Adey in Adey & Lebednik (1967, p. 83); depicted in Wilks & Woelkerling (1994, p. 206, fig. 1); additional data provided by Woelkerling (1993, p. 189).

Fig. 80. *Phymatolithon repandum* (**A**, LTB, 16209; **B, F**, LTB, 15836; **C**, LTB, 15795; **D, E, G**, LTB, 16205). **A.** Encrusting thallus on rock. **B.** Warty thallus on rock. **C.** Fruticose thallus on rock. **D.** Section of thallus showing epithallial cells and subepithallial initials that are as short as or shorter than the cells subtending them. **E.** Section of very young tetrasporangial conceptacle arising adventitiously from a group of vegetative cells (arrows) within the thallus. **F.** Section of mature tetrasporangial conceptacle. **G.** Portion of tetrasporangial conceptacle roof showing pore canals and bordering filaments.

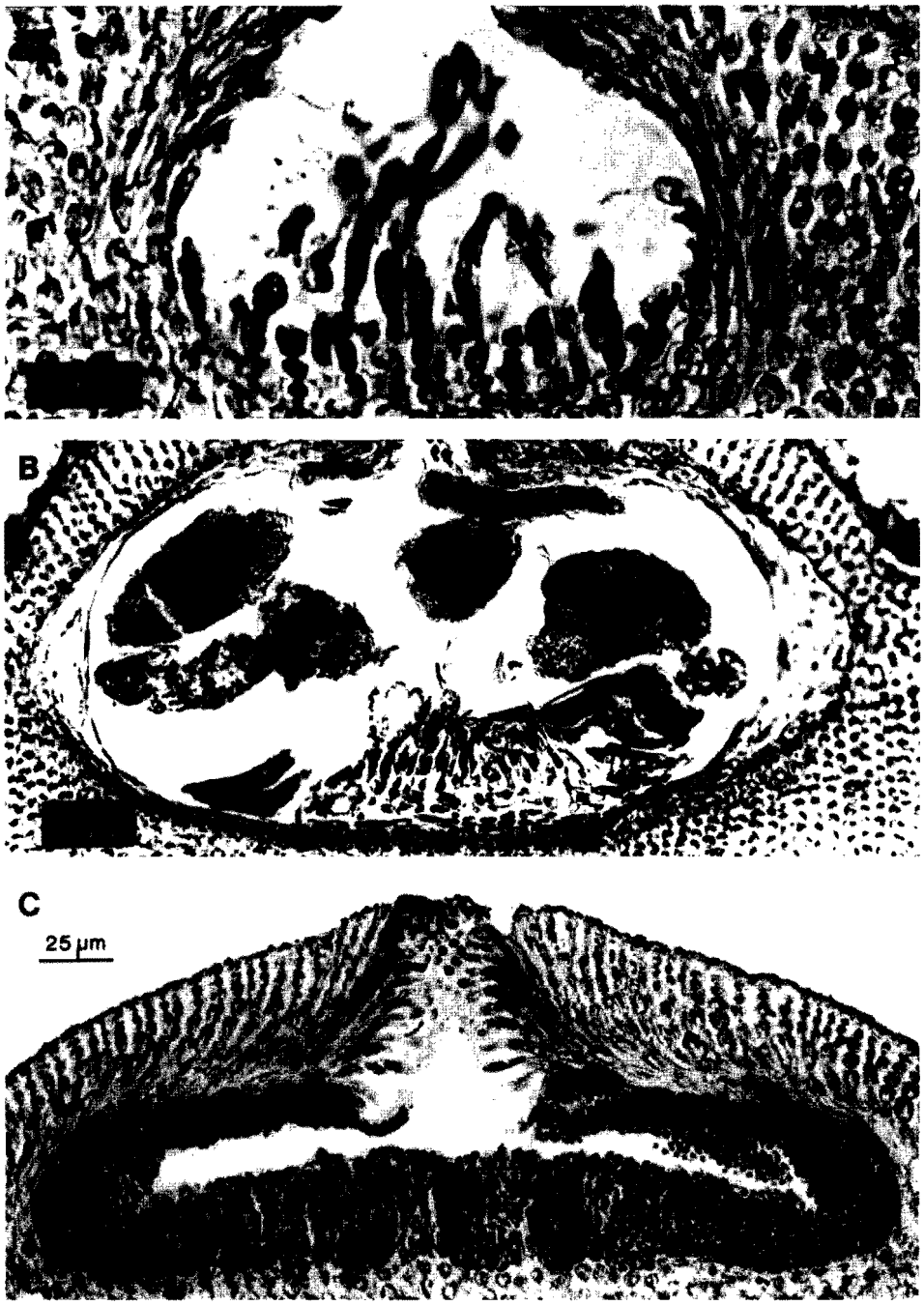


Fig. 81. *Phymatolithon repandum* (**A,** LTB, 16167; **B,** LTB, 15788; **C,** LTB, 15836). **A.** Section of female-carposporangial conceptacle with nearly mature carpogonial filaments. **B.** Section of female-carposporangial conceptacle with mature carposporophyte; most sporangia are no longer attached to the gonimoblast filaments. **C.** Section of male conceptacle with mature, branched and unbranched spermatangial filaments arising from chamber floor and unbranched spermatangial filaments arising from the roof.

Distribution: In Australia, from 10 km east of Eyre, W. Aust., to Cape Conran, Vic., and around Tasmania.

New Zealand.

Selected specimens: Reef 10.4 km E of Eyre, W. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 3.ii.1984; LTB, 14122, 14123, 14141). Point Sinclair, S. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 15.ii.1984; LTB, 14521). Hansen Bay, Kangaroo I., S. Aust., 0–1.5 m deep (*Campbell & Penrose*, 9.iv.1988; LTB, 15704, 15708). Beachport (reef W of Schnapper Point), S. Aust., 0–2 m deep (*Campbell, Penrose & Woelkerling*, 26.ii.1988; LTB, 15788, 15795). Beachport (Post Office Rock), S. Aust., 0–3 m deep (*Campbell & Penrose*, 6.xi.1987; LTB, 15836). Beachport (Woolley's Rocks), S. Aust., intertidal (*Penrose & Woelkerling*, 25.ii.1991; LTB, 16204, 16205, 16207, 16208). Blanket Bay, Otway National Park, Vic., 4 m deep (*Campbell, Penrose & May*, 14.xi.1985; LTB, 15235). Rye (Number 16 reef) (*Woelkerling & Wilks*, Feb. 1991; LTB, 16209). Flinders, Western Port, Vic., reef pool (*Woelkerling*, 13.i.1983; LTB, 12650). Kitty Miller Bay, Phillip I., Vic., intertidal (*Woelkerling, Penrose & Wilks*, 12.iv.1991; LTB, 16167, 16175, 16180, 16181). Cape Conran, Vic., reef pool (*Platt*, 29.xii.1982; LTB, 12633). Greens Beach, Tas., intertidal pool (*Platt*, 2.iii.1983; LTB, 13414). Binalong Bay, Bay of Fires, Tas., 0–2 m deep (*Platt & Woelkerling*, 23.ii.1983; LTB, 13203, 13194). Tessellated Pavement, Eaglehawk Neck, Tas., 1–2 m deep (*Platt & Woelkerling*, 26.ii.1983; LTB, 13247, 13250).

Phymatolithon repandum occurs intertidally on reef surfaces and in pools and is known subtidally to depths of 6 m in southern Australia. Thalli have been found on rock and glass; epiphytic and epizoic thalli have not been encountered. Thalli with young tetrasporangial and bisporangial conceptacles can sometimes be recognised in the field because senescent vegetative discs above developing conceptacles (Fig. 80E) lose pigmentation, turn white, and form conspicuous dots on the thallus surface. Tentative field identifications made on this basis need to be confirmed by sectioning.

Genus **MESOPHYLLUM** Lemoine 1928: 251

Thallus encrusting to warty, lumpy, fruticose, discoid, layered or foliose, epigenous and partially to completely affixed by cell adhesion or envelopment of host axes or unattached and free-living as rhodoliths; genicula absent. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; cell elongation apparently occurring mainly within actively dividing subepithallial initials that are usually as long as or longer than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions; secondary pit-connections absent; epithallial cells terminating most filaments at thallus surface, distal walls rounded or flattened but not flared; trichocytes occasional in some species; haustoria unknown.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia and carposporangia borne in uniporate conceptacles; tetrasporangia and bisporangia borne in multiporate conceptacles that apparently arise from groups of subepithallial initials; gametangia and carposporangia formed on separate thalli from tetrasporangia and bisporangia.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 2–4-celled filaments arising from the female conceptacle chamber floor. Mature carposporophytes apparently lacking a conspicuous central fusion cell and composed either of an irregularly shaped fusion cell that may appear discontinuous in section or of a several-celled fusion cell complex (not always evident) and of short gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, borne on the floor, walls and roof of male conceptacle chambers.

Tetrasporangia and bisporangia scattered across the conceptacle chamber floor, roofs formed by filaments interspersed amongst and peripheral to sporangial initials, each mature sporangium containing zonately arranged tetraspores or bispores and possessing an apical plug that blocks a roof pore prior to spore release.

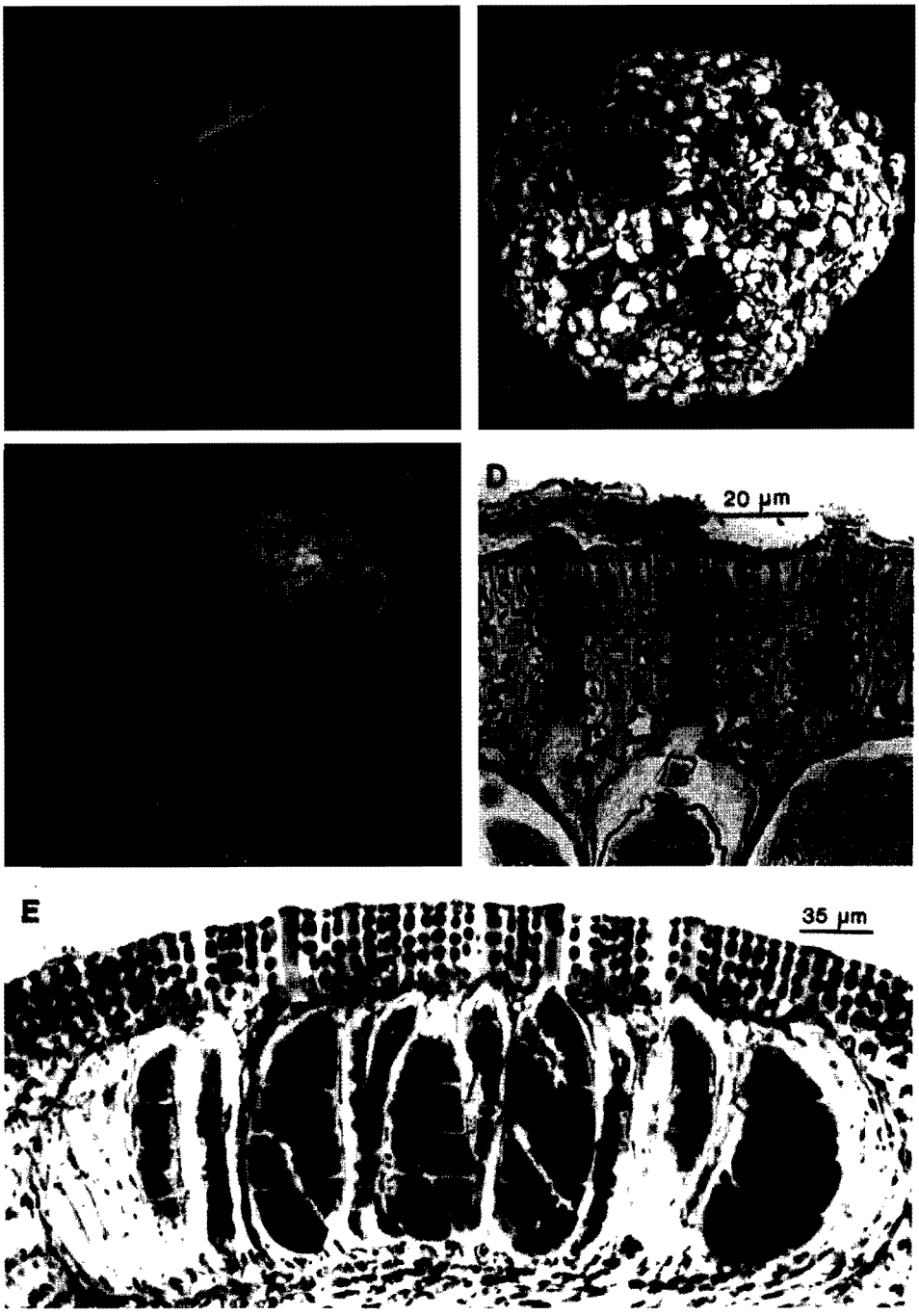


Fig. 82. *Mesophyllum engelhartii* (**A,** LTB, 15693; **B,** LTB, 15616; **C,** LTB, 13296; **D,** LTB, 10620; **E,** LTB, 13285). **A.** Encrusting thalli enveloping axes of *Gelidium*. **B.** Population of encrusting thalli on a sponge. **C.** Warty thallus attached to holdfast of *Phyllospora*. **D.** Portion of tetrasporangial conceptacle roof with pore canal and bordering filaments. **E.** Section of mature tetrasporangial conceptacle.

Lectotype species: *M. lichenoides* (Ellis)Lemoine 1928:251; designated by Ishijima (1942, p. 174). Basionym: *Corallium lichenoides* Ellis 1768:407, pl. 17 figs 9–11.

Mesophyllum, as delimited here, incorporates the conclusions of Woelkerling & Harvey (1992, pp. 395–397) who have updated the generic concept presented in Woelkerling (1988, p. 191). Over 140 species and infraspecific taxa have been ascribed to *Mesophyllum* (Woelkerling 1988, p. 195); most are poorly known. Woelkerling & Irvine (1986b) give a detailed account of the type species; further information on and references to additional accounts of *M. lichenoides* are included in Woelkerling & Harvey (1993, p. 596). Details relating to generic etymology, nomenclature, synonymy, *etc.* are provided by Woelkerling (1988, pp. 191–196). This account of southern Australian species follows Woelkerling & Harvey (1992; 1993).

KEY TO SPECIES OF *MESOPHYLLUM*

1. Tetrasporangial and bisporangial conceptacle roofs mound-like or flattened (Figs 83A, 85A), not differentiated into a peripheral rim and a central, sunken pore-plate 2
1. Tetrasporangial and bisporangial conceptacle roofs volcano-like, differentiated into a peripheral rim and a central somewhat sunken pore-plate (Figs 87A, 88D) 3

    2. Tetrasporangial and bisporangial conceptacle pore canals bordered by cells that are similar in size and shape to other roof cells above the chamber (Fig. 82D) ..... 1. *M. engelhartii*
    2. Tetrasporangial and bisporangial conceptacle pore canals bordered by cells (especially near the base of the canal) that are narrower and more elongate than adjacent roof cells (Fig. 84F) ..... 2. *M. incisum*

3. Tetrasporangial conceptacle pore canals bordered by cells that are similar in size and shape to other roof cells above the chamber (Fig. 86D) ..... 3. *M. macroblastum*
3. Tetrasporangial conceptacle pore canals bordered by cells (especially near the base of the canal) that are narrower and more elongate than adjacent roof cells (Fig. 89B, C) ..... 4. *M. printzianum*

1. **Mesophyllum engelhartii** (Foslie)Adey 1970: 23. Barry & Woelkerling 1995: 143. Woelkerling & Harvey 1993: 581, figs 1–11. Chamberlain & Keats 1995: 134, figs 1–51.
    Lithothamnion engelhartii Foslie 1900a: 18. Printz 1929: 40, pl. 7 figs 12–14 (as f. *typica*). Woelkerling 1993: 84.
    Lithothamnion engelhartii f. *imbricata* Foslie 1900a: 19. Woelkerling 1993: 120.
    Lithothamnion engelhartii f. *umbonata* Foslie 1900a: 18. Woelkerling 1993: 230.
    Lithothamnion patena f. *engelhartii* (Foslie)Heydrich 1907: 223 (as *engelhartii*).
    Lithothamnion discrepans Foslie 1907b: 8; Chamberlain & Keats 1995: 141, figs 5, 36–45.
    Lithothamnion fumigatum Foslie 1901a: 7. Woelkerling 1993: 100.
    Lithothamnion lemniscatum Foslie 1907b: 11. Woelkerling 1993: 137.
    Lithothamnion speciosum (Foslie)Foslie 1907b: 16.
    Lithothamnion synanablastum f. *speciosa* Foslie 1900a: 18. Chamberlain & Keats 1995: figs 4, 7, 12, 46–51.
    Lithothamnion versicolor Foslie 1907a: 3. Woelkerling 1993: 236.

Additional references involving these and other binomials, previous southern Australian records, misapplied names and known heterotypic synonyms are given by Woelkerling & Harvey (1993), and further references are given by Chamberlain & Keats (1995).

FIGS 82, 83

Thallus normally pinkish, encrusting to warty, layered or foliose, mostly 6–85 mm across and 0.05–22 mm thick or tall, epigenous and partially to completely ventrally affixed by cell adhesion; protuberant branches erect, mostly simple, 1–4 mm in diameter and 2.3–10 mm long; lamellate branches applanate or ascending, sometimes interwoven, simple or furcate, mostly 3–10 mm across and 5–16 mm long. *Structure* pseudoparenchymatous;

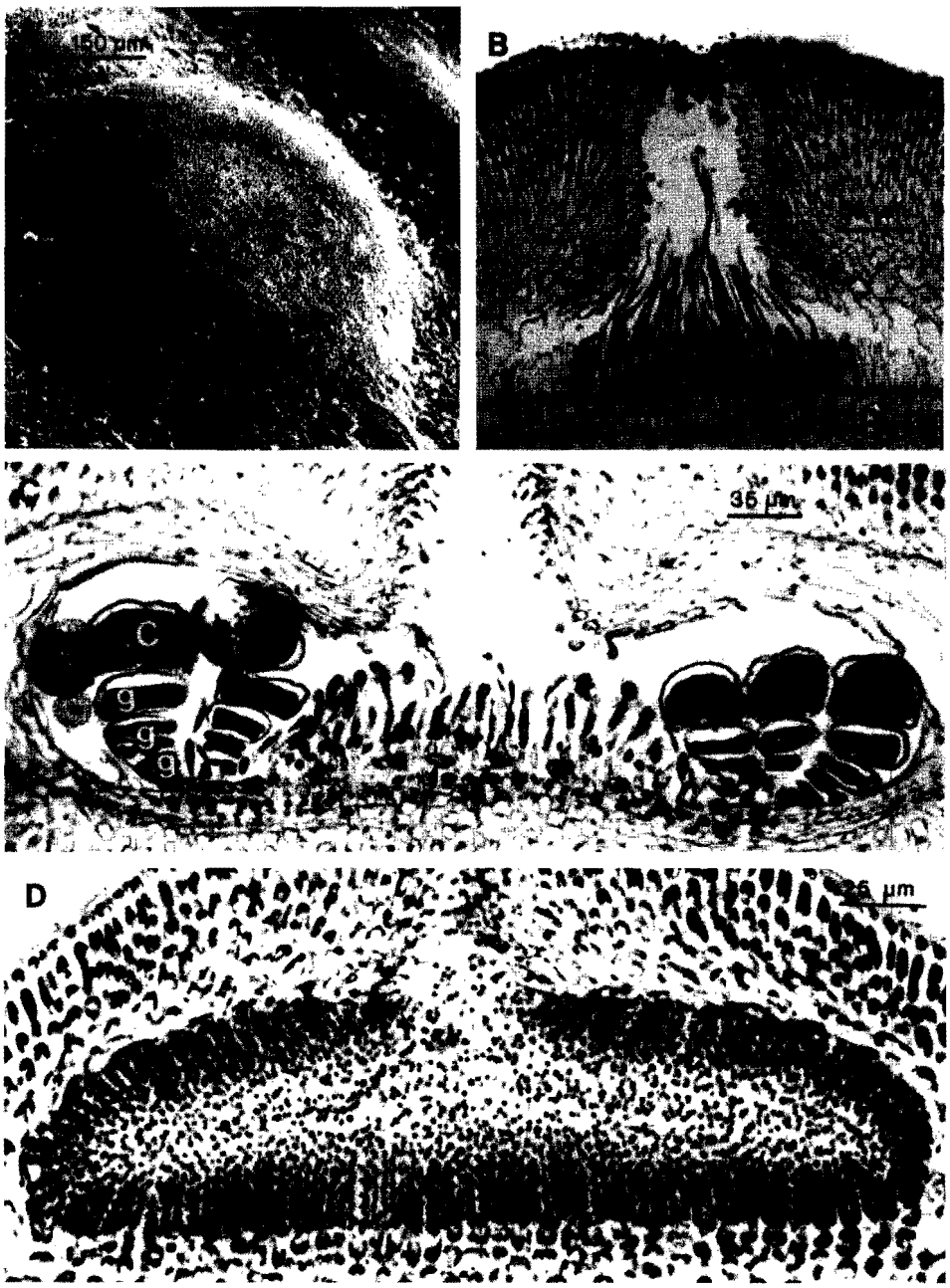


Fig. 83. *Mesophyllum engelhartii* (**A,** LTB, 13271; **B,** LTB, 15311; **C,** LTB, 15516; **D,** LTB, 13283). **A.** Surface view of tetrasporangial conceptacle showing pores. **B.** Section of female-carposporangial conceptacle with mature carpogonial filaments. **C.** Section of female-carposporangial conceptacle with mature carposporophyte showing sections of 'discontinuous' fusion cell (arrows), gonimoblast filaments (g) and carposporangia (C). **D.** Section of male conceptacle with mature, unbranched spermatangial filaments arising from chamber floor and roof.

organisation dorsiventral in crustose portions and lamellate branches but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 3–19 µm in diameter and 9–33 µm long; epithallial cells 3–5 µm in diameter and 4–9 µm long, terminating most filaments at the thallus surface, with distal walls rounded or flattened but not flared; cell elongation occurring mainly within actively dividing subepithallial initials that are usually as long as or longer than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions; secondary pit-connections, haustoria, and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporophytes produced in uniporate conceptacles; tetrasporangia and bisporangia produced in multiporate conceptacles.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 2–4-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above surrounding thallus surface, 100–180 µm thick, composed of 13–38 layers of cells above the chamber, conceptacle chambers 185–500 µm in diameter and 45–230 µm high. Carposporophytes lacking a conspicuous central fusion cell and apparently consisting of an irregularly shaped fusion cell (not always evident) that may look discontinuous in section or a several-celled fusion cell complex (evident only in young stages), and several-celled gonimoblast filaments bearing terminal carposporangia 30–95 µm in diameter. Spermatangial filaments unbranched, arising from the floor, walls and roof of male conceptacle chambers, mature male conceptacle roofs protruding above surrounding thallus surface, (32-) 40–55 (-135) µm thick, composed of 6–16 layers of cells above the chamber, conceptacle chambers (54-) 108–175 (-284) µm in diameter and 20–110 µm high.

Tetrasporangial/bisporangial conceptacle roofs protruding above surrounding surface, not differentiated into a peripheral rim and a central sunken pore-plate, 3–10 cells thick above the chamber, pore canals lined by cells that are similar in size and shape to other roof cells, conceptacle chambers 160–500 µm in diameter and 65–260 µm high; tetrasporangia scattered across the conceptacle chamber floor, each mature sporangium 24–81 µm in diameter and 59–173 µm long, containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release; bisporangia occasional, 22–65 µm in diameter and 68–110 µm long.

Type from Cape Jaffa, S. Aust.; lectotype in TRH (unnumbered; includes slide 350); designated by Adey in Adey & Lebednik (1967, p. 69); depicted in Printz (1929, pl. 7 fig. 14) and in Woelkerling & Harvey (1993, p. 607, fig. 1A); additional data provided by Woelkerling (1993, p. 84).

Distribution: Eagle Bluff, Shark Bay, W. Aust., to Kitty Miller Bay, Phillip I., Vic., and the eastern and southern coasts of Tasmania.

New Zealand, Auckland Islands; South Africa; Namibia.

Selected specimens: Eagle Bluff, Shark Bay., W. Aust., upper sublittoral (*Woelkerling*, 31.vii.1986; LTB, 15482, 15486). Mabel Cove, Rottnest I., W. Aust., reef top (*Woelkerling*, 9.ii.1978; LTB, 10640, 10643). Jeannies Lookout, Rottnest I., W. Aust., 1–3 m deep (*Woelkerling*, 12.ii.1978; LTB, 10620, 10628). Lucky Bay, Cape Le Grand National Park, W. Aust., 0–3 m deep (*Woelkerling, Platt & Jones*, 9.ii.1984; LTB, 14333). Eyre (Nine Mile Reef), W. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 1.ii.1984; LTB, 13970). Point Fowler (east shore), S. Aust., 2–3 m deep (*Platt & Jones*, 14.ii.1984; LTB, 14471). Point Westall, S. Aust., 2–3 m deep (*Platt & Jones*, 16.ii.1984; LTB, 14535). Snug Cove, Kangaroo I., S. Aust., 10–13 m deep (*Campbell & Penrose*, 12.iv.1988; LTB, 15616, 15617). Beachport (Post Office Rock), S. Aust., reef top (*Campbell, Penrose & Woelkerling*, 1.xii.1986; LTB, 15516). Beachport, S. Aust., 3–6 m deep (*Campbell & Penrose*, 26.ii.1988; LTB, 15693). Anglesea (Ingoldsby Reef), Vic., 0.5 m deep (*Beanland*, 19.i.1983; LTB, 13550). Rye (Number Sixteen reef), Vic., reef pools (*Woelkerling*, 31.iii.1985; LTB, 14759). Kitty Miller Bay, Phillip I., Vic., 1–2 m deep (*Woelkerling, Campbell & Penrose*, 2.xii.1985; LTB, 15311). Bluestone Bay, Freycinet Pen., Tas., 0–6 m deep (*Platt & Woelkerling*, 26.ii.1983; LTB, 13296). Eaglehawk Neck (Clydes I.), Tas., 0–6 m deep (*Woelkerling & Platt*, 26.ii.1983; LTB 13275, 13285 and *Platt & Woelkerling*, 26.ii.1983; LTB, 13270, 13271, 13283). Ninepin Point, D'Entrecasteaux Channel, Tas.,

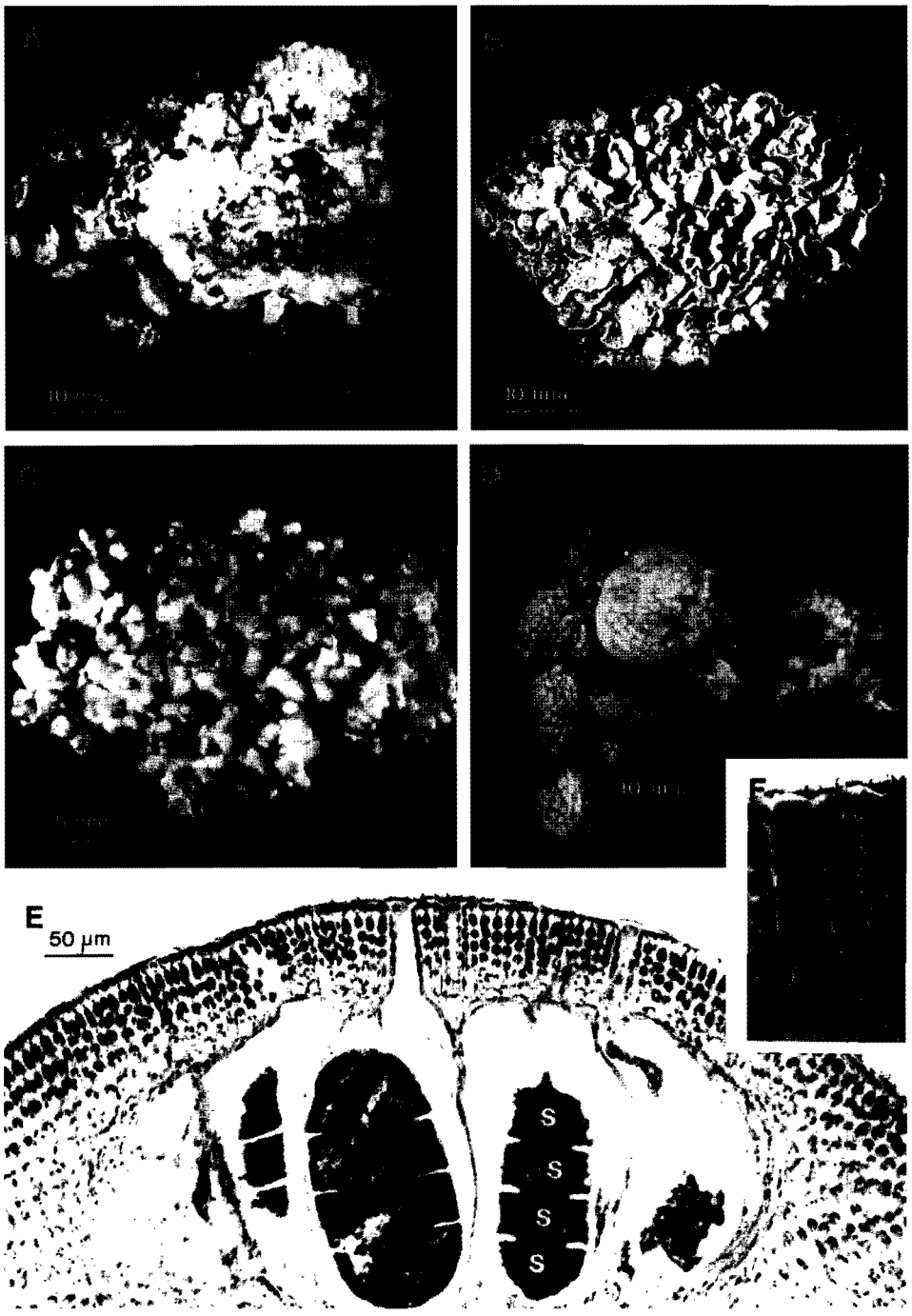


Fig. 84. *Mesophyllum incisum* (**A**, LTB, 14613; **B**, LTB, 11719; **C**, LTB, 13525; **D**, LTB, 11495; **E, F**, LTB, 13235). **A.** Encrusting to warty thallus on rock. **B.** Group of interwoven foliose thalli detached from rock. **C.** Warty to fruticose thallus detached from rock. **D.** Discoid to layered thalli detached from *Metamastophora*. **E.** Section of mature tetrasporangial conceptacle showing sporangia with zonately arranged spores (s). **F.** Portion of tetrasporangial conceptacle roof with pore canal and bordering filaments.

4–6 m deep (*Platt & Brown*, 18.ii.1983; LTB, 12734, 12752, 12753). Variety Bay (S shore), Bruny I., Tas., 2–4 m deep (*Platt, Woelkerling & Brown*, 17.ii.1983; LTB, 12936, 12950, 12951).

Mesophyllum engelhartii has been found intertidally on reef edges and in pools, and subtidally to depths of 15 m in southern Australia. Thalli occur on rock, molluscs, sponges and various green, brown, and red algae. In epiphytic and epizoic collections, dozens of individuals commonly occur on a single host and gametangial, tetrasporangial and bisporangial specimens are often present. Tetrasporangial conceptacle anatomy is very similar in *Mesophyllum engelhartii* and *Synarthrophyton patena*, and certain tetrasporangial thalli of the two species could be confused if viewed in isolation (A. Harvey *et al.* 1994, p. 341). Male thalli, however, can easily be told apart as spermatangial branches are unbranched in *Mesophyllum engelhartii* but branched in *Synarthrophyton patena*. Chamberlain & Keats (1995) provide a detailed account of the species in South Africa.

2. **Mesophyllum incisum** (Foslie)Adey 1970: 24. Woelkerling & Harvey 1992: 381, figs 1–36; 1993: 587, figs 12–16.
Lithothamnion patena f. *incisa* Foslie 1906: 8. Woelkerling 1993: 123.
Lithothamnion incisum (Foslie)Foslie 1907b: 12.
Polyporolithon patena var. *incisa* (Foslie)Chapman & Parkinson 1974: 202.

Additional references involving these binomials are provided by Woelkerling & Harvey (1993), and a detailed account of reproductive ontogeny in this species is contained in Woelkerling & Harvey (1992).

FIGS 62B, 84, 85

Thallus normally pinkish, encrusting to warty, lumpy, discoid, layered or foliose, mostly 2–200 mm across and 0.04–12 mm thick or tall, epigenous and partially to completely affixed by cell adhesion; protuberant branches simple, mostly 0.8–12 mm in diameter and 0.5–12 mm long; lamellate branches applanate to ascending or upright, often layered, mostly 3–23 mm across and 2–7 mm long. *Structure* pseudoparenchymatous, organisation dorsiventral in crustose portions and lamellate branches but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; each filament composed of cells 5–15 µm in diameter and 7–35 µm long; epithallial cells 5–12 µm in diameter and 5–10 µm long, terminating most filaments at the thallus surface, with distal walls rounded or flattened but not flared; cell elongation occurring mainly within actively dividing subepithallial initials that are usually as long as or longer than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions; trichocytes occasional, solitary or in small fields; secondary pit-connections and haustoria unknown.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporophytes produced in uniporate conceptacles; tetrasporangia and bisporangia produced in multiporate conceptacles.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above surrounding thallus surface, 75–185 µm thick, composed of 6–15 layers of cells above the chamber, conceptacle chambers 270–450 µm in diameter and 75–240 µm high. Carposporophytes lacking a conspicuous central fusion cell and apparently consisting of an irregularly shaped fusion cell that may look discontinuous in section and several-celled gonimoblast filaments bearing terminal carposporangia 25–155 µm in diameter. Spermatangial filaments unbranched, arising from the floor, walls and roof of male conceptacle chambers; mature male conceptacle roofs protruding above surrounding thallus surface, 45–90 µm thick, composed of 5–9 layers of cells above the chamber; conceptacle chambers 190–330 (-420) µm in diameter and 50–120 µm high.

Tetrasporangial/bisporangial conceptacle roofs protruding above surrounding surface, not differentiated into a peripheral rim and a central sunken pore-plate, 4–7 cells thick above the chamber; pore canals lined by cells (especially near the base of the canal) that are narrower and more elongate than adjacent roof cells; conceptacle chambers 340–655 µm in

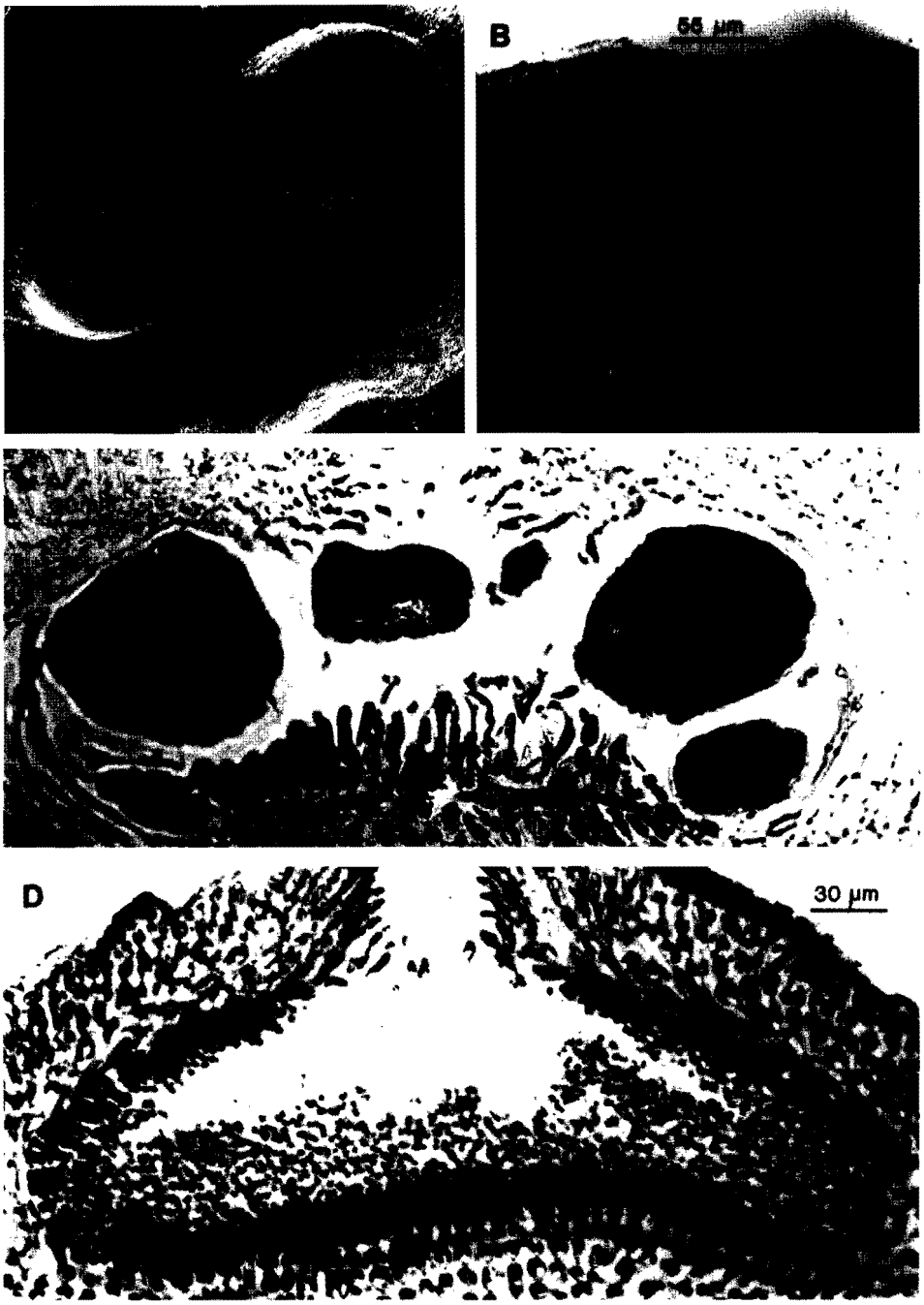


Fig. 85. *Mesophyllum incisum* (**A,** LTB, 11719; **B,** LTB, 13048; **C,** LTB, 11712; **D,** LTB, 14763). **A.** Surface view of tetrasporangial conceptacles. **B.** Section of female-carposporangial conceptacle with mature carpogonial filaments. **C.** Section of female-carposporangial conceptacle with mature carposporophyte. **D.** Section of male conceptacle with mature, unbranched spermatangial filaments arising from chamber floor and roof.

diameter and 130–265 μm high; tetrasporangia scattered across the conceptacle chamber floor; each mature sporangium 55–130 μm in diameter and 130–220 μm long, containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release; bisporangia occasional, 62–130 μm in diameter and 121–205 μm long.

Type from Bay of Islands, New Zealand; lectotype in TRH (Setchell No. 6354; includes two slides numbered 1175); designated by Woelkerling & Harvey (1992, p. 383); depicted in Woelkerling & Harvey (1992, p. 383, fig. 1) and Woelkerling & Harvey (1993, p. 618, fig. 12 A); additional data provided by Woelkerling (1993, p. 123).

Distribution: New Zealand, Chatham Islands, Snares Islands, Auckland Islands.

In Australia, from East Strickland Bay, Rottnest I., W. Aust., to Waterloo Bay, Wilsons Prom., Vic., and around Tasmania.

Selected specimens: East Strickland Bay, Rottnest I., W. Aust., reef pools (*Woelkerling*, 12.ii.1978; LTB, 11046). Garden Island (Five Fathom Bank), W. Aust., 12–15 m deep (*Cambridge*, 21.ii.1978; LTB, 11495). Lucky Bay, Cape Le Grand National Park, W. Aust., 0–3 m deep (*Woelkerling, Platt & Jones*, 9.ii.1984; LTB, 14287, 14292, 14296, 14345). Eyre (reef 7 km E of Twilight Cove), W. Aust., 0–3 m deep (*Woelkerling, Platt & Jones*, 2.ii.1984; LTB, 14080, 14091). Point Fowler (E shore), S. Aust., 2–3 m deep (*Platt & Jones*, 14.ii.1984; LTB, 14456). Point Westall, S. Aust., 2–3 m deep (*Platt & Jones*, 16.ii.1984; LTB, 14613). Tiparra Reef, Spencer Gulf, S. Aust., 8 m deep (*Shepherd*, 13.ii.1975; AD, A49395 = LTB, 13601). Nora Creina, S. Aust., 3–8 m deep (*Owen*, 3.ix.1971; AD, A39680 = LTB, 13595). Cape Northumberland, S. Aust., reef surface (*Womersley*, 8.xii.1991; AD, A61544). Port Fairy, Vic., lower eulittoral to upper sublittoral (*May*, 18.iii.1985; LTB, 14763; *Woelkerling*, 6.i.1977; LTB 12569 and 4.i.1979; LTB, 11712, 11714, 11719). Anglesea (Ingoldsby Reef), Vic., 9 m deep (*Beanland*, 5.iii.1983; LTB, 13509, 13523, 13525). Waterloo Bay (Wilsons Prom.), Vic. (*Leach*, 23.x.1977; LTB, 11446). Eddystone Point, Tas., 0–3 m deep (*Platt*, 23.ii.1983; LTB, 13193). Bluestone Bay, Freycinet Pen., Tas., 0–2.5 m deep (*Platt*, 21.ii.1983; LTB, 13048). Coles Bay, Freycinet Pen., Tas., 0–3 m deep (*Platt*, 21.ii.1983; LTB, 13112). Eaglehawk Neck (Tessellated Pavement), Tas., 1–2 m deep (*Platt & Woelkerling*, 26.ii.1983; LTB, 13228, 13235). Ninepin Point, D'Entrecasteaux Channel, Tas., 4–6 m deep (*Platt & Brown*, 18.ii.1983; LTB, 12753). Variety Bay, Bruny I., Tas., 2–4 m deep (*Platt*, 17.ii.1983; LTB, 13001).

Mesophyllum incisum has been found intertidally on reef surfaces and in pools and subtidally to depths of 15 m in southern Australia. It occurs on rock, sponges, and various algae. Gametangial, tetrasporangial and bisporangial thalli may be present in the same population and commonly are collected together on single host thalli.

3. **Mesophyllum macroblastum** (Foslie)Adey 1970: 25. Woelkerling & Harvey 1993: 590, figs 17–23.

Lithothamnion macroblastum Foslie 1897: 16. Woelkerling 1993: 140.

Additional references involving these binomials are provided by Woelkerling & Harvey (1993).

FIGS 86, 87

Thallus normally pinkish, encrusting to warty, somewhat lumpy or layered, mostly 30–85 mm across and 0.1–20 mm thick or tall, epigenous and partially to completely affixed by cell adhesion; protuberant branches simple, mostly 0.9–10 mm in diameter and 1.3–6 mm long; lamellate branches inconspicuous and tightly applanate, mostly 2–10 mm across and 2–14 mm long. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions and lamellate branches but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; each filament composed of cells 4–12 μm in diameter and 5–42 μm long; epithallial cells 3–5 μm in diameter and 3–6 μm long, terminating most filaments at the thallus surface, with distal walls rounded or flattened but not flared; cell elongation occurring mainly within actively dividing subepithallial initials that are usually as long as or longer than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions; secondary pit-connections, haustoria, and trichocytes unknown.

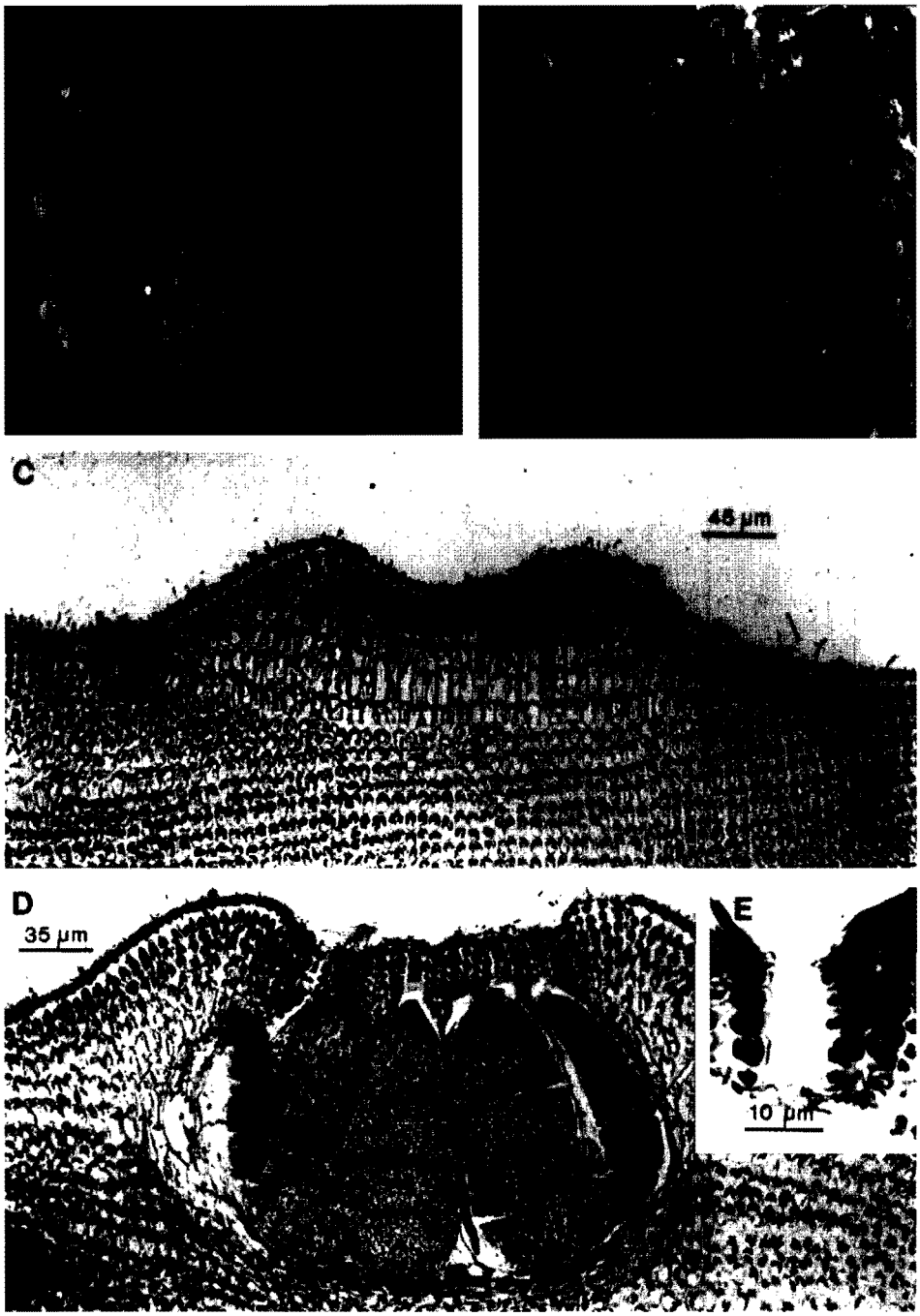


Fig. 86. *Mesophyllum macroblastum* (**A,** LTB, 13227; **B,** LTB, 12599; **C,** LTB, 13210; **D,** LTB, 13072; **E,** LTB, 13205). **A.** Encrusting to warty thallus on old holdfast of *Phyllospora.* **B.** Surface view of part of a layered thallus with inconspicuous applanate branches. **C.** Section of very young tetrasporangial conceptacle arising at thallus surface from a group of subepithallial initials. **D.** Section of mature tetrasporangial conceptacle. **E.** Portion of tetrasporangial conceptacle roof with pore canal and bordering filaments.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporophytes produced in uniporate conceptacles; tetrasporangia/bisporangia produced in multiporate conceptacles.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above surrounding thallus surface, 80–205 μm thick, composed of 12–30 layers of cells above the chamber; conceptacle chambers 175–540 μm in diameter and 54–270 μm high. Carposporophytes lacking a conspicuous central fusion cell and consisting of an irregularly shaped fusion cell (not always evident) that may look discontinuous in section, and several-celled gonimoblast filaments bearing terminal carposporangia 40–85 μm in diameter. Spermatangial filaments unbranched(?), arising from the floor, walls and roof of male conceptacle chambers; mature male conceptacle roofs protruding above surrounding thallus surface, 62–108 μm thick, composed of 11–16 layers of cells above the chamber; conceptacle chambers 243–310 μm in diameter and 65–105 μm high.

Tetrasporangial/bisporangial conceptacle roofs protruding above surrounding surface, differentiated into a peripheral rim and a central sunken pore-plate, 4–5 cells thick above the chamber; pore canals lined by cells that are similar in size and shape to other roof cells; conceptacle chambers 145–270 μm in diameter and 90–150 μm high; tetrasporangia/bisporangia scattered across the conceptacle chamber floor; each mature sporangium 29–81 μm in diameter and 81–135 μm long, containing zonately arranged tetraspores or bispores and possessing an apical plug that blocks a roof pore prior to spore release.

Type from Gulf of Naples, Italy; holotype in TRH (unnumbered; includes slide 191); depicted in Woelkerling & Harvey (1993, p. 623, fig. 17A); additional data provided by Woelkerling (1993, p. 140).

Distribution: Mediterranean shores of France and Italy.

In southern Australia, from the Head of the Great Australian Bight, S. Aust., to Walkerville, Vic., and the eastern and southern coasts of Tasmania.

Selected specimens: Head of Great Australian Bight, S. Aust., reef pools (*Womersley*, 4.ii.1954; AD, A19649 = LTB, 13707). Snapper Point, Kangaroo I., S. Aust. (*Campbell & Penrose*, 13.iv.1988; LTB, 15656). Robe, S. Aust., 3–6 m deep (*Baldock*, 15.v.1967; AD, A31493 = LTB, 13667). Red Rock Bay, Carpenter Rocks, S. Aust. (*Shepherd*, 26.i.1978; LTB, 12599). Cape Northumberland, S. Aust. (*Shepherd*, ii.1977; LTB, 11419). Port Fairy, Vic. (*Woelkerling*, 4.i.1979; LTB, 11436, 11720, 11721). Rye (Number Sixteen reef), Vic., reef pools (*Platt & Woelkerling*, 21.xii.1982; LTB, 12620 and *Harvey & Condon*, 11.ii.1993; LTB, 16596). Walkerville, Vic., 0–3 m deep (*Woelkerling et al.*, 30.xi.1983; LTB, 13906, 13917, 13923 (in error cited as 13293 in the legend to Fig. 22 in Woelkerling & Harvey 1993)). Binalong Bay, Tas., 0–4 m deep (*Platt*, 23.ii.1983; LTB, 13205, 13210). Bluestone Bay, Freycinet Pen., Tas., 0–4 m deep (*Platt*, 12.ii.1983; LTB, 13072). Eaglehawk Neck (Clydes I.), Tas., 0–6 m deep (*Platt*, 26.ii.1983; LTB, 13298, 13311). Eaglehawk Neck (Tessellated Pavement), Tas., 0–2 m deep (*Platt & Woelkerling*, 26.ii.1983; LTB, 13225, 13227). North shore, Safety Cove, Port Arthur, Tas., 0–3 m deep (*Platt & Woelkerling*, 25.ii.1983; LTB, 12831). Sister Bay, Southport, Tas., 3–4 m deep (*Platt et al.*, 16.ii.1983; LTB, 12877).

Mesophyllum macroblastum has been found in intertidal reef pools and subtidally to depths of 15 m on rock, glass, and the holdfasts of the brown algae *Ecklonia* and *Phyllospora* in southern Australia. Gametangial and tetrasporangial thalli may occur in the same populations, but isolated tetrasporangial thalli appear to occur more commonly. Bisporangia were found in one collection (LTB, 15656). Although most spermatangial filaments appear unbranched (Fig. 87D), one male conceptacle in LTB, 13298 recently examined by Derek Keats and the author appears to contain a branched spermatangial filament near the centre of the conceptacle chamber floor. Studies of mature and developing males in additional populations are required before the taxonomic significance of this observation can be fully assessed. Except for the type, records of occurrence in the Mediterranean require confirmation.

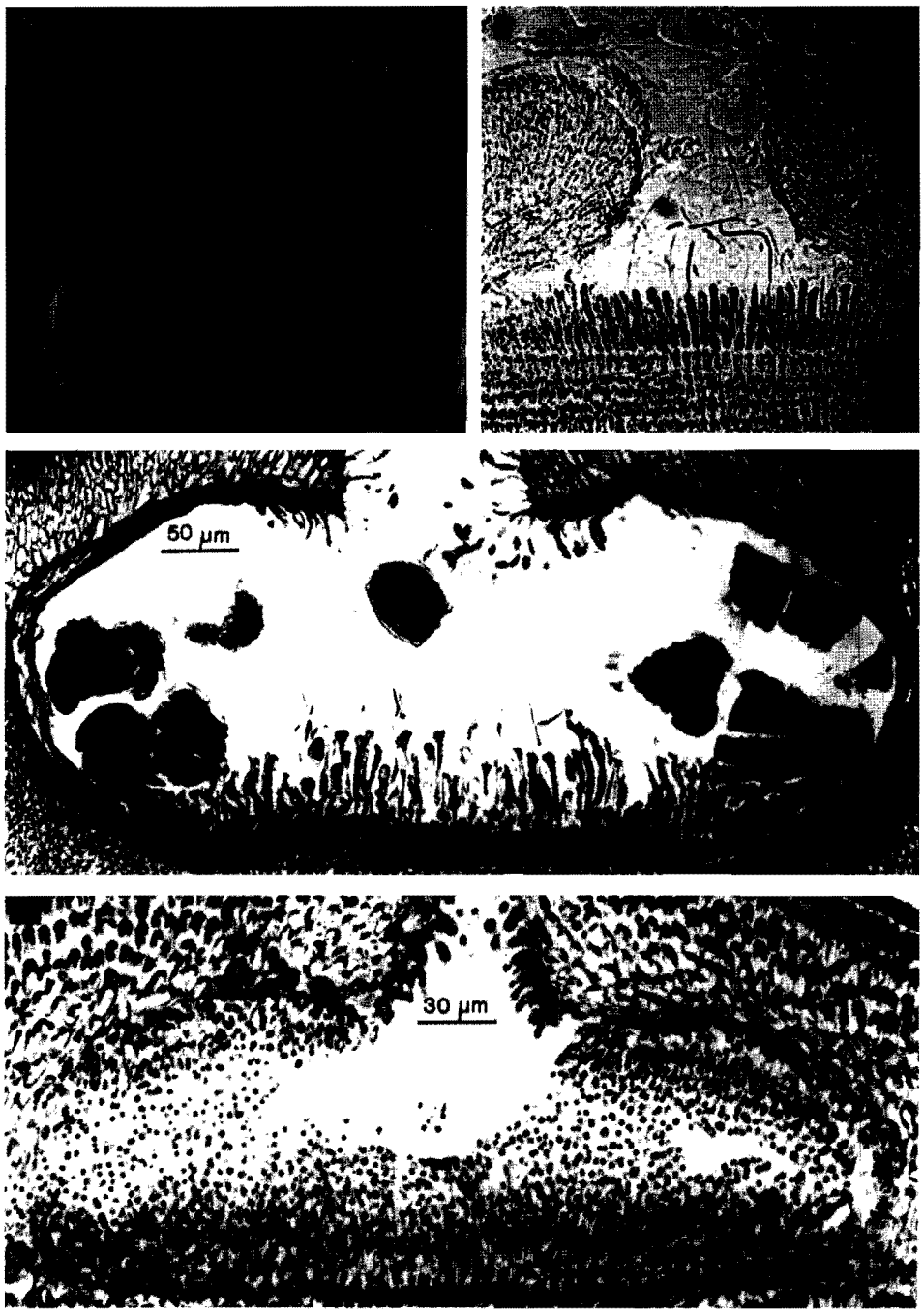


Fig. 87. *Mesophyllum macroblastum* (**A,** TRH, unnumbered; **B,** LTB, 13205; **C, D,** LTB, 13298). **A.** Surface view of tetrasporangial conceptacles with sunken pore plates. **B.** Section of female-carposporangial conceptacle with mature carpogonial filaments. **C.** Section of female-carposporangial conceptacle with mature carposporophyte. **D.** Section of male conceptacle with mature, unbranched spermatangial filaments arising from chamber floor and roof.

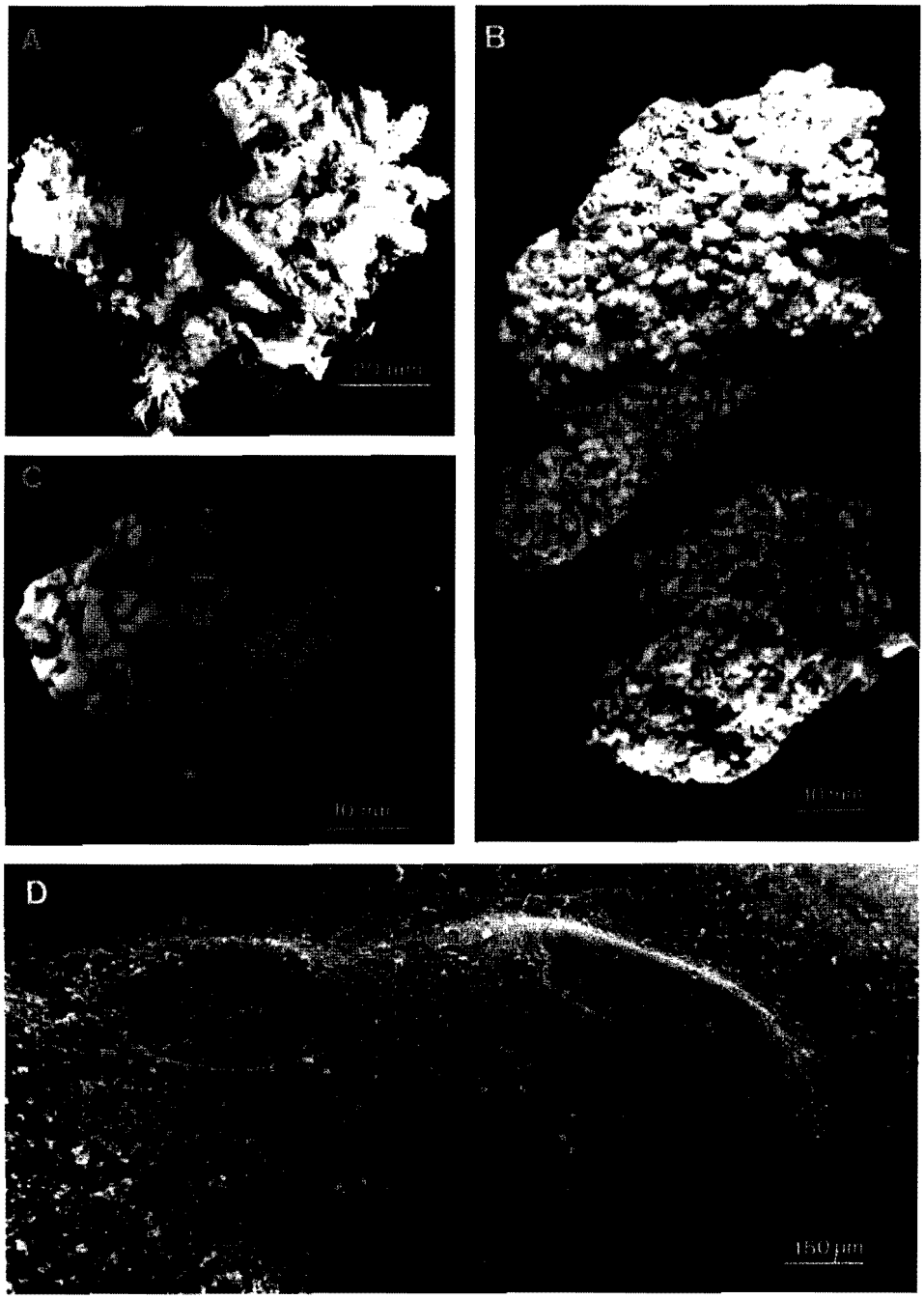


Fig. 88. *Mesophyllum printzianum* (**A,** LTB, 13297; **B,** LTB, 15249; **C,** LTB, 15834; **D,** LTB, 15507). **A.** Encrusting thalli on holdfast of *Ecklonia*. **B.** Warty thalli from holotype collection. **C.** Fruticose thallus detached from rock. **D.** Surface view of tetrasporangial conceptacles with sunken pore-plates.

4. **Mesophyllum printzianum** Woelkerling & Harvey 1993: 593, figs 24–29.

FIGS 63B, 64C, 88, 89

Thallus normally pinkish, encrusting to warty to fruticose, mostly 40–95 mm across and 0.2–25 mm thick or tall, epigenous and partially to completely affixed by cell adhesion; protuberant branches simple or branched, mostly 1.4–11 mm in diameter and 1.8–14 mm long. *Structure* pseudoparenchymatous, organisation dorsiventral in crustose portions but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 4–12 µm in diameter and 6–42 µm long; epithallial cells 3–5 µm in diameter and 4–6 µm long, terminating most filaments at the thallus surface, with distal walls rounded or flattened but not flared; cell elongation occurring mainly within actively dividing subepithallial initials that are usually as long as or longer than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions; trichocytes sometimes present, solitary or in small fields; secondary pit-connections and haustoria unknown.

Reproduction. Vegetative reproduction unknown. Gametangia and presumably carposporophytes produced in uniporate conceptacles; tetrasporangia produced in multiporate conceptacles. Bisporangia unknown.

Gametangial thalli probably dioecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonial stages and carposporophytes unknown. Spermatangial filaments unbranched, arising from the floor, walls and roof of male conceptacle chambers; mature male conceptacle roofs protruding above surrounding thallus surface, 54–94 µm thick, composed of 11–13 layers of cells above the chamber, conceptacle chambers 175–243 µm in diameter and 48–60 µm high.

Tetrasporangial conceptacle roofs protruding above surrounding surface, differentiated into a peripheral rim and a central sunken pore-plate, 3–6 cells thick above the chamber, pore canals lined by narrow elongate cells that differ in shape from other roof cells especially near the base of the canal, conceptacle chambers 185–420 µm in diameter and 175–190 µm high; tetrasporangia scattered across the conceptacle chamber floor; each mature sporangium 54–122 µm in diameter and 121–150 µm long, containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release.

Type from Blanket Bay, Otway National Park, Vic. (*Campbell, Penrose & May*, 14.xi.1985); holotype in LTB (15249); depicted in Woelkerling & Harvey (1993, p. 630, fig. 24A).

Distribution: Beachport, S. Aust., to Summerland Bay, Phillip I., Vic., and the eastern and southern coasts of Tasmania.

Selected specimens: Beachport (Post Office Rock), S. Aust., on reef, 0–3 m deep (*Campbell, Penrose & Woelkerling*, 1.xii.1986; LTB, 15507; *Campbell & Penrose*, 6.xi.1987; LTB, 15834 and *Harvey & Condon*, 15.ii.1993; LTB, 16594). Beachport (platform west of Post Office Rock), S. Aust., 0–1 m deep (*Woelkerling*, 6.xi.1987; LTB, 15821). Blanket Bay, Otway National Park, Vic., 2 m deep (*Campbell, Penrose & May*, 14.xi.1985; LTB, 15257). Rye (Number Sixteen reef), Vic., reef pool (*Platt & Woelkerling*, 21.xii.1982; LTB, 12622). Summerland Bay, Phillip I., Vic., 1–2 m deep (*Harvey & Harvey*, 22.ii.1993; LTB, 16591, 16592). Binalong Bay, Tas., 0–4 m deep (*Platt*, 23.ii.1983; LTB, 13207, 13212). Eaglehawk Neck (Clydes I.), Tas., 0–6 m deep (*Platt & Woelkerling*, 26.ii.1983; LTB, 13297). Safety Cove, Port Arthur, Tas., 0–2 m deep (*Platt*, 25.ii.1983; LTB, 12859 and *Platt & Woelkerling*, 25.ii.1983; LTB, 12850). Variety Bay (S shore), Bruny I., Tas., 2–4 m deep (*Platt*, 17.ii.1983; LTB, 13008).

Thalli of *Mesophyllum printzianum* have been found in intertidal rock pools and to depths of 6 m on rock and on the holdfasts of the brown alga *Phyllospora*.

Notes on other taxa reported from southern Australia

Woelkerling & Harvey (1993, pp. 596–600) provide information on nine additional species that at some stage were ascribed to *Mesophyllum* and reported from southern Australia. These include species whose status is uncertain, incorrect records, heterotypic synonyms of other species of *Mesophyllum* and species now known to belong to other genera or conspecific with taxa belonging to other genera.

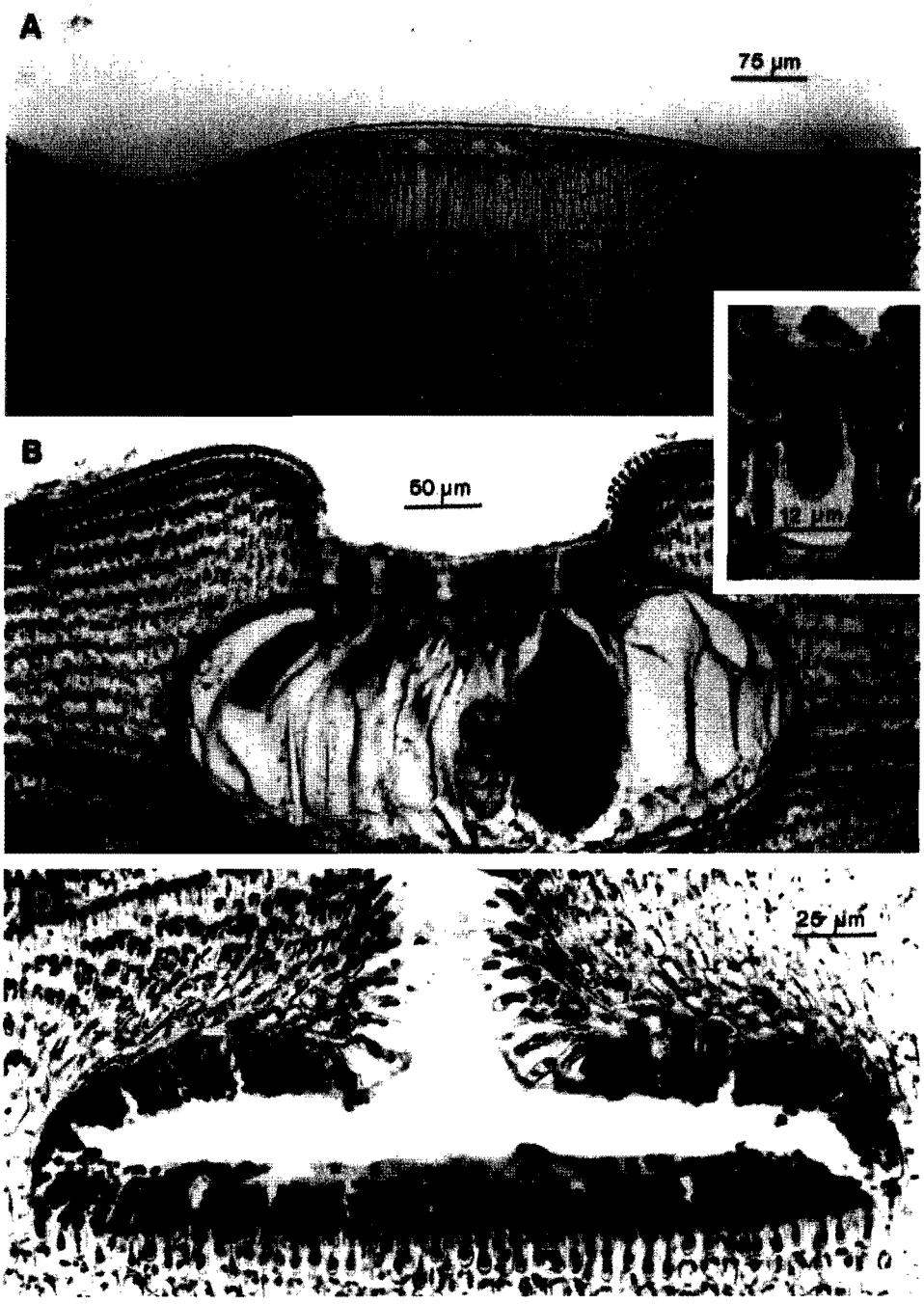


Fig. 89. *Mesophyllum printzianum* (**A, B,** LTB, 12850; **C,** LTB, 15507; **D,** LTB, 15249). **A.** Section of very young tetrasporangial conceptacle arising at thallus surface from a group of subepithallial initials. **B.** Section of mature tetrasporangial conceptacle. **C.** Portion of tetrasporangial conceptacle roof with pore canal and bordering filaments. **D.** Section of male conceptacle with mature, unbranched spermatangial filaments arising from chamber floor and roof.

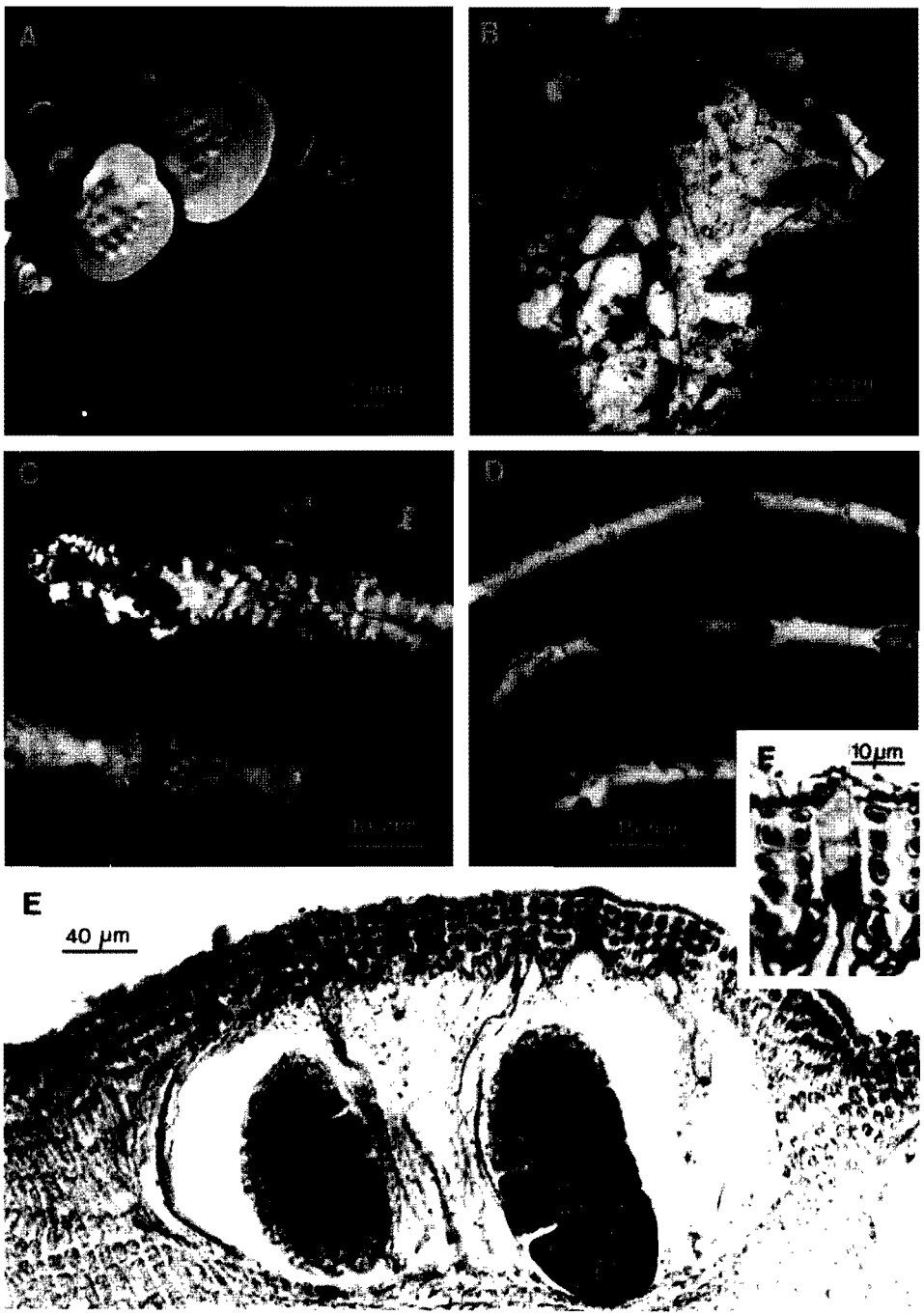


Fig. 90. *Synarthrophyton patena* (**A,** LTB, 16597; **B,** LTB, 13941; **C,** LTB, 11625; **D,** LTB, 13892; **E,** LTB, 12782; **F,** LTB, 15538). **A.** Discoid thalli on *Ballia*. **B.** Encrusting thallus on holdfast of *Ecklonia*. **C.** Encrusting to fruticose thalli enveloping axes of *Acrocarpia*. **D.** Encrusting thalli affixed to stems of *Amphibolis*. **E.** Section of mature tetrasporangial conceptacle. **F.** Portion of tetrasporangial conceptacle roof with pore canal and bordering filaments.

Genus SYNARTHROPHYTON Townsend 1979: 252

Thallus encrusting to discoid, warty, foliose or fruticose; epigenous and partially or completely affixed by cell adhesion or envelopment of host axes; genicula absent. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; cell elongation occurring mainly within actively dividing subepithallial initials that are usually as long as or longer than their immediate inward derivatives; fusions present between cells of contiguous filaments, secondary pit-connections absent; epithallial cells terminating most filaments at thallus surface, distal walls rounded or flattened but not flared; haustoria and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporangia borne in uniporate conceptacles; tetrasporangia borne in multiporate conceptacles that apparently arise from groups of subepithallial initials; gametangia and carposporangia formed on separate thalli from tetrasporangia. Report of bisporangia unconfirmed.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles or rarely in the same conceptacle. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature carposporophytes apparently composed of a fusion cell (not always evident) and short gonimoblast filaments bearing terminal carposporangia. Both unbranched and branched spermatangial filaments present, borne on the floor, walls and roof of male conceptacle chambers.

Tetrasporangia scattered across the conceptacle chamber floor, roofs formed by filaments interspersed amongst and peripheral to sporangial initials; each mature sporangium containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release.

Type species: *S. patena* (Hooker & Harvey *in* Harvey)Townsend 1979: 252.

Synarthrophyton is represented in southern Australia by a single species, *S. patena.* This account follows A. Harvey *et al.* (1994) and May & Woelkerling (1988). A second species, *S. schielianum* Woelkerling & Foster (1989), has been reported only from the Chatham Islands. Details relating to generic etymology, nomenclature, orthographic variants, *etc.* are provided by Woelkerling (1988, pp. 210–215). Bisporangial conceptacles, reported by Heydrich (1897b, p. 413) for *S. patena* (as *Lithothamnion*), have not been confirmed to occur (A. Harvey & Woelkerling 1994).

Synarthrophyton patena (Hooker & Harvey *in* Harvey)Townsend 1979: 252, figs 1–18. Adams 1994: 160, pl. 55, lower right. A. Harvey *et al.* 1994: 333, figs 1–24. May & Woelkerling 1988: 50, figs 1–40. Millar & Kraft 1993: 14.
Melobesia patena Hooker & Harvey *in* Harvey 1849: 111, pl. XL, lower left.
Mastophora patena (Hooker & Harvey *in* Harvey)Kützing 1858: 47.
Lithophyllum patena (Hooker & Harvey *in* Harvey)Rosanoff 1866: 88.
Lithothamnion patena (Hooker & Harvey *in* Harvey)Heydrich 1897a: 413.
Lithothamnion lichenoides f. *patena* (Hooker & Harvey *in* Harvey)Foslie 1898b: 7.
Lithothamnion lichenoides var. *patena* (Hooker & Harvey *in* Harvey)De Toni et Forti 1923: 59.
Polyporolithon patena (Hooker & Harvey *in* Harvey)Mason 1953: 317.
Mesophyllum patena (Hooker & Harvey *in* Harvey)Ricker 1987: 173.
Additional references involving these and other binomials, previous southern Australian records, misapplied names, and known heterotypic synonyms are listed in A. Harvey *et al.* (1994), May & Woelkerling (1988), and/or Townsend (1979).

PLATE 3 fig. 3; FIGS 90, 91

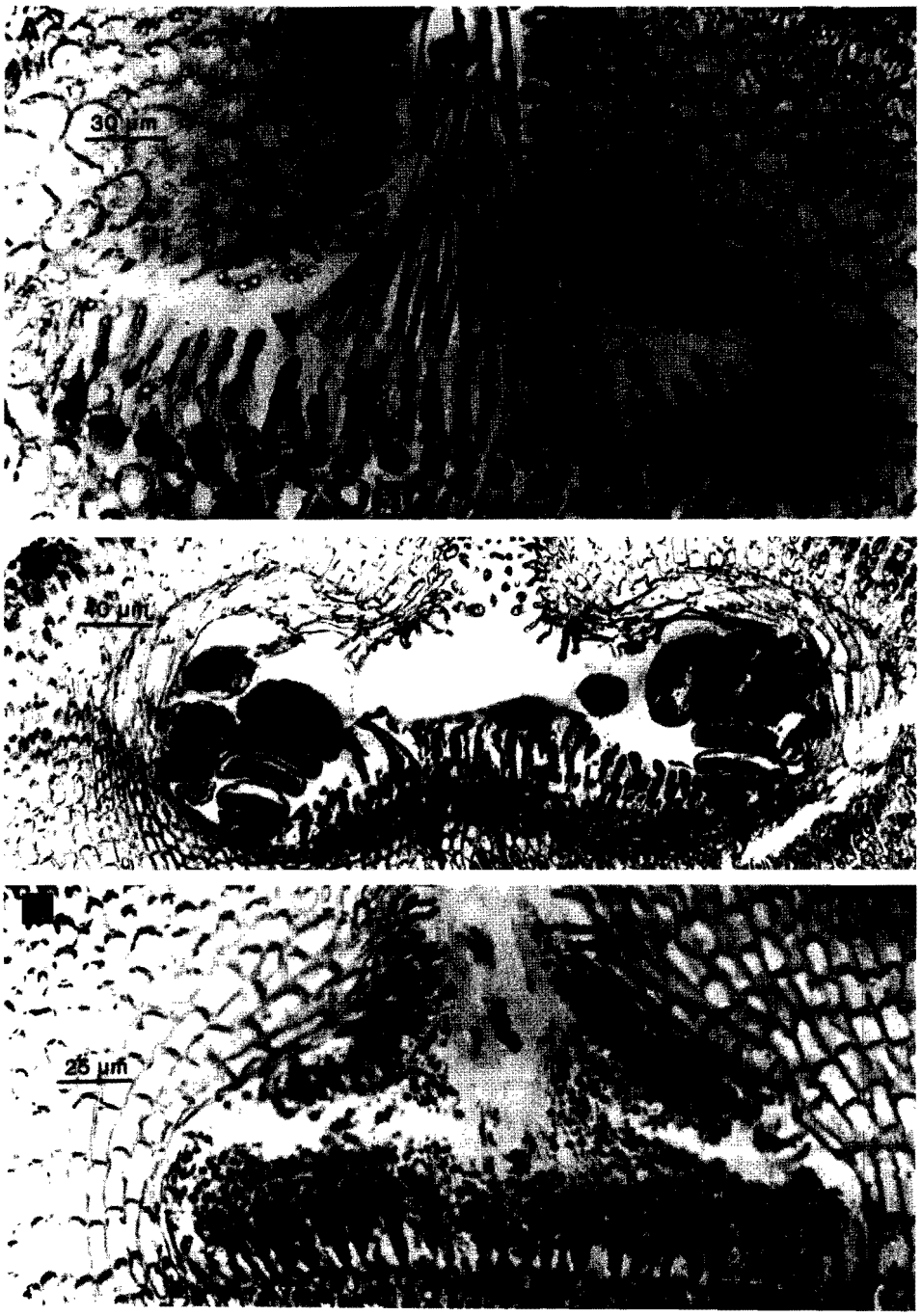


Fig. 91. *Synarthrophyton patena* (**A**, LTB, 14766; **B**, **C**, LTB, 15538). **A.** Section of female-carposporangial conceptacle with mature carpogonial filaments with (arrows) and without (arrowheads) trichogynes. **B.** Section of female-carposporangial conceptacle with mature carposporophyte showing sections of 'discontinuous' fusion cell (arrows). **C.** Section of male conceptacle with mature, branched spermatangial filaments arising from chamber floor and mostly unbranched spermatangial filaments arising from chamber roof.

Thallus normally dull pinkish, encrusting to discoid, warty or fruticose, mostly 2–65 mm across and 0.2–1.5 mm thick or tall, epigenous and partially or completely affixed by cell adhesion or by envelopment of host axes; protuberant branches simple or branched, mostly 1–4 mm in diameter and 2–4.5 mm long. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions but radial in protuberant branches; construction monomerous, consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 3–25 µm in diameter and 6–50 µm long; epithallial cells 5–15 µm in diameter and 3–12 µm long, terminating most filaments at the thallus surface, with distal walls rounded or flattened but not flared; cell elongation occurring mainly within actively dividing subepithallial initials that are usually as long as or longer than their immediate inward derivatives; cells of adjacent filaments joined by cell-fusions although sometimes difficult to detect; secondary pit-connections, haustoria, and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia and carposporophytes produced in uniporate conceptacles; tetrasporangia produced in multiporate conceptacles. Report of bisporangia not confirmed.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles or rarely in the same conceptacle. Carpogonia terminating 2- or 3-celled filaments arising from the conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above surrounding thallus surface, 120–190 µm thick, composed of 15–30 layers of cells above the chamber, conceptacle chambers 235–520 µm in diameter and 70–210 µm high. Carposporophytes apparently composed of a fusion cell (not always evident) and several-celled gonimoblast filaments bearing terminal carposporangia 40–80 µm in diameter. Both unbranched and branched spermatangial filaments present, arising from the floor, walls and roof of male (rarely bisexual) conceptacle chambers, mature male conceptacle roofs protruding above surrounding thallus surface, (30-) 80–90 µm thick, composed of (6-) 12–20 layers of cells above the chamber, conceptacle chambers (85-) 180–300 µm in diameter and (15-) 55–95 µm high.

Tetrasporangial conceptacle roofs protruding above surrounding surface, not differentiated into a peripheral rim and a central sunken pore-plate, 3–8 cells thick above the chamber, pore canals lined by cells that are similar in size and shape to other roof cells, conceptacle chambers 260–560 µm in diameter and 120–210 µm high; tetrasporangia scattered across the conceptacle chamber floor, each mature sporangium 35–100 µm in diameter and 70–250 µm long, containing zonately arranged tetraspores and possessing an apical plug that blocks a roof pore prior to spore release.

Type from Flat Point (near Castlepoint), New Zealand; lectotype in TCD (Colenso 1331); designated and depicted by Chapman & Parkinson (1974, pl. 72); also depicted in May & Woelkerling (1988, p. 53, fig. 1) and Ricker (1987, fig. 73d).

Distribution: New Zealand; southern Africa; the Chatham Islands; various subantarctic islands (A. Harvey *et al.* 1994).

In Australia, Cape Vlaming, Rottnest I., W. Aust., to Long Reef, N.S.W., and around Tasmania.

Selected specimens: Cape Vlaming, Rottnest I., W. Aust., reef edge on *Laurencia* (*Woelkerling*, 8.ii.1978; LTB, 10961). Eyre ('Nine Mile Reef'), W. Aust., 2–3 m deep on holdfast of *Ecklonia radiata* (*Woelkerling, Platt & Jones*, 1.ii.1984; LTB, 13941). Foul Ground, 7.2 km S of Wedge I., S. Aust., 21–37 m deep on *Ballia callitricha* (*Baldock*, 4.i.1964; AD, A27196). Port Elliot, S. Aust. (*Womersley*, 9.ii.1975; AD, A46065 = LTB, 13745). Hansen Bay, Southwest R., Kangaroo I., S. Aust., upper sublittoral on *Acrocarpia* (*Woelkerling*, 21.ii.1979; LTB, 11625). Cape Buffon, S. Aust., 2 m deep on *Ballia callitricha* (*Collings & Kildea*, 27.ix.1992; AD, A62775 —"Marine Algae of southern Australia" No. 334). Cape Northumberland, S. Aust., reef edge on *Gelidium* (*Campbell, Penrose & Woelkerling*, 2.xii.1986; LTB, 15538). Peterborough, Vic., drift on *Ballia callitricha* (*Woelkerling*, 10.iii.1993; LTB, 16597). Warrnambool, Vic., drift on *Camontagnea oxyclada* (*Womersley*, 13.iv.1959; AD, A22931). Anglesea (Ingoldsby Reef), Vic., 6 m deep on *Ballia callitricha* (*May*, 9.vi.1985; LTB, 14766). Flinders, Vic., reef pools on *Amphibolis* (*Woelkerling*, 19.xi.1983; LTB,

13892). Little Squally Cove, Deal I., Bass Strait, Tas., 21 m deep on *Ballia callitricha* (*Houridis*, 14.iii.1993; AD, A63277). Ninepin Point, D'Entrecasteaux Channel, Tas., 4–6 m deep on *Haliptilon* (*Platt*, 18.ii.1983; LTB, 12782). N of Cape Surville, Forestier Pen., Tas., 8–12 m deep (*Gowlett-Holmes*, 5.v.1995; AD, A64409). Lady Bay, Southport, Tas., drift on *Ballia callitricha* (*Wollaston & Mitchell*, 27.ii.1964; AD, A27537). Long Reef, N.S.W., on *Ballia callitricha* (*May*, 3.xii.1944; NSW, A3540).

Synarthrophyton patena occurs epiphytically on a variety of green, brown and red algae, and on seagrasses, tunicates, molluscs and sponges in southern Australia. It has been found in intertidal pools and subtidally to depths of 37 m. Populations involving many individuals often occur on a single host thallus, and both gametangial and tetrasporangial specimens often are present in the same collection. Thalli of *Synarthrophyton patena* growing on *Ballia* or *Camontagnea* commonly form distinctive, largely detached, discoid thalli that can be recognised in the field from external features; no other known southern Australian non-geniculate coralline found on *Ballia* has this growth form. Tetrasporangial conceptacle anatomy is very similar in *Synarthrophyton patena* and *Mesophyllum engelhartii*, and certain tetrasporangial thalli of the two species could be confused if viewed in isolation (A. Harvey *et al.* 1994, p. 341). Male thalli, however, can easily be told apart as spermatangial branches are both branched and unbranched in *Synarthrophyton patena* but only unbranched in *Mesophyllum engelhartii.*

SUBFAMILY CHOREONEMATOIDEAE Woelkerling 1987a: 125

by W.J. Woelkerling

Thallus largely unconsolidated, vegetative portions endophytic but conceptacles protruding above the host surface; genicula absent. *Structure* filamentous to partly pseudoparenchymatous with diffuse construction; cells of adjacent filaments not joined by cell-fusions or secondary pit-connections.

Reproduction. Vegetative reproduction unknown. Gametangia and tetrasporangia borne in uniporate conceptacles. Bisporangia unknown.

Gametangial thalli dioecious. Carpogonial filaments 2- or 3-celled, arising from the female conceptacle chamber floor. Carposporophytes developing within female conceptacles after karyogamy, composed of carposporangia terminating short gonimoblast filaments that arise from a central fusion cell. Spermatangial filaments unbranched, produced from the floor, walls and roof of male conceptacle chambers.

Tetrasporangia borne on separate thalli from gametangia and carposporangia, with apical plugs that collectively block the conceptacle pore prior to spore release, tetrasporangia each containing four zonately arranged spores. Conceptacle roofs formed from filaments peripheral to developing sporangia.

Type genus: *Choreonema* Schmitz 1889: 455.

The Choreonematoideae includes a single genus and species (Woelkerling 1987a, 1988). *Chaetolithon* Foslie (1898b, p. 7), based on a single southern Australian collection, is considered to be a heterotypic synonym of *Choreonema* (Woelkerling 1987b).

Genus CHOREONEMA Schmitz 1889: 455

Thallus largely unconsolidated, vegetative portions endophytic but conceptacles produced external to the host. *Structure* filamentous to partly pseudoparenchymatous; organisation vaguely dorsiventral; construction diffuse, consisting of short, simple or branched endophytic filaments that may become partially consolidated in areas of conceptacle production but collectively lack any regularised internal structure; cell elongation characteristics uncertain; cell-fusions, secondary pit-connections, epithallial cells, haustoria and trichocytes unknown.

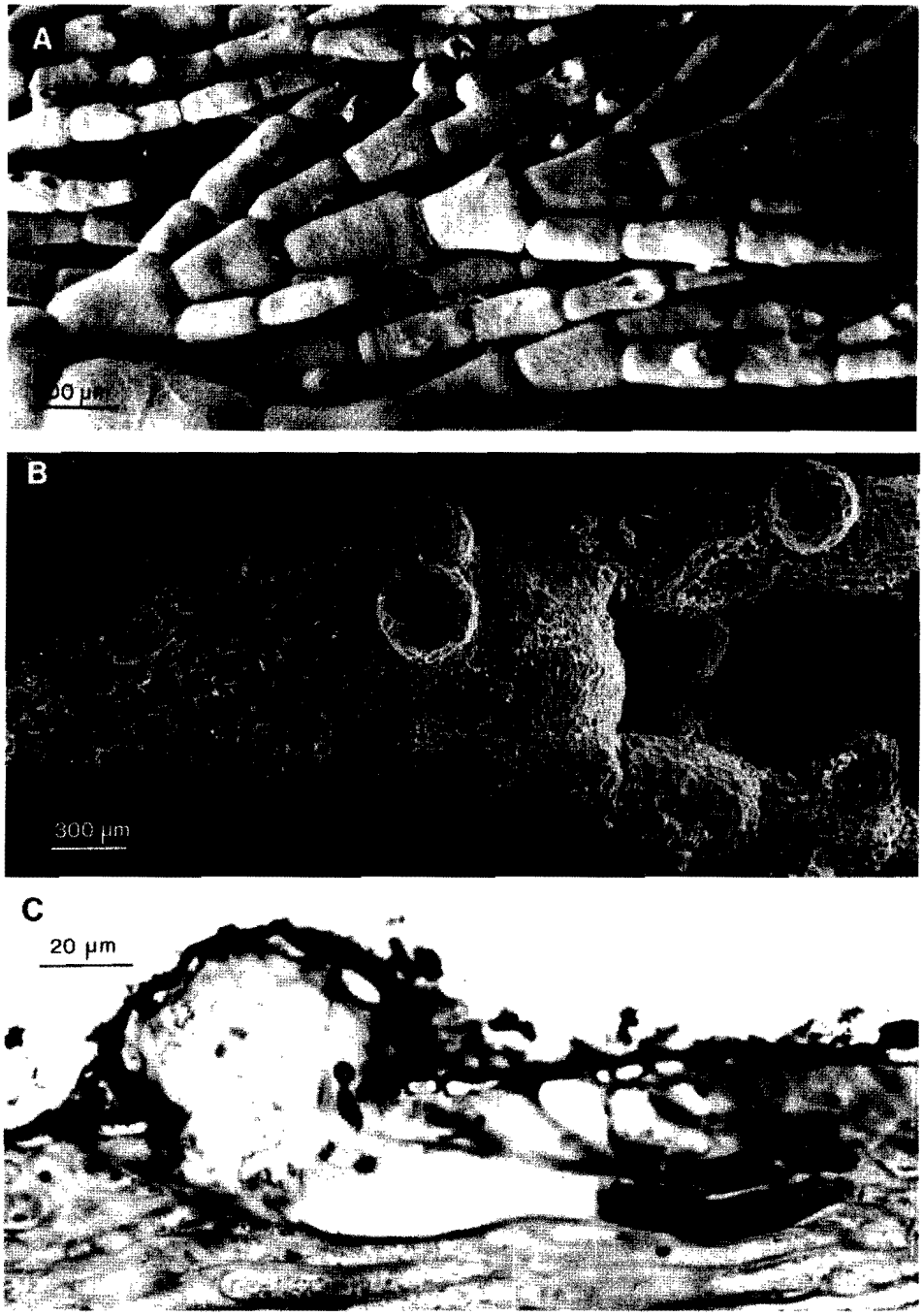


Fig. 92. *Choreonema thuretii* (**A**, LTB, 14777; **B**, LTB, 11566; **C**, LTB, 11737). **A.** Habit of *Choreonema* on *Haliptilon roseum*. **B.** Surface view of conceptacles of *Choreonema* on intergenicula of *Haliptilon*. **C.** Section of endophytic vegetative thallus with developing conceptacle protruding above host surface.

Reproduction. Vegetative reproduction unknown. Gametangia and tetrasporangia formed in uniporate, calcified conceptacles produced external to the host, roofs composed of a single layer of cohering filaments. Bisporangia unknown.

Gametangial thalli dioecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Carposporophytes composed of a central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, produced on floor, walls and roof of male conceptacle chambers.

Tetrasporangia scattered across the conceptacle chamber floor, roofs arising from filaments peripheral to the sporangial initials, each mature sporangium containing zonately arranged tetraspores and possessing an apical plug that helps to block the roof pore prior to spore release.

Type species: *C. thuretii* (Bornet *in* Thuret & Bornet)Schmitz 1889: 455. Basionym: *Melobesia thuretii* Bornet *in* Thuret & Bornet 1878: 96.

Choreonema contains one species. *Endosiphonia* Ardissone 1883 (non Zanardini 1878) is an older but illegitimate name for *Choreonema*. Details relating to generic etymology, nomenclature, synonymy and infrageneric classification are provided by Woelkerling (1988, pp. 90, 91). The following account is based mainly on data in Woelkerling (1987a).

Choreonema thuretii (Bornet *in* Thuret & Bornet)Schmitz 1889: 455. Adams 1994: 160. Afonso-Carrillo *et al.* 1986: 207, figs 1–5. Cabioch 1980: 707, figs A–D. Chamberlain & Irvine 1994a: 34, figs 10, 11. Minder 1910: 1, figs 1–9. Suneson 1937: 53, figs 33–35, pl. 3 figs 10–12. Woelkerling 1987a: 111, figs 1–25.
Melobesia thuretii Bornet *in* Thuret & Bornet 1878: 96, pl. 50 figs 1–8.
Endosiphonia thuretii (Bornet *in* Thuret & Bornet)Ardissone 1883: 451.
Melobesia deformans Solms-Laubach 1881: 57, pl. 1 fig. 5, pl. 3 figs 12, 26.
Lithothamnion deformans (Solms-Laubach)Foslie 1898a: 4.
Chaetolithon deformans (Solms-Laubach)Foslie 1898b:7. Woelkerling 1987b: 277, figs 1–7.

FIGS 92, 93

Thallus largely unconsolidated, mostly 0.3–2 mm in greatest extent, vegetative portions endophytic but conceptacles produced external to the host. *Structure* filamentous to partly pseudoparenchymatous; construction diffuse, consisting of several-celled simple or branched filaments with cells mostly 5–20 µm in diameter and 20–65 µm long; cell elongation characteristics uncertain; cell-fusions and secondary pit-connections absent; epithallial cells, haustoria, and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia and tetrasporangia formed in uniporate conceptacles produced external to the host. Bisporangia unknown.

Gametangial thalli dioecious. Carpogonia terminating 2-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above the host surface, 15–20 µm thick, composed of one layer of cells above the chamber, conceptacle chambers 75–80 µm in diameter and 50–60 µm high. Mature carposporophytes composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia 15–30 µm in diameter. Spermatangial filaments unbranched, arising from the floor, walls and roof of male conceptacle chambers, mature male conceptacle roofs protruding above the host surface, 15–20 µm thick, composed of one layer of cells above the chamber, conceptacle chambers 55–70 µm in diameter and 50–60µm high.

Tetrasporangial conceptacle roofs protruding above the host surface, 15–20 µm thick above the chamber and composed of one layer of cells, conceptacle chambers 60–80 µm in diameter and 50–55 µm high; tetrasporangia scattered across the conceptacle chamber floor; each mature sporangium 8–20 µm in diameter and 35–50 µm long, containing zonately arranged tetraspores and possessing an apical plug that helps to block the single conceptacle pore prior to spore release.

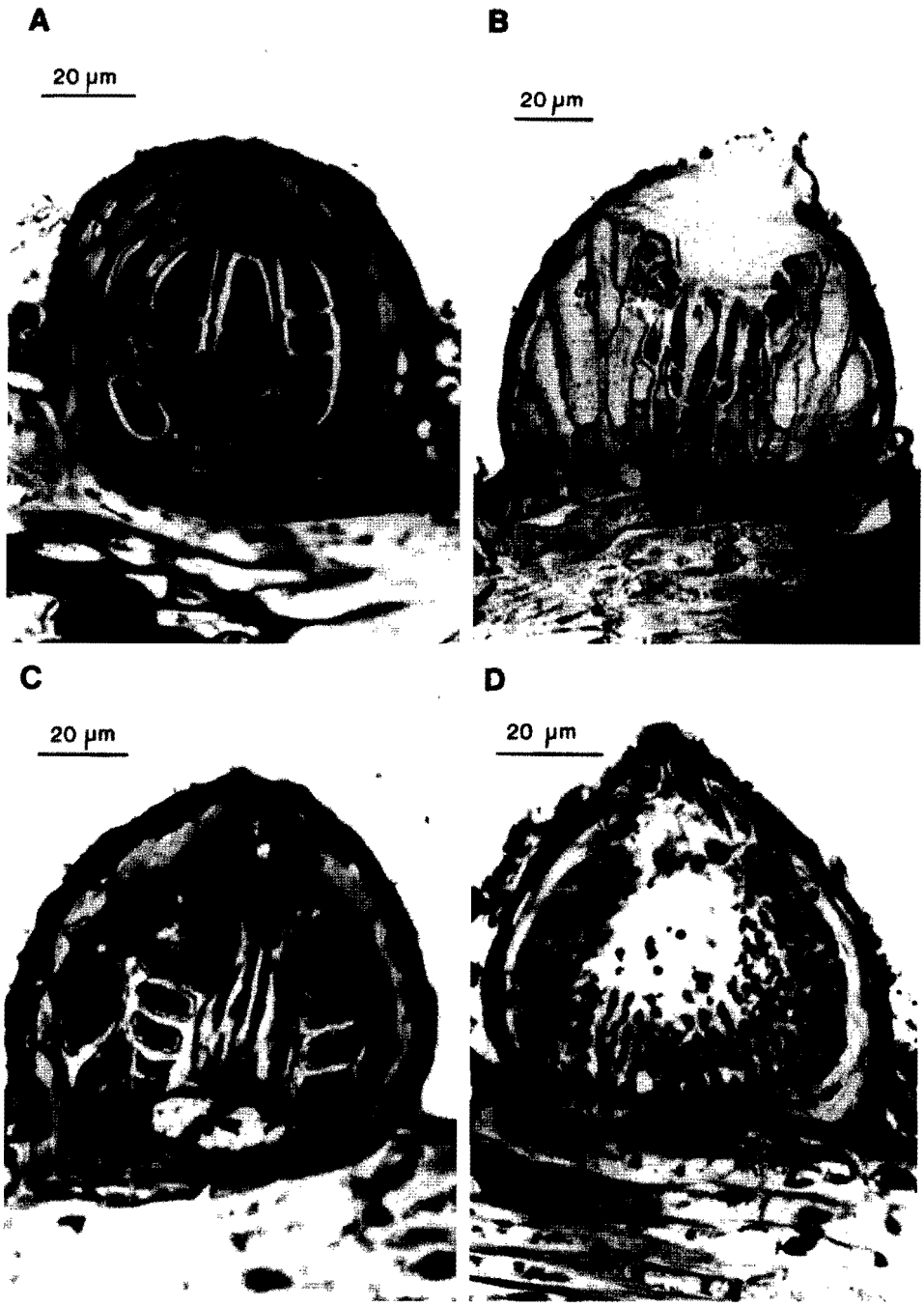


Fig. 93. *Choreonema thuretii* (**A, C,** LTB, 11566; **B,** LTB, 11567; **D,** LTB, 10585). **A.** Section of mature tetrasporangial conceptacle. **B.** Section of female-carposporangial conceptacle with mature carpogonial filaments. **C.** Section of female-carposporangial conceptacle with mature carposporophyte. **D.** Section of male conceptacle with spermatangial filaments arising from chamber floor and walls.

Type from Pointe de Querqueville, France; lectotype in PC (unnumbered); designated by Woelkerling (1987a, p. 113); depicted in Woelkerling (1987a, p. 114, fig. 1).

Distribution: Widespread (Woelkerling 1987a, p. 115; 1988, p. 91).

In western and southern Australia, Kalbarri, W. Aust., to Gabo I., Vic., and around Tasmania.

Selected specimens: Kalbarri, W. Aust., 2–3 m deep on *Jania* (*Woelkerling*, 22.ii.1978; LTB, 11706). Jeannies Lookout, Rottnest I., W. Aust., 2–3 m deep on *Haliptilon* (*Woelkerling*, 11.ii.1978; LTB, 10920). Point Valliant, Two People Bay, W. Aust., 0–1 m deep on *Jania* (*Woelkerling*, 2.ii.1978; LTB, 10585). Rossiter Bay, Esperance, W. Aust., 1–2 m deep on *Jania* (*Woelkerling*, 28.i.1978; LTB, 10797). Point Malcolm, SW of Israelite Bay, W. Aust., 0–2 m deep on *Jania* (*Woelkerling, Platt & Jones*, 7.ii.1984; LTB, 14188). St Francis I., S. Aust., 0–2 m on *Jania* (*Shepherd*, 6.i.1971; AD, A38127 = LTB, 14771). Pearson I., S. Aust., 20–25 m deep on *Jania* (*Shepherd*, 8.i.1969; AD, A56898 = LTB, 14952). Pennington Bay, Kangaroo I., S. Aust., reef surface on *Haliptilon* (*Womersley*, 25.i.1944; AD, A56905 = LTB, 14777). Cape Willoughby, Kangaroo I., S. Aust., upper sublittoral on *Jania* and *Haliptilon* (*Woelkerling*, 25.ii.1979; LTB, 11566 and 11567 respectively). Port Fairy, Vic., lower eulittoral on *Haliptilon* (*Woelkerling*, 4.i.1979; LTB, 11716). Rye (Number 16 reef), Vic., upper sublittoral on *Haliptilon* (*Woelkerling*, 14.ii.1977; LTB, 11336). Walkerville, Vic., lower eulittoral on *Haliptilon* (*Woelkerling*, 28.xii.1978; LTB, 11737). Gabo I, Vic., 8 m deep on *Haliptilon* (*Shepherd*, 19.ii.1973; AD, A56904 = LTB, 14951). Hunter I., Tas., reef pools on *Haliptilon* (*Bennett*, 14.i.1954; AD, A56896 = LTB, 14946). Coles Bay, Tas., upper sublittoral on *Jania* (*Womersley*, 4.xi.1982; AD, A56885 = LTB, 14945). Triabunna, Tas., sublittoral on *Jania* (*Cribb*, 18.iii.1950; AD, A56889 = LTB, 14949). Cape Sorrell, Tas., lower eulittoral on *Haliptilon* (*Bennett*, 4.ii.1955; AD, A56981 = LTB, 14944).

Choreonema thuretii has been found on the geniculate corallines *Haliptilon roseum* and less often on *Jania verrucosa* and *J. micrarthrodia* in southern Australia; host thalli containing the endophyte have been collected intertidally from pools and rock platforms and subtidally to depths of 25 m. In southern Australian collections, deformation of host axes in areas endophytised by *C. thuretii* is rare; this contrasts with reports of host distortion in European populations (Cabioch 1980; Chamberlain & Irvine 1994a, p. 36). The apical plugs on tetrasporangia stain well with toluidine blue but not with potassium permanganate (Woelkerling 1987a). Woelkerling (1987b) concluded that *Chaetolithon deformans*, known from a single southern Australian collection, is conspecific with *Choreonema thuretii*, and thus that *Chaetolithon* is a heterotypic synonym of *Choreonema*.

SUBFAMILY LITHOPHYLLOIDEAE Setchell 1943: 134 (as 'Lithophylleae')

by W.J. Woelkerling

Thallus encrusting to warty, lumpy, fruticose, discoid, layered, ribbon like or foliose; prostrate to erect; partially endophytic, epigenous, or unattached and free-living as rhodoliths; genicula absent. *Structure* pseudoparenchymatous with monomerous or dimerous construction or both; cells of adjacent filaments joined by secondary pit-connections; cell-fusions absent or rare.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia, tetrasporangia and bisporangia borne in uniporate conceptacles.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles or rarely in the same conceptacle. Carpogonial filaments mostly 2- or 3-celled, arising from the female conceptacle chamber floor. Carposporophytes developing within female conceptacles after karyogamy, composed of carposporangia terminating short gonimoblast filaments that arise from a central fusion cell. Spermatangial filaments unbranched, confined to the male conceptacle chamber floor.

Tetrasporangia and bisporangia borne on separate thalli from gametangia and carposporangia, lacking apical plugs, tetrasporangia each containing four zonately arranged spores, bisporangia each containing two bispores. Conceptacle roofs formed from filaments interspersed amongst and peripheral to developing sporangia or only from filaments peripheral to developing sporangia.

Type genus: *Lithophyllum* Philippi 1837: 387.

The Lithophylloideae (see Woelkerling 1988, Campbell & Woelkerling 1990, Woelkerling & Campbell 1992) includes three genera: *Ezo*, known only from Japan; *Tenarea*, known only from the eastern Mediterranean; and *Lithophyllum*, which is widespread. *Titanoderma*, recognised by Chamberlain (1991) and Chamberlain & Irvine (1994b), is considered to be a heterotypic synonym of *Lithophyllum* for reasons outlined by Campbell & Woelkerling (1990), Woelkerling & Campbell (1992, pp. 17–18), John *et al.* (1994, pp. 59–60), and Braga & Aguirre (1995, p. 271).

Genus LITHOPHYLLUM Philippi 1837: 387

Thallus encrusting to warty, lumpy, fruticose, layered or foliose, epigenous and partially to completely affixed by cell adhesion or envelopment of host axes or unattached and free-living as rhodoliths; genicula absent. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions and lamellate branches but radial in protuberant branches; construction monomerous, dimerous or both; monomerous portions consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; dimerous portions consisting of two distinct groups of laterally cohering filaments/cells: a unistratose ventral layer in which each filament is composed of palisade cells, non-palisade cells or both, and secondly epithallial cells or multicellular filaments arising dorsally and more or less perpendicularly from cells of ventral layer filaments; cell elongation characteristics uncertain; cells of adjacent filaments joined by secondary pit-connections, cell-fusions rare or absent; epithallial cells terminating most filaments at thallus surface, distal walls rounded or flattened but not flared; haustoria unknown; trichocytes uncommon, occurring singly.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia, carposporangia, tetrasporangia and bisporangia borne in uniporate conceptacles; gametangia and carposporangia formed on separate thalli from tetrasporangia and bisporangia.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles or rarely in the same conceptacle. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Carposporophytes composed of a central fusion cell and short gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, confined to the male conceptacle chamber floor.

Tetrasporangia and bisporangia scattered across the conceptacle chamber floor or peripheral to a central columella; mode of roof formation uncertain in most species; each mature sporangium lacking an apical plug and containing zonately arranged tetraspores or two bispores.

Lectotype species: *L. incrustans* Philippi 1837: 388; designated by Foslie (1898a: 6).

Over 650 species and infraspecific taxa have been ascribed to *Lithophyllum* (Woelkerling & Campbell 1992, p. 2); most are poorly known. The most recent detailed account of the type species is that of Chamberlain & Irvine (1994b, pp. 75–81, frontispiece, figs 6, 7C, 19C, 27–29, Tables 2, 3). Woelkerling (1983b, pp. 315–317, figs 15–23) provides an in depth account of the holotype collection of *L. incrustans*; Edyvean & Moss (1984) give data on conceptacle development, and the population biology and ecology of *L. incrustans* has been studied by Edyvean & Ford (1984a, 1984b, 1986a, 1986b, 1987) and Ford *et al.* (1983). Details relating to generic etymology, nomenclature, synonymy, infrageneric classification, *etc.* are provided by Woelkerling (1988, pp. 97–104, 111–113). This account of southern Australian species updates Woelkerling & Campbell (1992), who considered *Titanoderma* to be a heterotypic synonym of *Lithophyllum* (also see Campbell & Woelkerling 1990). Woelkerling (1991) has concluded that *Perispermon* is also a heterotypic synonym of *Lithophyllum*.

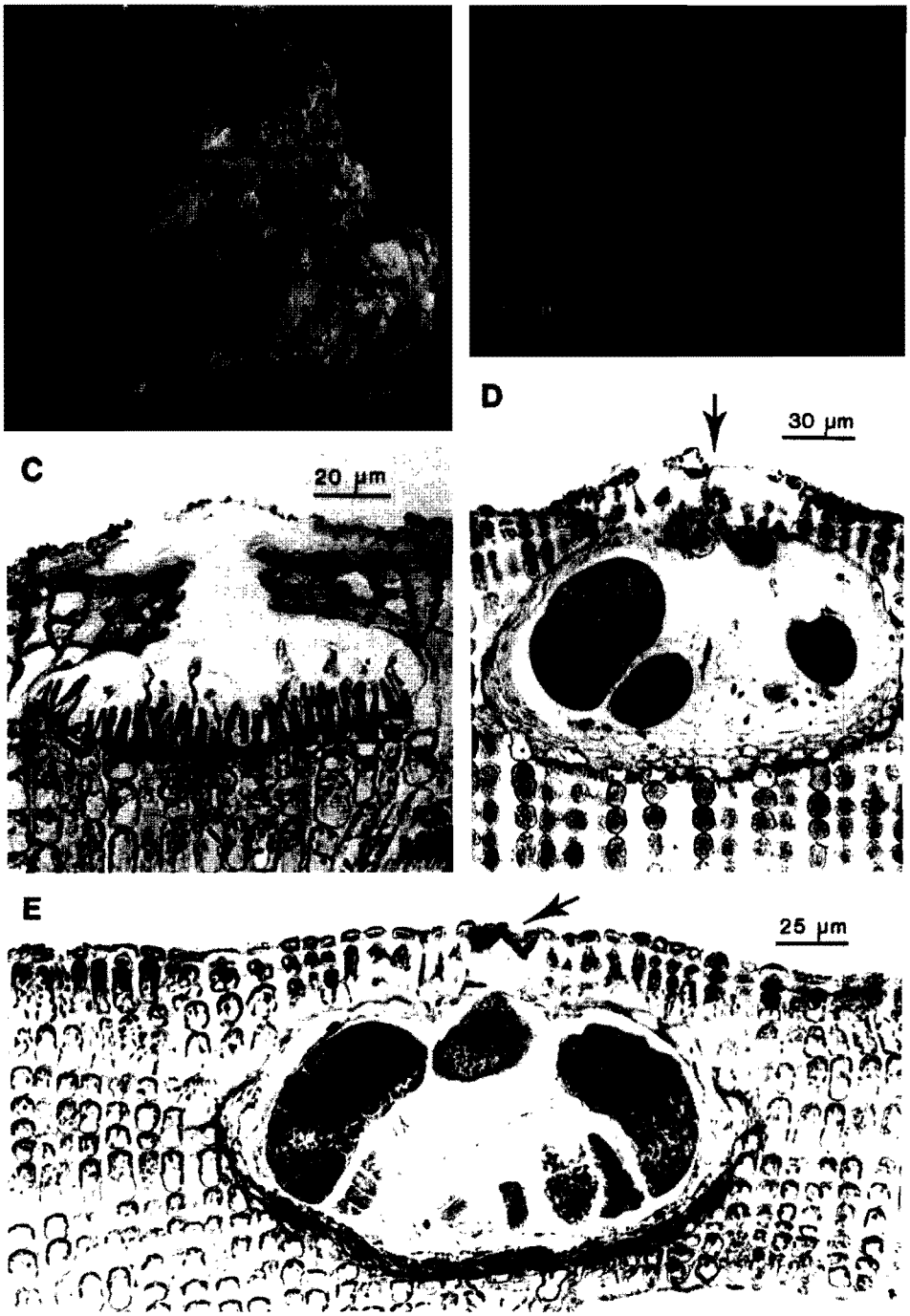


Fig. 94. *Lithophyllum johansenii* (**A, E,** LTB, 11724; **B, D,** LTB, 13134; **C,** LTB, 12446). **A.** Encrusting to lumpy thallus from holotype collection. **B.** Encrusting thallus on rock. **C.** Section of male conceptacle with unbranched spermatangial filaments arising from chamber floor. **D.** Fracture through sporangial conceptacle showing occluded pore (arrow) in surface view. **E.** Section of mature tetrasporangial conceptacle with occluded pore canal (arrow).

KEY TO SPECIES OF *LITHOPHYLLUM*

1. Pore canals of mature tetrasporangial and bisporangial conceptacles completely occluded by enlarged cells (Figs 94E; 95D, E; 97E) 2
1. Pore canals of mature tetrasporangial and bisporangial conceptacles lined with cells that may project somewhat into but do not completely occlude the entire canal (Figs 98C, 100F, 102E, 104E), although the canal sometimes appears blocked by mucilaginous material 4

2. Floors of tetrasporangial and bisporangial conceptacle chambers usually situated 8–20 cells below the surrounding thallus surface (Fig. 94E); conceptacle roofs usually more or less flush with the surrounding thallus surface; vegetative filaments arising from the single ventral layer of filaments in a dimerous thallus, commonly composed of 10 or more cells ..... 1. *L. johansenii*
2. Floors of tetrasporangial and bisporangial conceptacle chambers usually situated 1–3 cell layers below the surrounding thallus surface (Figs 95E, 97E); conceptacle roofs commonly protruding above the surrounding thallus surface; vegetative filaments arising from the single ventral layer of filaments in a dimerous thallus rare and only 2 or 3 cells long, often replaced by epithallial cells only 3

3. Pore canal occluded by a cluster of overlapping, more or less tubular and sometimes clasping or inflexed cells that are derived from at least the first two rows of roof filaments flanking the pore canal and that usually project beyond the surrounding roof surface (Fig. 95D, E) ..... 2. *L. chamberlainianum*
3. Pore canal occluded by 2 or 4 angular cells that are derived only from the row of roof filaments immediately flanking the pore canal and that do not project beyond the surrounding roof surface (Fig. 97D, E) ..... 3. *L. irvineanum*

4. Floors of tetrasporangial and bisporangial conceptacle chambers usually situated 1–3 (-5) cell layers below the surrounding thallus surface (Fig. 100F) 5
4. Floors of tetrasporangial and bisporangial conceptacle chambers usually situated 6 or more cell layers below the surrounding thallus surface (Figs 102E, 104E) ... 6

5. Thallus composed of a number of overlapping layers of flattened and horizontally expanded branches that give a terraced appearance in surface view (Fig. 98B); dimerous development limited to epithallial cells in vegetative parts of thallus ..... 4. *L. prototypum*
5. Thallus lacking overlapping layers of flattened and horizontally expanded branches or with sporadic branches that do not form numerous overlapping layers giving a terraced appearance in surface view; dimerous development commonly but not always involving multicellular filaments ..... 5. *L. pustulatum*

6. Tetrasporangial and bisporangial conceptacle chambers (155-) 190–235 (-280) µm in diameter; conceptacle roofs commonly 2–4 cells thick above the chamber ..... 6. *L. corallinae*
6. Tetrasporangial and bisporangial conceptacle chambers (255-) 320–410 (-445) µm in diameter; conceptacle roofs commonly 4–7 cells thick above the chamber ..... 7. *L. frondosum*

1. **Lithophyllum johansenii** Woelkerling & Campbell 1992: 61, figs 36–41.

FIG. 94

Thallus normally pinkish, encrusting to warty, lumpy or layered, mostly 30–40 mm across and 0.2–1.0 mm tall or thick, epigenous and completely affixed by cell adhesion; lamellate branches applanate and inconspicuous. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, consisting of a single ventral layer of branched, laterally cohering, filaments each composed of palisade and/or non-palisade cells 8–12 µm long and 5–25 µm high, and additionally of simple or branched,

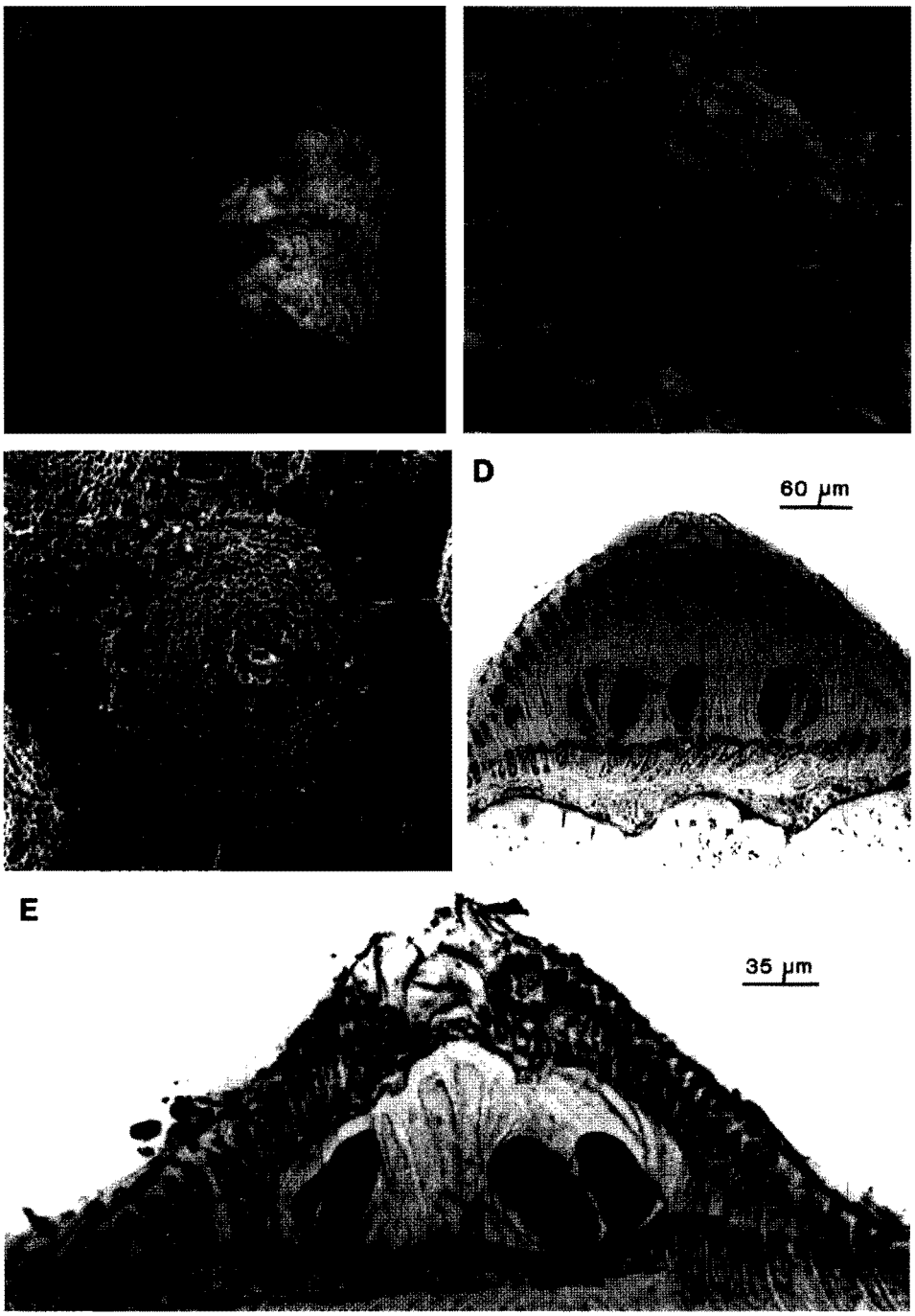


Fig. 95. *Lithophyllum chamberlainianum* (**A, B,** LTB, 15851; **C–E,** LTB, 14334). **A.** Encrusting thallus on a *Turbo* shell. **B.** Layered thallus with applanate branches on a *Turbo* shell. **C.** Surface view of tetrasporangial conceptacle with occluded pore canal. **D.** Section of tetrasporangial conceptacle with occluded pore canal and sporangia scattered across the chamber floor and interspersed amongst sterile cells. **E.** Section of tetrasporangial conceptacle with occluded pore canal and sporangia peripheral to a central columella of sterile cells.

laterally cohering, filaments that arise dorsally and more or less perpendicularly from most cells of ventral layer filaments and are each usually composed of 10 or more cells 5–10 µm in diameter and 8–30 µm long; epithallial cells 6–9 µm in diameter and 4–6 µm long, terminating most filaments at the thallus surface, with distal walls rounded or flattened but not flared; cells of adjacent filaments joined by secondary pit-connections; cell-fusions, haustoria, and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia, tetrasporangia and bisporangia produced in uniporate conceptacles; gametangia formed on thalli separate to those bearing tetrasporangia or bisporangia.

Gametangial thalli probably dioecious. Carpogonia and carposporophytes unknown. Spermatangial filaments unbranched, borne across the conceptacle chamber floor, mature male conceptacle roofs flush with or slightly protruding above surrounding thallus surface, 12–25 µm thick, composed of 2–3 layers of cells above the chamber, male conceptacle chambers 80–100 µm in diameter and 32–47 µm high.

Tetrasporangial/bisporangial conceptacle roofs more or less flush with surrounding surface, 2–4 cells thick above the chamber, pore canals completely occluded by 2 or 4 enlarged angular cells that arise from the row of roof filaments flanking the pore canal and that do not project above the surrounding roof surface; conceptacle chambers 130–155 (-196) µm in diameter and 65–108 µm high, floor of mature chambers mostly 8–20 cells below thallus surface; tetrasporangia and bisporangia scattered across the conceptacle chamber floor, each mature sporangium 27–35 (-45) µm in diameter, 45–70 µm long, containing zonately arranged tetraspores or bispores.

Type from Port Fairy, Vic. (*Woelkerling*, 4.i.1979); holotype in LTB (11724); depicted in Woelkerling & Campbell (1992, p. 62, fig. 36A).

Distribution: From Cape Willoughby, Kangaroo I., S. Aust., to Port Fairy, Vic., and Coles Bay, Tas.

Known specimens: The type. Cape Willoughby, Kangaroo I., S. Aust., upper sublittoral (*Woelkerling*, 25.ii.1979; LTB, 11576). Port MacDonnell, S. Aust., intertidal pools (*Woelkerling*, 6.i.1977; LTB, 12446, 12459). Coles Bay, Tas., 0–2.5 m deep (*Platt & Woelkerling*, 21.ii.1983; LTB, 13134).

Lithophyllum johansenii has been found on rock and on the holdfasts of the brown alga *Ecklonia radiata* in intertidal pools and subtidally to depths of 2.5 m. Male thalli are known from a single dried collection (LTB, 12446). Bisporangia have not been found on the same thalli as tetrasporangia, and it is unknown whether bispores give rise to new bisporangial thalli or to gametangial thalli.

2. **Lithophyllum chamberlainianum** Woelkerling & Campbell 1992: 34, figs 16–21. Barry & Woelkerling 1995: 137.

FIGS 95, 96

Thallus normally pinkish, encrusting to layered, mostly 0.05–2.5 mm across and 0.04–0.5 mm thick, epigenous and partially or completely affixed by cell adhesion or envelopment of host axes; lamellate branches applanate and inconspicuous. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, consisting of a single ventral layer of branched, laterally cohering, filaments each usually composed of palisade cells 5–18 µm long and (13-) 20–75 (-90) µm high, and additionally of epithallial cells that arise dorsally and more or less perpendicularly from most cells of ventral layer filaments and are 4–12 µm in diameter and 2–7 µm long with distal walls rounded or flattened but not flared; cells of adjacent filaments joined by secondary pit-connections; cell-fusions, haustoria and trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia, tetrasporangia and bisporangia produced in uniporate conceptacles; gametangia and carposporangia formed on thalli separate to those bearing tetrasporangia and bisporangia.

Gametangial thalli probably dioecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above surrounding thallus surface, 60–110 µm thick, composed

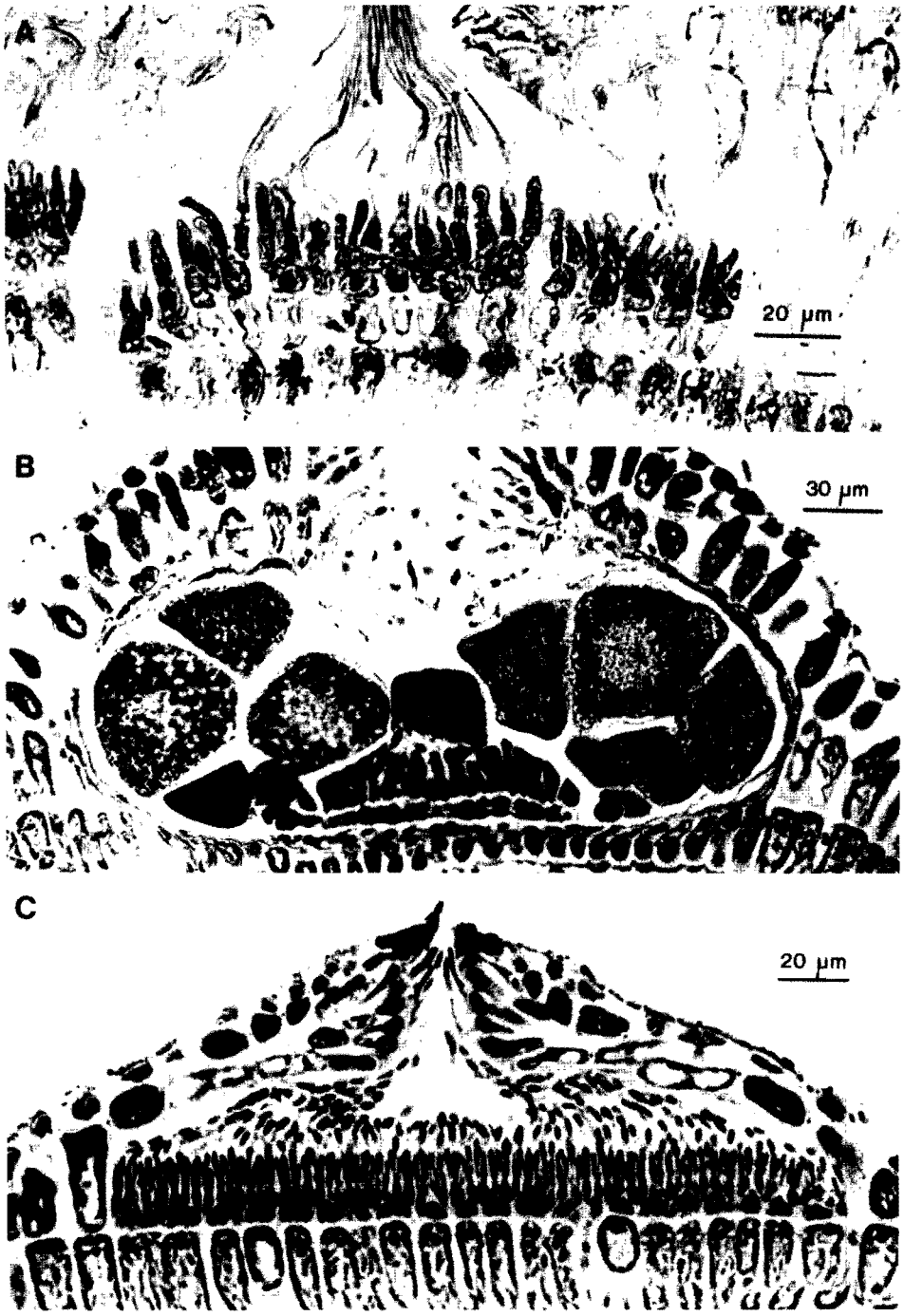


Fig. 96. *Lithophyllum chamberlainianum* (**A**, LTB, 14335; **B**, LTB, 13094; **C**, LTB, 14334). **A.** Section of female-carposporangial conceptacle with mature carpogonial filaments. **B.** Section of female-carposporangial conceptacle with mature carposporophyte. **C.** Section of male conceptacle with unbranched spermatangial filaments arising from chamber floor.

of 7–10 layers of cells above the chamber, conceptacle chambers 160–225 (-259) μm in diameter and 81–115 (-209) μm high. Carposporophytes composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia 20–30 (-52) μm in diameter. Spermatangial filaments unbranched, borne across the male conceptacle chamber floor, mature male conceptacle roofs protruding above surrounding thallus surface, 35–60 μm thick, composed of 5–7 layers of cells above the chamber, male conceptacle chambers 160–200 μm in diameter and 29–55 μm high.

Tetrasporangial/bisporangial conceptacle roofs protruding above surrounding surface, 2–4 (-5) cells thick above the chamber, pore canals completely occluded by a conglomerate of elongate, more or less tubular and sometimes inflexed cells that arise from at least the first two rows of roof filaments flanking the pore canal and that usually project above the surrounding roof surface, conceptacle chambers (145-) 175–210 (-252) μm in diameter and (60-) 80–120 (-159) μm high, floor of mature chambers usually one cell below thallus surface; tetrasporangia and bisporangia scattered across the conceptacle chamber floor or peripheral to a central columella, each mature sporangium (16-) 20–35 (-47) μm in diameter and (35-) 55–95 (-118) μm long, containing zonately arranged tetraspores or bispores.

Type from Lucky Bay, Cape Le Grand National Park, E of Esperance, W. Aust. (*Woelkerling, Platt & Jones*, 9.ii.1984); holotype in LTB (14334); depicted in Woelkerling & Campbell (1992, p. 35, fig. 16A).

Distribution: Shark Bay, W. Aust., to Refuge Cove, Wilsons Prom., Vic., and the northern and eastern coasts of Tasmania.

Selected specimens: Herald Bight, Shark Bay, W. Aust., on *Amphibolis* (*Harlin*, 12.ix.1984; LTB, 16637) and on *Penicillis* (*Woelkerling*, 28.vii.1986; LTB, 16629). Lucky Bay, Cape Le Grand National Park, W. Aust., 0–3 m deep (*Woelkerling, Platt & Jones*, 9.ii.1984; LTB, 14315, 14327, 14328, 14335, 14366). Eyre ("Nine Mile Reef"), W. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 1.ii.1984; LTB, 13940, 13944, 13945, 13959). Point Fowler, Fowlers Bay, S. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 14.ii.1984; LTB, 14393). Chinaman's Hat Island Bay, Yorke Pen., S. Aust. (*Woelkerling*, 30.xii.1976; LTB, 11266). Penneshaw, Kangaroo I., S. Aust., 1–2 m deep on shells (*Campbell & Penrose*, 13.iv.1988; LTB, 15672). Beachport, S. Aust., 0–2 m deep (*Campbell & Penrose*, 24.ii.1988; LTB, 15851 and 26.ii.1988; LTB, 15751, 15762). Flinders, Vic., 1–2 m deep (*Woelkerling*, 15.ii.1985; LTB, 15269). Port Fairy, Vic. (*Woelkerling*, 4.i.1979; LTB, 11708, 11717). Refuge Cove, Wilsons Prom., Vic. (*Leach*, 22.x.1977; LTB, 11248). Rocky Cape National Park, Tas., 0–1 m deep (*Platt*, 2.iii.1983; LTB, 13444). Greens Beach (N Coast), Tas., 1 m deep (*Platt*, 2.iii.1983; LTB, 13398). Eddystone Point, Tas., 0–3 m deep (*Platt & Woelkerling*, 23.ii.1983; LTB, 13148, 13152, 13158). Coles Bay, Freycinet Pen., Tas., 0–2.5 m deep (*Platt & Woelkerling*, 21.ii.1983; LTB, 13094).

Lithophyllum chamberlainianum has been found on limpets, snails, abalone shells, the seagrass *Amphibolis antarctica* and a variety of algae in intertidal pools and subtidally to depths of 10 m. Thalli generally conform to the contours of the substrate and thus may be horizontally expanded or sleeve-like in appearance. Dense aggregations occur in some collections while isolated individuals occur in others.

3. **Lithophyllum irvineanum** Woelkerling & Campbell 1992: 56, figs 33–35.

FIG. 97

Thallus normally pinkish, encrusting to layered, mostly 3–35 mm across and 0.05–1.0 mm thick or tall, epigenous and completely affixed by cell adhesion; lamellate branches applanate and inconspicuous. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, consisting of a single ventral layer of branched, laterally cohering, filaments each usually composed of palisade cells 5–12 μm long and (15-) 25–70 (-80) μm high, and additionally of epithallial cells or rarely two-celled filaments that arise dorsally and more or less perpendicularly from most cells of ventral layer filaments and are each composed of a terminal epithallial cell 4–9 μm in diameter and 2–6 μm long and rarely a subtending cell 5–12 μm in diameter and 30–60 μm long; distal walls of epithallial cells rounded or flattened but not flared; cells of adjacent filaments joined by secondary pit-connections; cell-fusions, haustoria and trichocytes unknown.

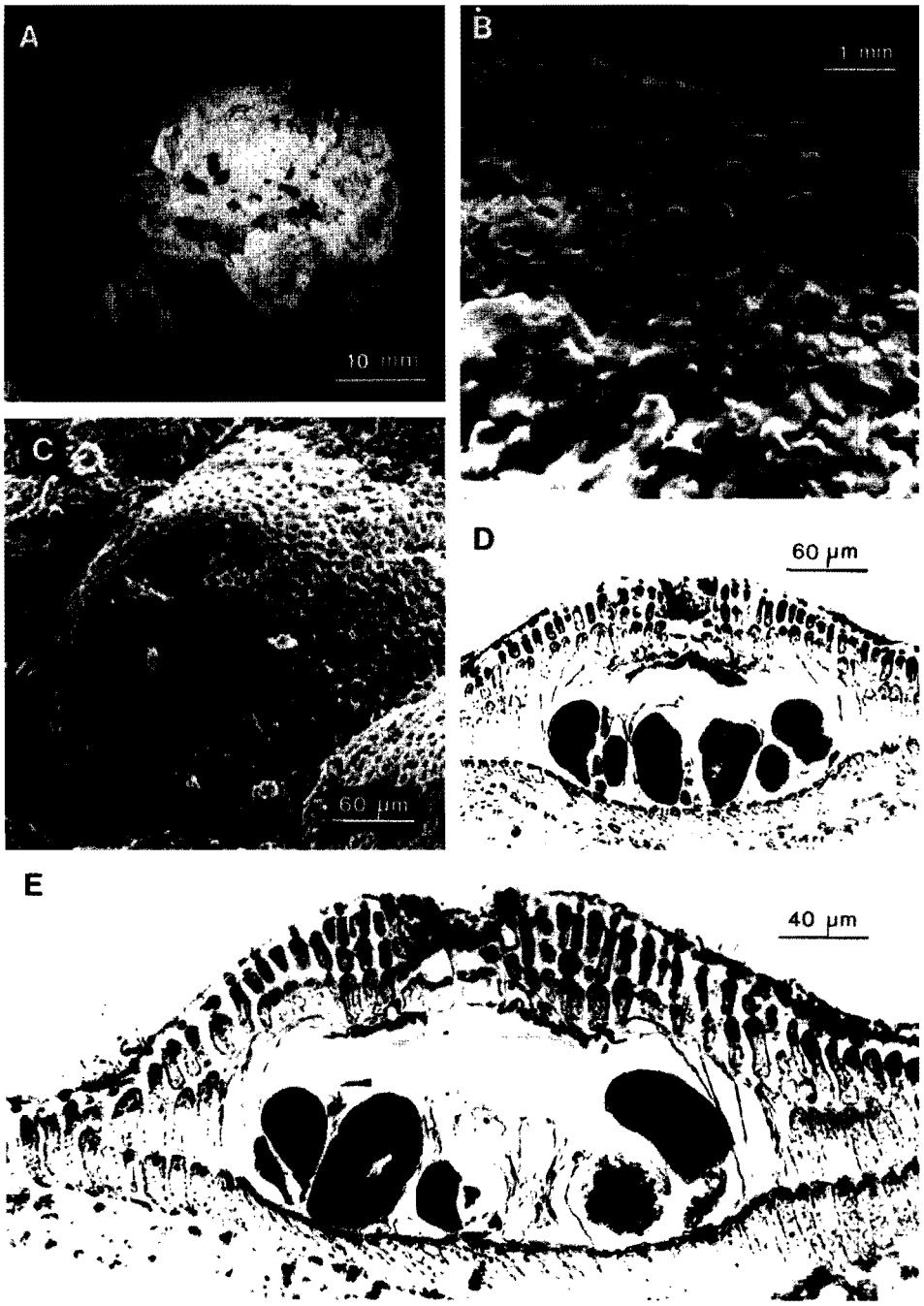


Fig. 97. *Lithophyllum irvineanum* (**A–E**, LTB, 15676, holotype). **A.** Encrusting thalli on a snail. **B.** Surface view of layered thallus showing applanate branches. **C.** Surface view of tetrasporangial conceptacle. **D.** Section of mature tetrasporangial conceptacle lacking a columella and with tetrasporangia across the conceptacle chamber floor. **E.** Section of mature tetrasporangial conceptacle with a columella and peripherally situated tetrasporangia. Note enlarged cells occluding pore canal.

Reproduction. Vegetative reproduction, gametangial thalli, carposporophytes and tetrasporophytes unknown. Bisporangia produced in uniporate conceptacles.

Bisporangial conceptacle roofs protruding above surrounding surface, (2-) 3–4 cells thick above the chamber, pore canals completely occluded by 2 or 4 enlarged angular cells that arise from the row of roof filaments flanking the pore canal and that do not project above the surrounding roof surface; conceptacle chambers (180-) 215–245 (-263) μm in diameter and 82–125 μm high, floor of mature chambers usually 1 (-3) cells below thallus surface; bisporangia scattered across the conceptacle chamber floor or peripheral to a central columella, each mature sporangium (29-) 40–55 μm in diameter and 68–88 (-101) μm long, containing two bispores.

Type from Beachport (Three Mile Rocks), S. Aust. (*Campbell & Penrose*, 26.ii.1988); holotype in LTB (15676); depicted in Woelkerling & Campbell (1992, p. 57, fig. 33A).

Distribution: Dempster Point, Israelite Bay, W. Aust., to Beachport, S. Aust.

Known specimens: Dempster Point, Israelite Bay, W. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 6.ii.1984; LTB, 14247). Reef 10 km E of Eyre, W. Aust., 0–1 m deep (*Woelkerling, Platt & Jones*, 3.ii.1984; LTB, 14107). Point Westall, S. Aust., 2–3 m deep (*Platt & Jones*, 16.ii.1984; LTB, 14580, 14607). Elliston, S. Aust., 11 and 5 m deep (*Turner*, 28.x.1981; LTB, 15446 and 31.x.1981; LTB, 15390). Pennington Bay, Kangaroo I., S. Aust. (*Womersley*, 22.i.1948; AD, A7908, mixed with *L. corallinae*). Beachport (Three Mile Rocks), S. Aust., 3–6 m deep (*Campbell & Penrose*, 26.ii.1988; LTB, 15676).

Lithophyllum irvineanum has been found on snails, mussel shells, holdfasts of the brown alga *Ecklonia radiata* and on the red alga *Osmundaria* at depths of 1–11 m. Thalli generally conform to the contours of the substrate and thus may be horizontally expanded or sleeve-like in appearance.

4. **Lithophyllum prototypum** (Foslie)Foslie 1905c: 129. Woelkerling & Campbell 1992: 67, figs 42–49.
Dermatolithon prototypum (Foslie)Foslie 1900c: 22.
Goniolithon prototypum (Foslie)Setchell & Mason 1943: 89.
Lithothamnion prototypum Foslie 1897: 18. Woelkerling 1993: 179.
Melobesia prototypa (Foslie)Foslie 1898b: 11.
Tenarea prototypa (Foslie)Adey 1970: 7.
Titanoderma prototypum (Foslie)Woelkerling *et al.* 1985: 333. Chamberlain 1991: 6, 13, figs 5, 6. D. Littler *et al.* 1989: 218.
Lithophyllum tessellatum Lemoine 1930: 68.
Tenarea tessellata (Lemoine)M. Littler *ex* Adey *et al.* 1982: 35, figs 21, 22. M. Littler 1971: 355, figs 1–10.
Titanoderma tessellatum (Lemoine)Woelkerling *et al.* 1985: 333. Woelkerling 1988: 110, 114, figs 88, 94, 96.

Additional references are given by Woelkerling & Campbell (1992).

FIGS 98, 99

Thallus normally pinkish, encrusting to layered or rarely with isolated lumpy outgrowths, mostly 20–50 mm across and 0.1–0.9 mm thick, epigenous and partially or completely affixed by cell adhesion; lamellate branches usually present, applanate, conspicuous and giving the thallus surface a terraced appearance. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, consisting of a single ventral layer of branched, laterally cohering, filaments each usually composed of palisade cells 5–14 μm long and 15–50 (-70) μm high, and additionally of epithallial cells that arise dorsally and more or less perpendicularly from most cells of ventral layer filaments and are 4–9 μm in diameter and 2–6 μm long with distal walls rounded or flattened but not flared; cells of adjacent filaments joined by secondary pit-connections; cell-fusions and haustoria unknown; trichocytes rare, occurring singly or in groups.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia and tetrasporangia produced in uniporate conceptacles; gametangia and carposporangia formed on thalli separate to those bearing tetrasporangia. Bisporangia unknown.

Gametangial thalli probably dioecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above surrounding thallus surface, 65–85 µm thick, composed of 7–10 layers of cells above the chamber; conceptacle chambers 405–495 µm in diameter and 103–150 µm high. Carposporophytes composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia 37–88 µm in diameter. Spermatangial filaments unbranched, borne across the male conceptacle chamber floor; mature male conceptacle roofs protruding above surrounding thallus surface, 30–40 µm thick, composed of 2–3 layers of cells above the chamber, chambers 133–185 µm in diameter and (22-) 37–60 µm high.

Tetrasporangial conceptacle roofs protruding above surrounding surface, 2–3 cells thick above the chamber, pore canals lined with non- or slightly protruding cells that do not occlude the canal, conceptacle chambers 375–440 µm in diameter and 125–150 µm high, floor of mature chambers usually one cell below thallus surface; tetrasporangia usually peripheral to a central columella, each mature sporangium 30–45 µm in diameter and (60-) 71–103 (-110) µm long, containing zonately arranged spores.

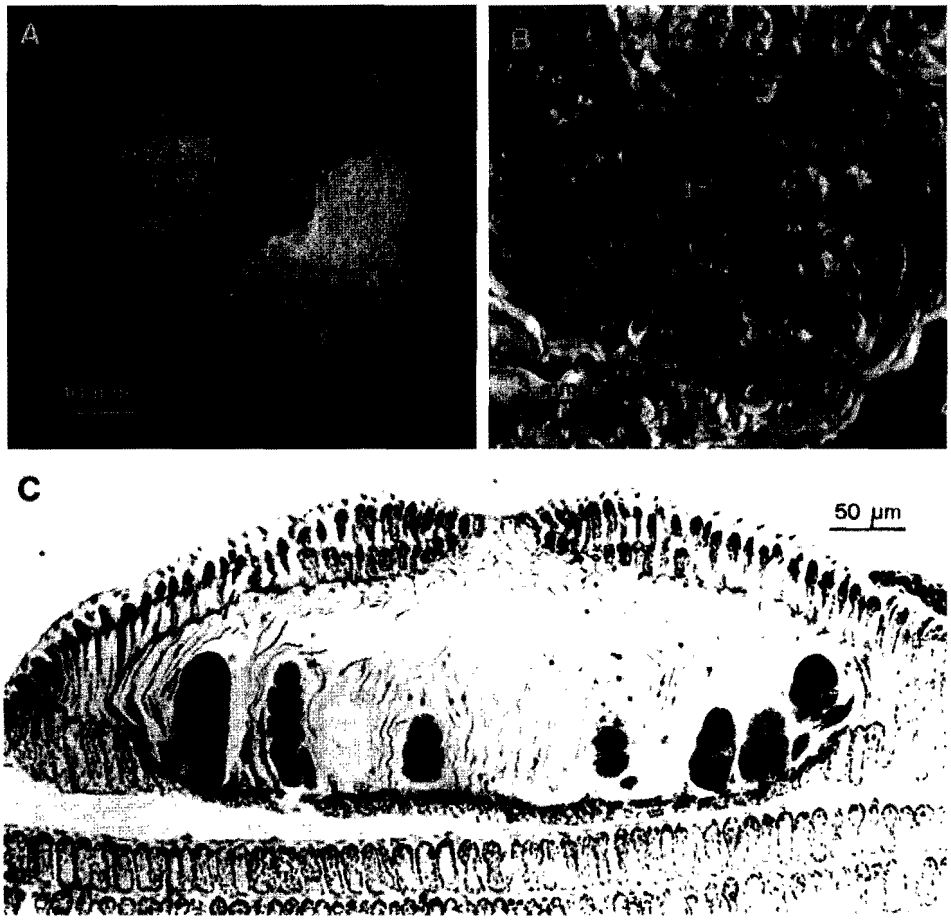


Fig. 98. *Lithophyllum prototypum* (**A**, TRH, unnumbered holotype; **B**, LTB, 15444; **C**, LTB, 14494). **A.** Holotype collection. **B.** Surface view of layered thallus showing terracing of applanate branches. **C.** Section of mature tetrasporangial conceptacle.



Fig. 99. *Lithophyllum prototypum* (**A**, LTB, 15649; **B**, LTB, 15443; **C**, LTB, 14179). **A.** Section of part of a female-carposporangial conceptacle with mature carpogonial filaments. **B.** Section of part of a female-carposporangial conceptacle with mature carposporophyte. **C.** Section of male conceptacle with unbranched spermatangial filaments arising from chamber floor.

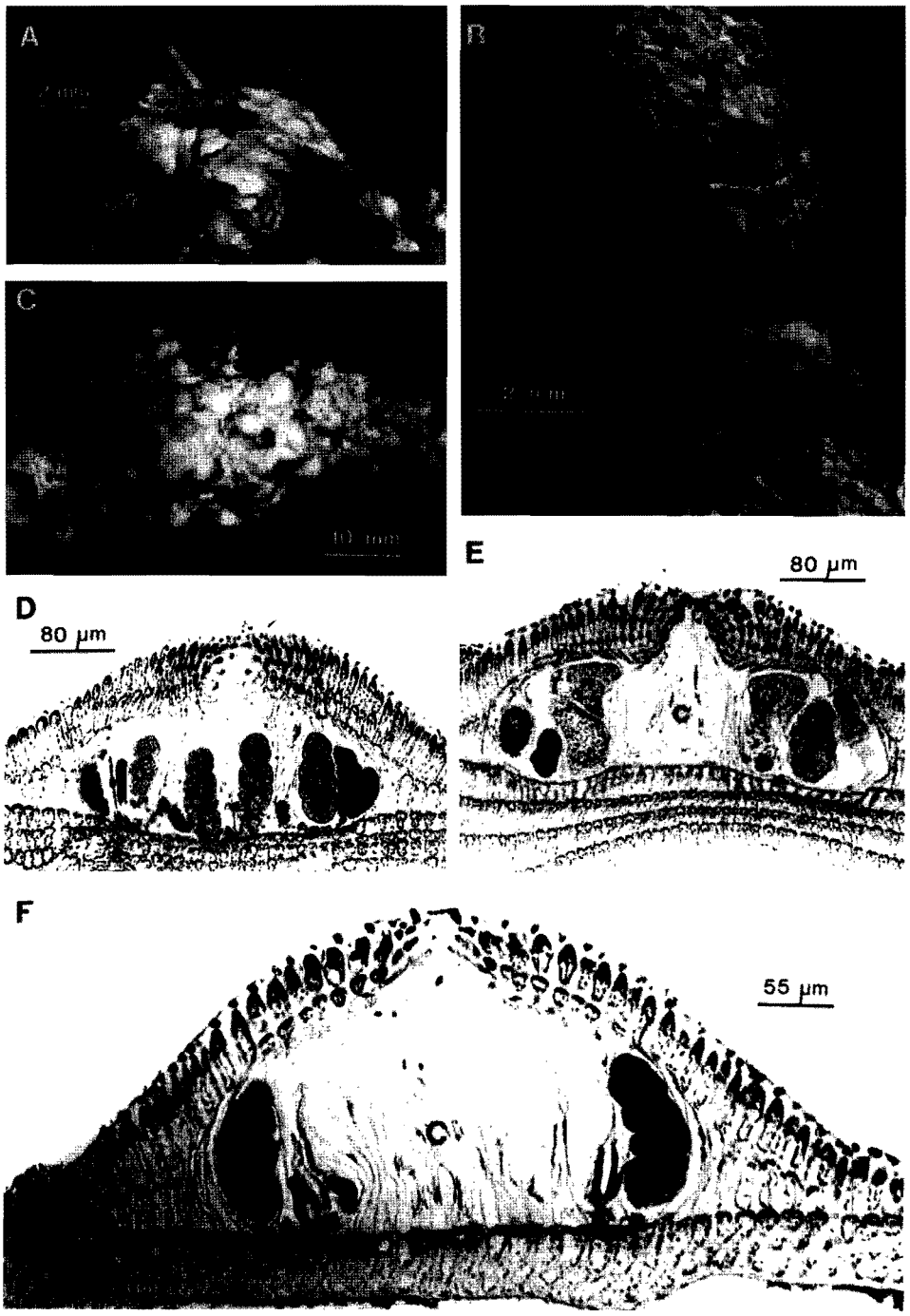


Fig. 100. *Lithophyllum pustulatum* (**A, F,** LTB, 14365; **B,** LTB, 13054; **C, E,** LTB, 14581; **D,** LTB, 14396). **A.** Encrusting thalli on a red alga. **B.** Layered thalli on *Hormosira*. **C.** Warty to lumpy thallus on rock. **D–F.** Sections of mature tetrasporangial conceptacles. Note variation in roof anatomy and the presence (E, F) or absence (D) of a columella and the occurrence of sporangia either peripherally or across the chamber floor (C = columella).

Type from St Croix, US Virgin I.; holotype in TRH (unnumbered); depicted in Printz (1929, pl. 72 fig. 8) and Woelkerling & Campbell (1992, p. 68, fig. 42A); additional data provided by Woelkerling (1993, p. 179).

Distribution: Caribbean islands; Bermuda; Florida; Mexico; Panama; Galapagos Islands; Midway I.; Hawaii.

In Australia, Green I. Bay, Rottnest I., W. Aust., to Beachport, S. Aust.

Selected specimens: Green I. Bay, Rottnest I., W. Aust. (*Woelkerling*, 12.ii.1978; LTB, 11318). Esperance (Observatory Point), W. Aust., 2–3 m deep (*Woelkerling, Platt, & Jones*, 5.ii.1984; LTB, 14168, 14179, 14184). Head of Great Australian Bight, S. Aust., drift (*Woelkerling, Platt, & Jones*, 13.ii.1984; LTB, 14378). Point Sinclair, S. Aust., 0–2 m deep (*Woelkerling, Platt, & Jones*, 15.ii.1984; LTB, 14494). Speeds Point, Sceale Bay, S. Aust., 20 m deep on abalone (comm. S. Shepherd, Oct. 1981; LTB, 15443). Searcy Bay (S of Sceale Bay), S. Aust., 20 m deep (comm. S. Shepherd, Oct. 1981; LTB, 15444). Encounter Bay, S. Aust., 1 m deep (*Littler*, 31.xii.1975; AD, A47021 = LTB, 13885). Snug Cove, Kangaroo I., S. Aust., 10–13 m deep (*Campbell & Penrose*, 12.iv.1988; LTB, 15629, 15649). Beachport (Post Office Rock), S. Aust., 2 m deep (*May*, 1.xii.1986; LTB, 15910).

Lithophyllum prototypum has been found epiphytically on *Sporolithon durum* and on rock, abalone shells, snails, sponges and bottles at depths of 1–20 m in southern Australia. Gametangial and tetrasporangial thalli can occur within single populations. Based on a comparative study of relevant types, Woelkerling & Campbell (1992, pp. 71, 72, figs 42, 43) concluded that *Lithophyllum tessellatum* Lemoine was a heterotypic synonym of *L prototypum*. In Hawaii, thalli of *L. prototypum* have been recorded intertidally and subtidally to depths of 40 m on various substrates including other algae (see Adey *et al.* 1982, as *Tenarea tessellata;* M. Littler 1973, as *T. tessellata;* Magruder & Hunt 1979, as *T. tessellata*); while Hoek *et al.* (1978, as *Tenarea prototypa*) found thalli at depths of 55–60m off Curaçao, Netherlands Antilles.

5. **Lithophyllum pustulatum** (Lamouroux)Foslie 1904c: 8. Barry & Woelkerling 1995: 138. Campbell & Woelkerling 1990: 115, figs 1,4. Millar & Kraft 1993: 14. Suneson 1943: 39, figs 22, 23, pl. 6 figs 26, 27. Woelkerling & Campbell 1992: 78, figs 50–60.
   Melobesia pustulata Lamouroux 1816: 315.
   Dermatolithon pustulatum (Lamouroux)Foslie 1898b: 11.
   Epilithon pustulatum (Lamouroux)Lemoine 1921: 10.
   Tenarea pustulata (Lamouroux)Adey 1965: 88 (invalid).
   Titanoderma pustulata (Lamouroux)Nägeli 1858: 532. Chamberlain 1991: 26, figs 2, 4, 7–15, 19–48, 52a–i, 53–207. Chamberlain & Irvine 1994b: 96, figs 39–49. Woelkerling *et al.* 1985: 329, figs 29–39.

Additional references involving these and other binomials, previous southern Australian records, and heterotypic synonyms are given by Woelkerling & Campbell (1992).

FIGS 100, 101

Thallus normally pinkish, encrusting to layered or rarely warty or lumpy, mostly 1–100 mm across and 0.05–2.5 mm thick or tall, epigenous and partially or completely affixed by cell adhesion; lamellate branches applanate and inconspicuous. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, consisting of a single ventral layer of branched, laterally cohering, filaments each composed of palisade and/or non-palisade cells 5–25 μm long and (12-) 25–75 (-100) μm high, and additionally of epithallial cells or more commonly of simple or branched, laterally cohering, filaments that arise dorsally and more or less perpendicularly from cells of ventral layer filaments and are each usually composed of cells 5–14 μm in diameter and (5-) 16–55 (-65) μm long; epithallial cells 3–12 μm in diameter and 2–8 μm long, terminating most filaments at the thallus surface, with distal walls rounded or flattened but not flared; cells of adjacent filaments joined by secondary pit-connections; cell-fusions, haustoria, and trichocytes not observed.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia, tetrasporangia and bisporangia produced in uniporate conceptacles; gametangia and carposporangia formed on thalli separate to those bearing tetrasporangia and bisporangia.

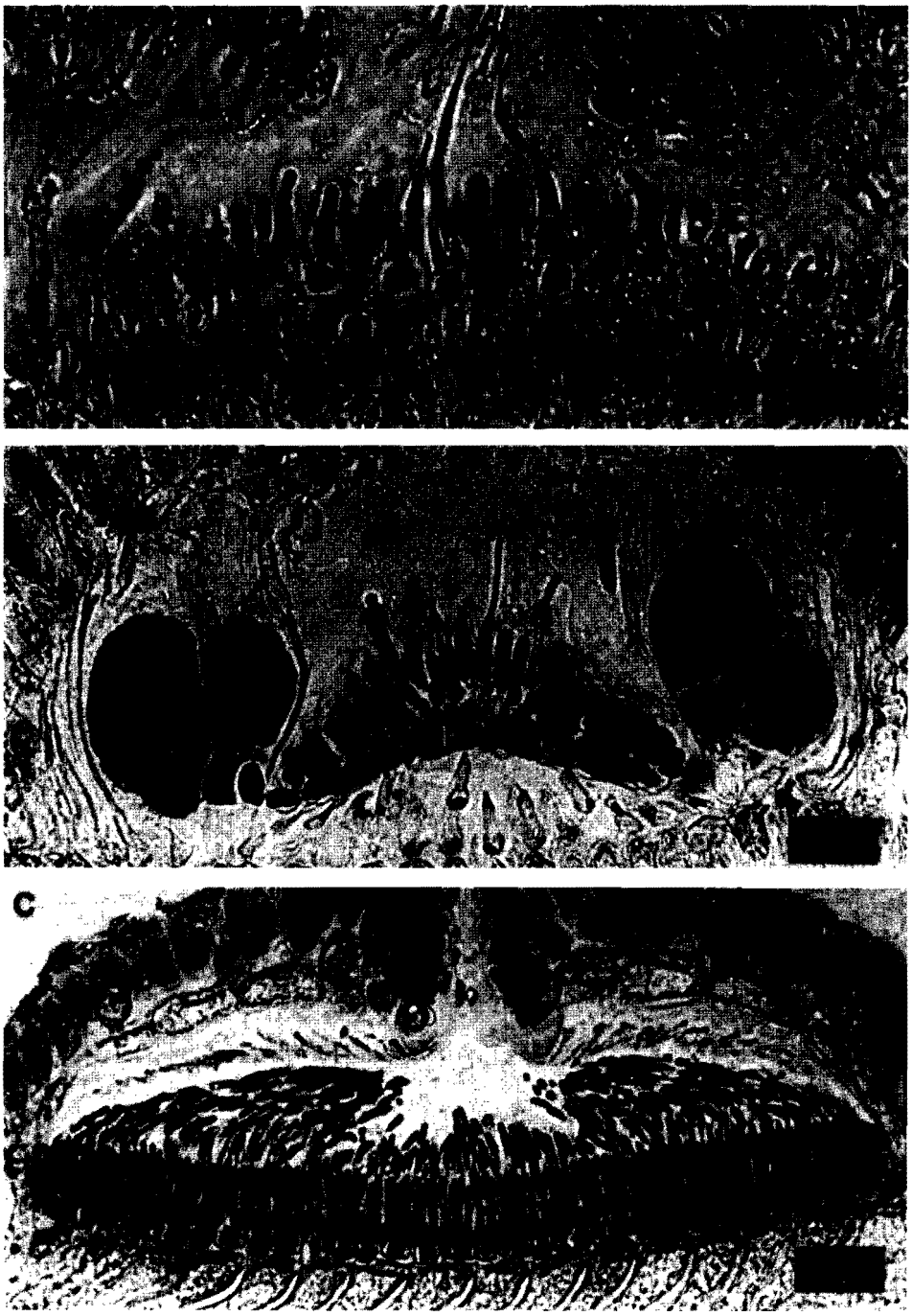


Fig. 101. *Lithophyllum pustulatum* (**A–C**, LTB, 14365). **A.** Section of part of a female-carposporangial conceptacle with mature carpogonial filaments. **B.** Section of part of a female-carposporangial conceptacle with mature carposporophyte (F = fusion cell). **C.** Section of male conceptacle with unbranched spermatangial filaments arising from chamber floor.

Gametangial thalli probably dioecious. Carpogonia terminating 2- or 3-celled filaments arising from the conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above surrounding thallus surface, 60–100 μm thick, composed of 6–8 layers of cells above the chamber, conceptacle chambers 220–300 μm in diameter and 85–110 (-177) μm high. Carposporophytes composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia 30–75 μm in diameter. Spermatangial filaments unbranched, borne across the male conceptacle chamber floor; mature male conceptacle roofs protruding above surrounding thallus surface, 40–65 μm thick, composed of 7–9 layers of cells above the chamber, male conceptacle chambers (53-) 220–450 μm in diameter and 50–90 μm high.

Tetrasporangial/bisporangial conceptacle roofs protruding above surrounding surface, 2–7 cells thick above the chamber, pore canals lined with non- or somewhat protruding cells that do not completely occlude the canal, conceptacle chambers (162-) 390–500 (-556) μm in diameter and 110–180 μm high, floor of mature chambers usually 1–3 (-5) cells below thallus surface; tetrasporangia and bisporangia scattered across the conceptacle chamber floor or peripheral to a central columella, each mature sporangium 35–85 μm in diameter and 95–140 μm long, containing zonately arranged tetraspores or bispores.

Type from an unknown locality in France; lectotype in CN (Herb. Lamouroux, unnumbered); designated by Woelkerling, Chamberlain & Silva (1985, p. 325); depicted in Woelkerling, Chamberlain & Silva (1985, p. 328, fig. 29) and Woelkerling & Campbell (1992, p. 80, fig. 50A).

Distribution: Widespread, but many published records involve misidentifications; see Chamberlain (1991) and Woelkerling & Campbell (1992).

In Australia, Herald Bight, Shark Bay, W. Aust., to Cape Green, N.S.W., and Bluestone Bay, Tasmania. An additional collection (not seen) has been reported from Narrabeen, New South Wales (Millar & Kraft 1993, p. 14).

Selected specimens: Herald Bight, Shark Bay, W. Aust., 1–2 m deep (*Harlin*, 12.ix.1984; LTB, 16631, 16634, 16639, 16640, 16686). Cape Vlaming, Rottnest I., W. Aust., reef pools (*Woelkerling*, 8.ii.1978; LTB, 12667). Lucky Bay, Cape Le Grand National Park, W. Aust., 0–3 m deep (*Woelkerling, Platt, & Jones*, 9.ii.1984; LTB, 14301, 14361, 14365, 14367). Eyre ("Nine Mile Reef"), W. Aust., 2–3 m deep (*Woelkerling, Platt, & Jones*, 1.ii.1984; LTB, 13953, 13956). Head of Great Australian Bight, S. Aust., drift (*Woelkerling, Platt, & Jones*, 13.ii.1984; LTB, 14377, 14380). Point Fowler, Fowlers Bay, S. Aust., 2–3 m deep (*Woelkerling, Platt, & Jones*, 14.ii.1984; LTB, 14464, 14390, 14396, 14398). Point Westall, S. Aust., 2–3 m deep (*Platt & Jones*, 16.ii.1984; LTB, 14581). Pondalowie Bay, Yorke Pen., S. Aust., upper sublittoral (*Woelkerling*, 31.xii.1976; LTB, 12473). Vivonne Bay, Kangaroo I., S. Aust., large pool, S side Ellen Point (*Womersley*, 17.i.1948; AD, A7907 = LTB, 13594). Beachport (Post Office Rock), S. Aust., 0–3 m deep (*Campbell & Penrose*, 6.xi.1987; LTB, 15843). Warrnambool, Vic., low eulittoral (*Pope & Bennett*, 16.viii.1948; AD, A12125 = LTB, 13700). Point Lonsdale, Vic., reef pools (*Turner*, 6.i.1979; LTB, 11542). Bluestone Bay, Freycinet Pen., Tas., intertidal pools (*Platt & Woelkerling*, 21.ii.1983; LTB, 13054, 13055). Green Cape, N.S.W., 1–2 m deep (*Platt*, 31.xii.1982; LTB, 12635).

Lithophyllum pustulatum has been found in Australia on rock, sponges, abalone shells, snails, seagrasses and various red and brown algae in intertidal pools and subtidally to depths of 5 m. Gametangial, carposporangial, tetrasporangial and bisporangial thalli can occur in the same population, but bisporangia and tetrasporangia were not found on the same thallus. In the British Isles, Chamberlain (1991, as *Titanoderma*) and Chamberlain & Irvine (1994b, as *Titanoderma*) found only bisporangial thalli. Woelkerling & Campbell (1992, p. 95) and Chamberlain & Irvine (1994b, p. 99) both suggest that the British populations are probably apomictic and that this has led to the occurrence of taxonomically recognizable varieties that appear morphologically stable. In southern Australia, Woelkerling & Campbell (1992) found that populations were highly and continuously variable making it impossible to identify clear-cut varieties.

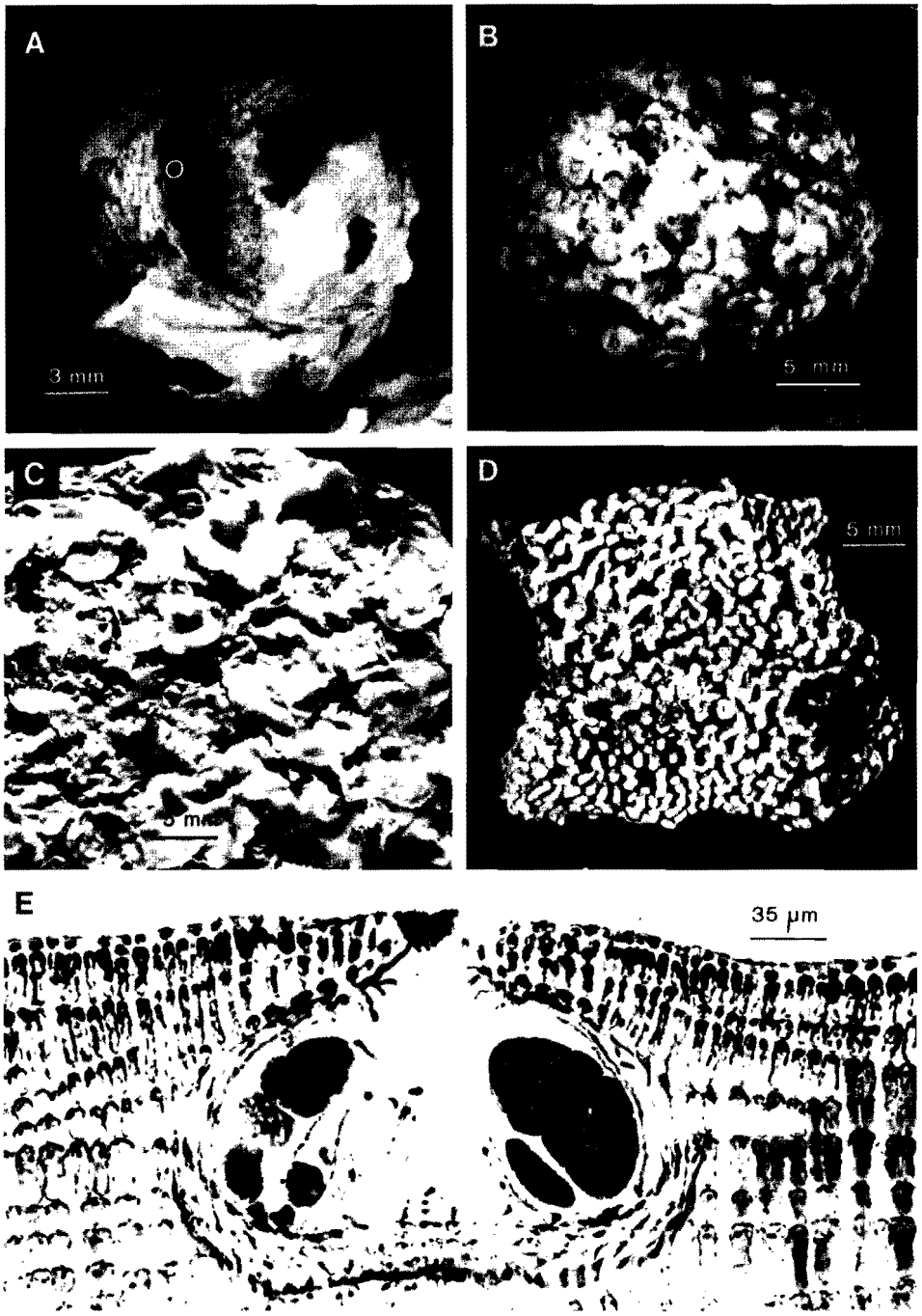


Fig. 102. *Lithophyllum corallinae* (**A, E,** LTB, 15578; **B,** LTB, 13236; **C,** LTB, 13306; **D,** LTB, 13621). **A.** Encrusting thalli on a snail. **B.** Warty to lumpy thalli on rock. **C.** Encrusting to layered thalli on an abalone shell. **D.** Fruticose thallus detached from rock. **E.** Section of mature tetrasporangial conceptacle with a central columella and peripherally situated tetrasporangia.

6. **Lithophyllum corallinae** (Crouan & Crouan)Heydrich 1897b: 47. Woelkerling & Campbell 1992: 41, figs 22–32.
Melobesia corallinae Crouan & Crouan 1867: 150, 252, pl. 20 gen 133 bis figs 6–11.
Dermatolithon corallinae (Crouan & Crouan)Foslie *in* Børgesen 1902: 402.
Tenarea corallinae (Crouan & Crouan)Notoya 1974: 47 (invalid).
Titanoderma corallinae (Crouan & Crouan)Woelkerling *et al.* 1985: 333. Chamberlain 1991: 66, figs 3, 16–18, 52j, 208–224. Chamberlain & Irvine 1994b: 90, figs 34, 35.

Additional references involving these and other binomials are given by Campbell & Woelkerling (1992).

FIGS 62E, 63G, 102, 103

Thallus normally pinkish, encrusting to layered, warty, lumpy or fruticose, mostly 10–50 mm across and 0.2–1 (-5) mm thick or tall, epigenous and partially or completely affixed by cell adhesion; protuberant branches simple or branched, mostly 1–7 mm in diameter and 3–7 mm long; lamellate branches applanate and inconspicuous, mostly 3–12 mm across and 1–2 mm long. *Structure* pseudoparenchymatous, organisation dorsiventral in crustose portions and lamellate branches but radial in protuberant branches; construction dimerous, dimerous and monomerous or largely monomerous; dimerous portions consisting of a single ventral layer of branched, laterally cohering, filaments each composed of palisade and/or non-palisade cells 5–20 µm long and (13-) 20–65 (-82) µm high, and additionally of simple or branched, laterally cohering, filaments that arise dorsally and more or less perpendicularly from cells of ventral layer filaments and are each usually composed of cells 5–16 µm in diameter and 5–40 (-55) µm long; monomerous portions consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, with each filament composed of cells 5–14 µm in diameter and 5–35 (-55) µm long; epithallial cells 4–9 µm in diameter and 2–6 µm long, terminating most filaments at the thallus surface, with distal walls rounded or flattened but not flared; cells of adjacent filaments joined by secondary pit-connections; cell-fusions and haustoria unknown; trichocytes rare, single.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia, tetrasporangia and bisporangia produced in uniporate conceptacles; gametangia and carposporangia formed on thalli separate to those bearing tetrasporangia and bisporangia.

Gametangial thalli monoecious or dioecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs flush with or somewhat protruding above surrounding thallus surface, 50–115 µm thick, composed of 5–12 layers of cells above the chamber, conceptacle chambers 185–233 (-305) µm in diameter and 60–110 (-140) µm high. Carposporophytes composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia 27–40 (-57) µm in diameter. Spermatangial filaments unbranched, borne in groups of 1–3 on initials across the male conceptacle chamber floor, mature male conceptacle roofs flush with or slightly protruding above surrounding thallus surface, 25–40 µm thick, composed of 2–5 layers of cells above the chamber, male conceptacle chambers 115–145 µm in diameter and 30–50 µm high.

Tetrasporangial/bisporangial conceptacle roofs non- or slightly protruding above surrounding surface, mostly 2–4 cells thick above chamber, pore canals lined with somewhat projecting cells that do not completely occlude the canal, conceptacle chambers (155-) 190–235 (-280) µm in diameter and 68–105 (-136) µm high, floor of mature chambers usually 6 or more cells below thallus surface; tetrasporangia and bisporangia scattered across the conceptacle chamber floor or peripheral to a central columella, each mature sporangium (15-) 25–55 (-95) µm in diameter and (35-) 50–95 (-125) µm long, containing zonately arranged tetraspores or bispores.

Type from Brest, France; lectotype in CO (unnumbered); designated by Chamberlain (1991, p. 67); depicted in Chamberlain (1991, p. 64, fig. 208) and Woelkerling & Campbell (1992, p. 43, fig. 22A).

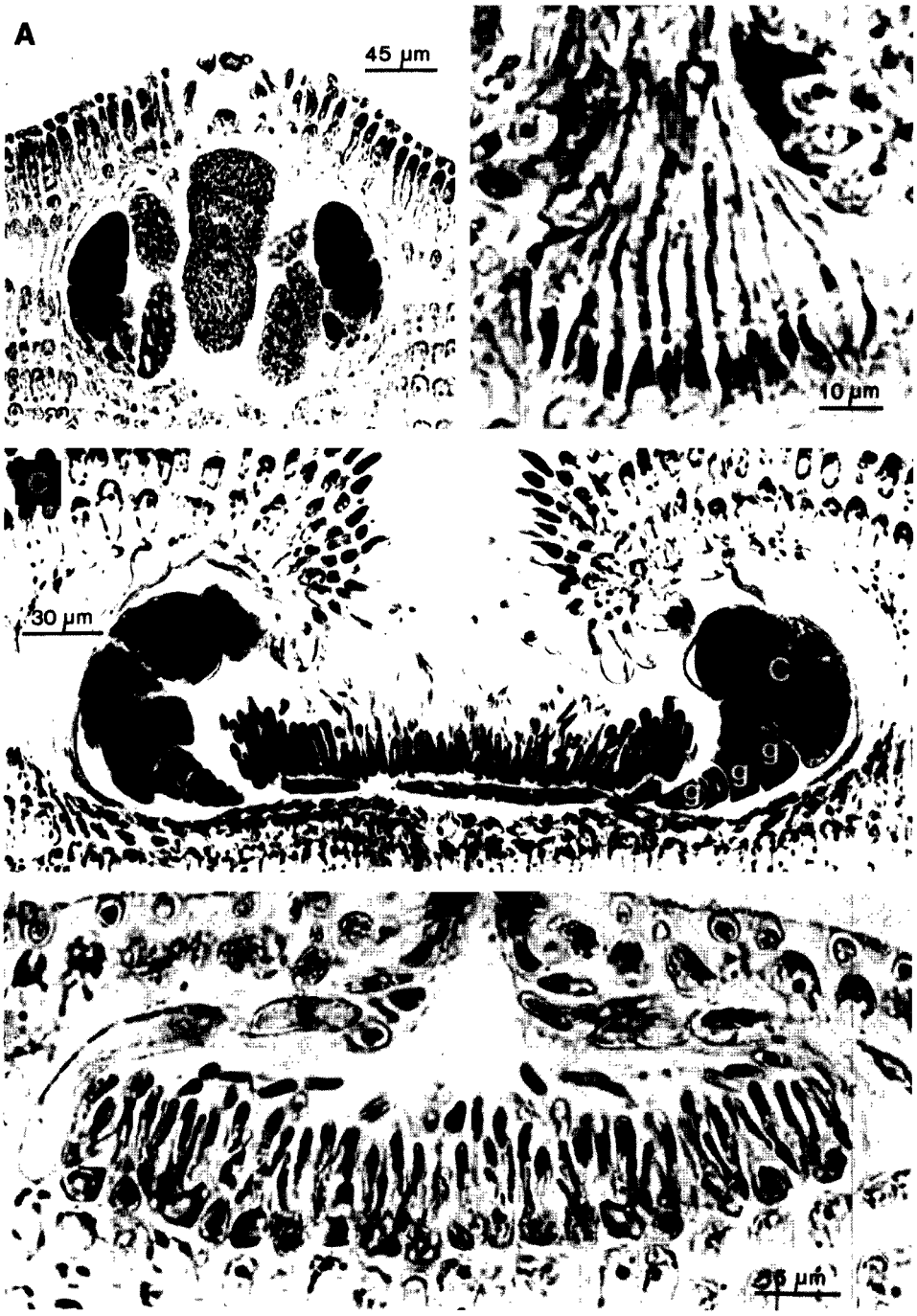


Fig. 103. *Lithophyllum corallinae* (**A, D,** LTB, 13174; **B, C,** LTB, 15578). **A.** Section of mature tetrasporangial conceptacle lacking a central columella and with tetrasporangia situated across the conceptacle chamber floor. **B.** Section of female-carposporangial conceptacle with mature carpogonial filaments. **C.** Section of female-carposporangial conceptacle with mature carposporophyte (g = gonimoblast filaments; C = carposporangium). **D.** Section of male conceptacle with unbranched spermatangial filaments arising from chamber floor.

Distribution: Probably widespread; many records outside Europe, however, require confirmation [see Chamberlain (1991) and Woelkerling & Campbell (1992)].

In Australia, Eyre, W. Aust., to Anglesea, Vic., and the E coast of Tasmania.

Selected specimens: Eyre ("Nine Mile Reef"), W. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 1.ii.1984; LTB, 13974). Point Sinclair, S. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 15.ii.1984; LTB, 14507). Elliston, S. Aust., 5 m deep (*Turner*, 28.x.1981; LTB, 15360). Vivonne Bay, Kangaroo I., S. Aust., low eulittoral (*Womersley*, 14.i.1947; AD, A12978 = LTB, 13587 and *Campbell & Penrose*, 8.iv.1988; LTB, 15884). Penneshaw, Kangaroo I., S. Aust., 0–1.5 m deep (*Campbell & Penrose*, 13.iv.1988; LTB, 15669). Nora Creina, S. Aust. (*Woelkerling*, 6.xi.1987; LTB, 15578). Bridgewater Bay, Vic., lower eulittoral (*Womersley*, 21.viii.1953; AD, A19053 = LTB, 13646 and 14.iv.1959; AD, A22633 = LTB, 13621). Apollo Bay (Haylings Reef), Vic. (*Pope & Bennett*, 17.i.1949; AD, A15243 = LTB, 13703). Anglesea (Potato Patch Reef), Vic., 8–9 m deep (*Beanland*, 31.viii.1982; LTB, 12721). Eddystone Point, Tas., 0–3 m deep (*Platt & Woelkerling*, 23.ii.1983; LTB, 13171, 13172, 13174, 13176). Eaglehawk Neck (Tessellated Pavement), Tas., 1–2 m deep (*Platt & Woelkerling*, 26.ii.1983; LTB, 13236, 13240). Eaglehawk Neck (Clydes I.), Tas., 0–6 m deep (*Platt*, 26.ii.1983; LTB, 13306).

Lithophyllum corallinae has been found in southern Australia on rock, snails, limpets, abalone shells and sea urchins in intertidal pools, on reef edges and subtidally to depths of 9 m. Gametangial, carposporangial, tetrasporangial and bisporangial thalli can occur in the same population. Bisporangia and tetrasporangia, however, were not found on the same individual. All southern Australian thalli examined were dioecious and epiphytic populations were not found. In the British Isles, in contrast, both monoecious and dioecious thalli occur and only epiphytic collections are known (Chamberlain & Irvine 1994b, p. 93). Woelkerling & Campbell (1992, p. 97) report that, rarely, intermediates can occur between *L. corallinae and L. frondosum* (as *L. bermudense*) and conclude that further studies of the relationships of these two species are required.

7. **Lithophyllum frondosum** (Dufour)Furnari, Cormaci & Alongi 1996: 115.

Melobesia frondosa Dufour 1861: 39. Dufour 1864: 60. Woelkerling, Penrose & Chamberlain 1993: 326, figs 12–15.

Lithophyllum bermudense Foslie & Howe 1906: (132), pl. 81 fig. 3, pl. 85 fig. 3, pl. 92. Barry & Woelkerling 1995: 137. Campbell & Woelkerling 1990: 119, fig. 13. Millar & Kraft 1993: 14. Woelkerling & Campbell 1992: 18, figs 2–15. Woelkerling 1993: 38.

Dermatolithon bermudense (Foslie & Howe)Foslie & Howe *in* Foslie 1909: 58.

Tenarea bermudense (Foslie & Howe)Adey 1970: 6.

Titanoderma bermudense (Foslie & Howe)Woelkerling, Chamberlain & Silva 1985: 333.

FIGS 62D, 63E, 104, 105

Thallus normally pinkish, encrusting to layered, foliose, warty, lumpy or fruticose, mostly 4–200 mm across and 0.1–60 mm thick or tall, partially to completely affixed by cell adhesion or unattached and free-living as rhodoliths; protuberant branches simple or branched, mostly 2–27 mm in diameter and 2–29 mm long; lamellate branches applanate or ascending and sometimes coalescent, mostly 3–12 mm across and 1–8 mm long. *Structure* pseudoparenchymatous, organisation dorsiventral in crustose portions and lamellate branches but radial in protuberant branches; construction dimerous, dimerous and monomerous or largely monomerous; dimerous portions consisting of a single ventral layer of branched, laterally cohering, filaments each composed of palisade and/or non-palisade cells 5–25 μm long and (16-) 25–60 (-100) μm high, and additionally of simple or branched, laterally cohering, filaments that arise dorsally and more or less perpendicularly from cells of ventral layer filaments and are each usually composed of cells 3–15 μm in diameter and (3-) 8–50 (-60) μm long; monomerous portions consisting of a single system of branched, laterally cohering, filaments that collectively contribute to a ventrally or centrally situated core and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, with each filament composed of cells 5–14 μm in diameter and 5–50 (-70) μm long; epithallial cells 4–12 μm in diameter and 2–6 μm long, terminating most filaments at the thallus surface, with distal walls rounded or flattened but

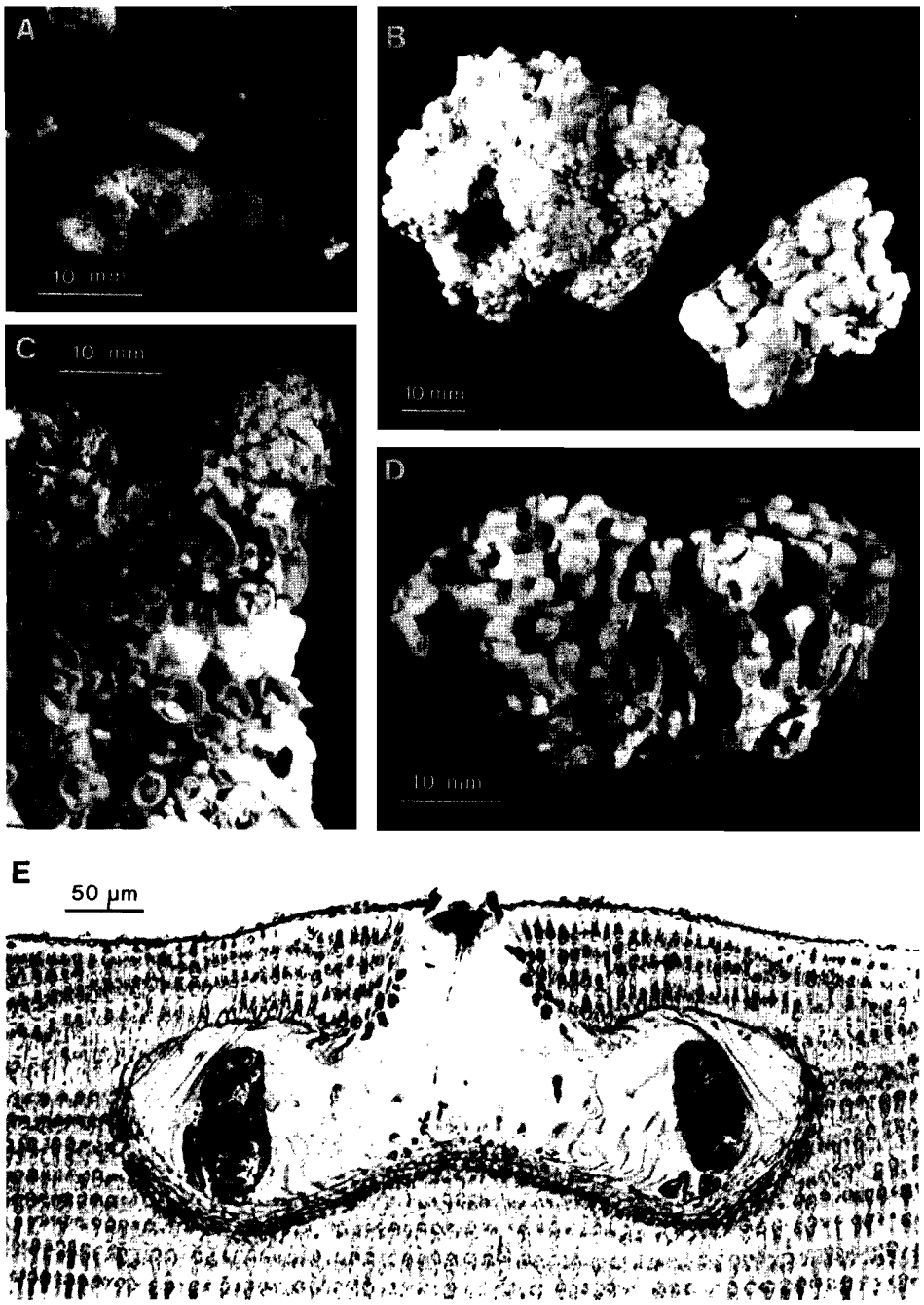


Fig. 104. *Lithophyllum frondosum* (**A,** LTB, 14061; **B,** LTB, 10604; **C,** LTB, 13260; **D,** LTB, 10668; **E,** LTB, 13187). **A.** Encrusting thalli on the red alga *Osmundaria*. **B.** Warty to lumpy thalli detached from rock. **C.** Warty to foliose thallus on rock. **D.** Portion of fruticose thallus detached from rock. **E.** Section of mature tetrasporangial conceptacle.

not flared; cells of adjacent filaments joined by secondary pit-connections; cell-fusions, haustoria, and trichocytes unknown.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia, carposporangia and tetrasporangia produced in uniporate conceptacles; gametangia and carposporangia formed on thalli separate to those bearing tetrasporangia. Bisporangia unknown.

Gametangial thalli probably dioecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs flush with or slightly protruding above surrounding thallus surface, 65–110 μm thick, composed of 7–11 layers of cells above the chamber, conceptacle chambers (169-) 300–385 μm in diameter and (65-) 85–115 (-125) μm high. Carposporophytes composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal (rarely catenate) carposporangia 30–55 μm in diameter. Spermatangial filaments unbranched, borne in groups of 1–3 on initials across the male conceptacle chamber floor, mature male conceptacle roofs flush with or slightly protruding above surrounding thallus surface, 18–40 μm thick, composed of 4–5 layers of cells above the chamber, male conceptacle chambers (100-) 140–160 μm in diameter and 25–60 μm high.

Tetrasporangial conceptacle roofs non- or slightly protruding above surrounding surface, mostly 3–7 cells thick above chamber, pore canals lined with somewhat projecting cells that do not completely occlude the canal, conceptacle chambers (255-) 320–410 (-445) μm in diameter and (65-) 90–125 (-160) μm high, floor of mature chambers usually 7 or more cells below thallus surface; tetrasporangia scattered across the conceptacle chamber floor or peripheral to a central columella, each mature sporangium 25–45 (-55) μm in diameter and (31-) 75–125 (-135) μm long, containing zonately arranged tetraspores.

Type from St Nazzaro (near Genoa), Italy; lectotype in PC (unnumbered, Thuret-Bornet Herbarium, fascicle 132, filed under *Lithophyllum expansum*); designated by Woelkerling *et al.* 1993: 327.

The type of *L. bermudense*, from Spanish Point, Bermuda (*Howe*, 21.vi.1900) is Howe 199 in TRH.

Distribution: Mediterranean Sea; Bermuda; Florida; Caribbean islands; Juan Fernandez I.

In Australia, Eagle Bluff, Shark Bay, W. Aust., to Newport, N.S.W., and from the northern and eastern coasts of Tasmania.

Selected specimens: Eagle Bluff, Shark Bay, W. Aust., 1–2 m deep (*Woelkerling*, 31.vii.1986; LTB, 15482, 15486). Cape Vlaming, Rottnest I., W. Aust., reef edge (*Woelkerling*, 8.ii.1978; LTB, 10601, 10603, 10604, 10619). North Point Reef, Rottnest I., W. Aust., reef edge (*Woelkerling*, 10.ii.1978; LTB, 10664, 10668). Point Valliant, Two People Bay, W. Aust., 0–1 m deep (*Woelkerling*, 2.ii.1978; LTB, 10725). Twilight Cove, Eyre, W. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 2.ii.1984; LTB, 14031, 14038, 14043, 14061). Eucla, W. Aust., drift (*Woelkerling*, 26.i. 1978; LTB, 10523). Head of Great Australian Bight, S. Aust., drift (*Woelkerling, Platt & Jones*, 13.ii.1984; LTB, 14381). Point Sinclair, S. Aust., reef pools (*Womersley*, 26.i.1951; AD, A15212 = LTB, 13636 and 8.ii.1954; AD, A19647). Point Westall, S. Aust., 2–3 m deep (*Platt & Jones*, 16.ii.1984; LTB, 14527, 14530, 14549). Port Lincoln (Boston I.), S. Aust., reef top (*Woelkerling*, 14.v.1968; AD, A32622 = LTB, 14683). Cape Willoughby, Kangaroo I., S. Aust., 0–2 m deep (*Campbell & Penrose*, 6.iv.1988; LTB, 15588, 15589). Beachport (Post Office Rock), S. Aust., on reef, 0–6 m deep (*Campbell, Penrose & Woelkerling*, 1.xii.1986; LTB, 15510; *Woelkerling*, 6.xi.1987; LTB, 15822; *Campbell & Penrose*, 26.ii.1988; LTB, 15682). Blanket Bay, Otway National Park, Vic., 2 m deep (*Campbell, Penrose & May*, 14.xi.1985; LTB, 15251). Anglesea (Ingoldsby Reef), Vic., upper sublittoral (*Beanland*, 13.xii.1982; LTB, 15295, 15296). Cape Paterson (Eagles Nest), Vic., reef top (*Woelkerling*, 27.xi.1976; LTB, 12510). Rocky Cape National Park, Tas., 0–1 m deep (*Platt*, 2.iii.1983; LTB, 13435). Eddystone Point, Tas., 0–3 m deep (*Platt*, 23.ii.1983; LTB, 13187, 13188, 13189, 14648). Coles Bay, Freycinet Pen., Tas., 0–2.5 m deep (*Platt & Woelkerling*, 21.ii.1983; LTB, 13111, 13115, 13130, 13144). Eaglehawk Neck (Clydes I.), Tas., at low tide (Platt, 26.ii.1983; LTB, 13260). Eaglehawk Neck (Tessellated Pavement), Tas., 1–2 m deep (*Platt & Woelkerling*, 26.ii.1983; LTB, 13241, 13243, 13253). Sister Bay (Convict Burial Ground), Southport, Tas., 3–4 m deep (*Platt*, 16.ii.1983; LTB, 12913, 12914, 12915, 12924, 14654). Newport, N.S.W., drift (*Womersley*, 30.v.1950; AD, A13077 = LTB, 14684).

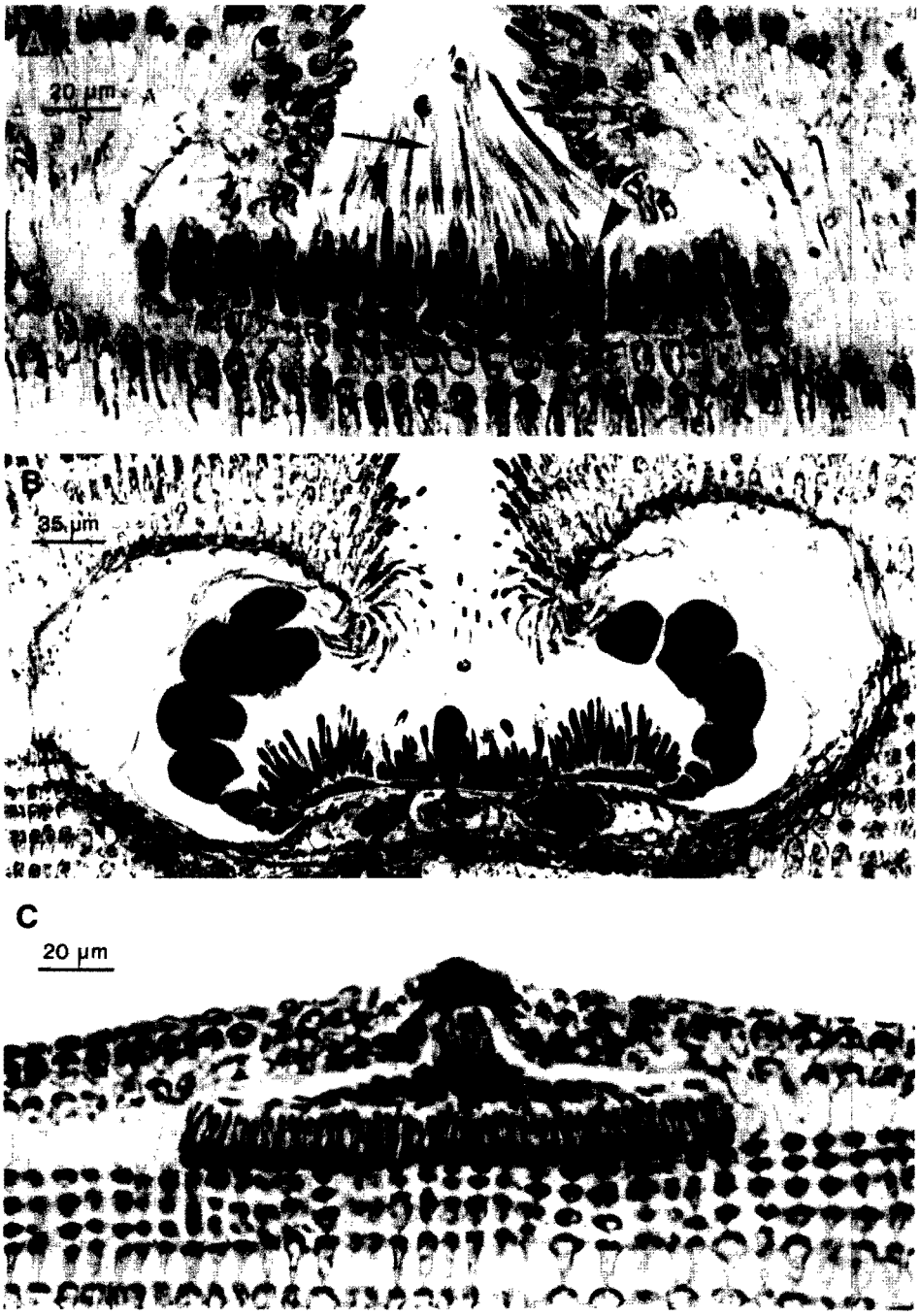


Fig. 105. *Lithophyllum frondosum* (**A**, LTB, 13253; **B**, LTB, 12924; **C**, LTB, 15296). **A.** Section of female-carposporangial conceptacle with mature carpogonial filaments and carpogonia with (arrows) and without (arrowheads) trichogynes. **B.** Section of female-carposporangial conceptacle with mature carposporophyte. **C.** Section of male conceptacle with unbranched spermatangial filaments arising from chamber floor.

Lithophyllum frondosum has been found in southern Australia on rock, or occasionally on molluscs, algae or seagrasses or unattached; it occurs in intertidal pools and along reef edges in heavy surf and subtidally to depths of 13 m. Of the known southern Australian species of *Lithophyllum, L. frondosum* is the most variable morphologically and anatomically. Woelkerling & Campbell (1992, p. 97) reported that, rarely, intermediates can occur between *L. frondosum* (as *L. bermudense*) and *L. corallinae* and conclude that further studies of the relationships of these two species are required. Furnari *et al.* (1996) provide an account of this species in the Mediterranean.

Notes on other taxa reported from southern Australia

Woelkerling & Campbell (1992, pp. 97–101) provide information on 12 additional species and infraspecific taxa that at some stage were ascribed to *Lithophyllum* and reported from southern Australia. These include taxa whose status is uncertain, incorrect records, and taxa now known to belong to other genera or conspecific with taxa belonging to other genera.

SUBFAMILY MASTOPHOROIDEAE Setchell 1943: 134 (as 'Mastophoreae')

by W.J. Woelkerling (with some genera by D.L. Penrose)

Thallus partly unconsolidated to encrusting, warty, lumpy, fruticose, discoid, layered, foliose or arborescent, prostrate to erect; partially endophytic, epigenous or unattached and free-living as rhodoliths; genicula absent. *Structure* pseudoparenchymatous with monomerous or dimerous construction or both, or rarely partly filamentous with diffuse construction; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent or rare.

Reproduction. Vegetative reproduction by thallus fragmentation or propagules. Gametangia, carposporangia, tetrasporangia and bisporangia borne in uniporate conceptacles.

Gametangial thalli monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles or rarely in the same conceptacle. Carpogonial filaments 2- to 3-celled, arising from the female conceptacle chamber floor. Carposporophytes developing within female conceptacles after karyogamy, composed of carposporangia terminating short gonimoblast filaments that arise from a conspicuous central fusion cell or from an irregularly shaped fusion cell that may look discontinuous in section. Spermatangial filaments unbranched, confined to the male conceptacle chamber floor or more rarely produced both on floor and roof.

Tetrasporangia and bisporangia usually borne on separate thalli from gametangia and carposporangia, lacking apical plugs; tetrasporangia and bisporangia usually with zonately arranged spores. Conceptacle roofs formed from filaments interspersed amongst and peripheral to developing sporangia or only from filaments peripheral to developing sporangia.

Type genus: *Mastophora* Decaisne 1842a: 365.

The Mastophoroideae includes eight genera, all of which are represented in southern Australia. The key to genera is adapted from that of Penrose & Chamberlain (1993, p. 303). Information on the historical background of the subfamily has been provided by Johansen (1981) and Woelkerling (1988).

KEY TO GENERA OF MASTOPHOROIDEAE

1. Vegetative thallus endophytic; epithallial cells absent from vegetative portions; haustoria present ..... LESUEURIA
1. Vegetative thallus epigenous or growing unattached; epithallial cells present in vegetative portions; haustoria absent 2

2. Thallus possessing a conspicuous ventral or central layer of filaments composed of palisade cells 3
2. Thallus lacking a conspicuous ventral or central layer of filaments composed of palisade cells 5

3. Thallus, at least in older parts, composed of many layers of cells, anchored to substrate at only one point by a holdfast and producing a distinct stipe..... METAMASTOPHORA
3. Thallus mostly 2–3 (-5) cells thick except near conceptacles or points of branching, anchored to substrate by cell adhesion or rhizoids or growing unattached 4

4. Tetrasporangial and bisporangial conceptacles with a central columella, roofs formed only by filaments peripheral to the sporangial initials, sporangia confined to the periphery of the conceptacle chamber floor ..... MASTOPHORA
4. Tetrasporangial and bisporangial conceptacles lacking a central columella, roofs formed by filaments surrounding and interspersed amongst sporangial initials, sporangia scattered across the conceptacle chamber floor ..... LITHOPORELLA

5. Tetrasporangial and bisporangial conceptacle pore canals lined by cells that are orientated more or less perpendicularly to the roof surface and do not protrude laterally into the pore canal ..... HYDROLITHON
5. Tetrasporangial and bisporangial conceptacle pore canals lined by cells that are orientated more or less parallel to the roof surface and protrude laterally into the pore canal 6

6. Tetrasporangial and bisporangial conceptacle roofs formed by filaments surrounding and interspersed amongst sporangial initials; southern Australian specimens epiphytic ..... PNEOPHYLLUM
6. Tetrasporangial and bisporangial conceptacle roofs formed only by filaments peripheral to the sporangial initials; southern Australian specimens epilithic, epizoic or unattached 7

7. Spermatangia formed on only the floors of male conceptacle chambers; gonimoblast filaments arising from peripheral surfaces of fusion cells ..... SPONGITES

7. Spermatangia formed both on the floors and roofs of male conceptacle chambers; gonimoblast filaments arising from dorsal surfaces of fusion cells ..... NEOGONIOLITHON

Genus **LESUEURIA** Woelkerling & Ducker 1987: 193

Thallus partly to largely unconsolidated; vegetative portions endophytic but conceptacles produced externally to the host; genicula absent. *Structure* filamentous to partly pseudoparenchymatous, without apparent dorsiventral, radial or isobilateral organisation; construction diffuse, consisting of branched endophytic filaments that may become partially consolidated but collectively lack any regularised internal structure; cell elongation characteristics uncertain; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; epithallial cells absent from vegetative portions of thallus but terminating most conceptacle roof filaments, with distal walls rounded or flattened but not flared; haustoria occasional, penetrating cells of host; trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia and tetrasporangia borne in uniporate conceptacles produced externally to the host. Bisporangia unknown.

Gametangial thalli presumably dioecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Carposporophytes arising within female conceptacles after karyogamy; composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, produced on the floor of male conceptacle chambers.

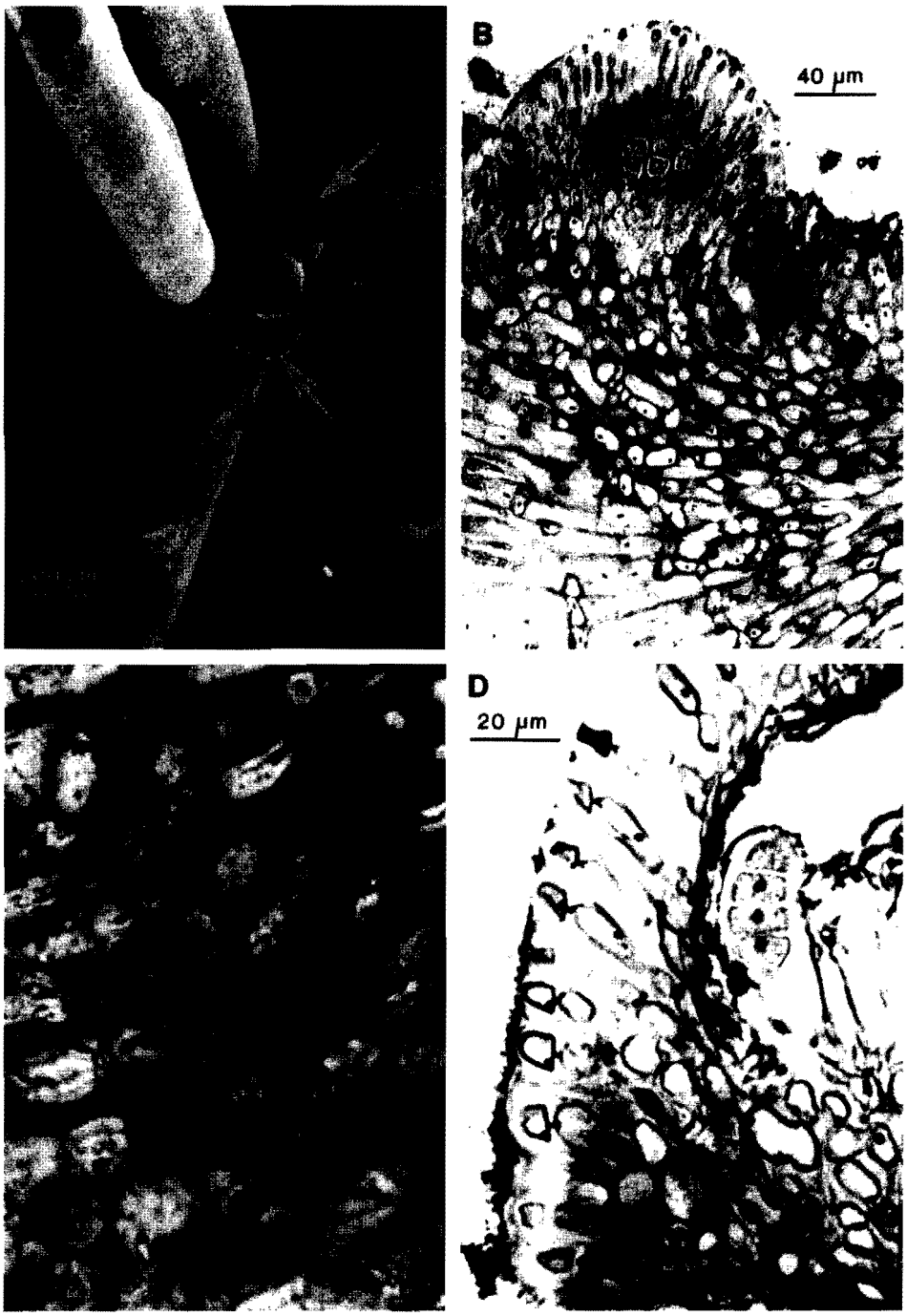


Fig. 106. *Lesueuria minderiana* (**A, B, D,** LTB, 10851; **C,** LTB, 10760). **A.** Surface view of thallus showing conceptacles (arrows) protruding from surface of host geniculum of *Metagoniolithon*. Vegetative portion of thallus is endophytic. **B.** Section of host geniculum showing endophytic, diffuse thallus of *Lesueuria minderiana*. **C.** Haustorium (H) of *L. minderiana* penetrating host cell. **D.** Portion of roof of a tetrasporangial conceptacle showing terminal epithallial cells. Epithallial cells have not been found on vegetative filaments.

Tetrasporangia formed peripheral to a central columella, roofs formed only by filaments peripheral to sporangial initials, each mature sporangium lacking an apical plug and containing four zonately arranged tetraspores.

Type species: *L. minderiana* Woelkerling & Ducker 1987: 193.

Lesueuria contains one known species reported only from southern Australia. The following account is based mainly on data in Woelkerling & Ducker (1987).

Lesueuria minderiana Woelkerling & Ducker 1987: 193, figs 1–24. Woelkerling 1988: 123, figs 106–110.

FIGS 62G, 106, 107

Thallus largely unconsolidated, mostly 0.1–0.4 mm in greatest extent, vegetative portions endophytic but conceptacles produced externally to the host. *Structure* filamentous to partly pseudoparenchymatous; construction diffuse, consisting of simple or branched, laterally cohering, filaments with cells mostly 7–16 µm in diameter and 8–30 µm long; cell elongation characteristics uncertain; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; epithallial cells mostly 8–11 µm in diameter and 5–11 µm long, absent from vegetative portions of thallus but terminating most conceptacle roof filaments, with distal walls rounded or flattened but not flared; haustoria occasional, penetrating cells of host; trichocytes unknown.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia and tetrasporangia formed in uniporate conceptacles produced externally to the host. Bisporangia unknown.

Gametangial thalli probably dioecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above the host surface, 40–70 µm thick, composed of 3–7 layers of cells above the chamber, conceptacle chambers 60–150 µm in diameter and 50–70 µm high. Carposporophytes developing within female conceptacles after karyogamy, mature carposporophytes composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia 19–27 µm in diameter. Spermatangial filaments unbranched, arising from the floor of male conceptacle chambers, mature male conceptacle roofs protruding above the host surface, 30–65 µm thick, composed of 3–7 layers of cells above the chamber, conceptacle chambers 90–110 µm in diameter and 35–60 µm high.

Tetrasporangial conceptacle roofs protruding above the host surface, 40–80 µm thick above the chamber and composed of 3–7 layers of cells, conceptacle chambers 100–190 µm in diameter and 65–115 µm high; tetrasporangia peripheral to a central columella, each mature sporangium 15–25 µm in diameter and 35–50 µm long, containing four zonately arranged tetraspores.

Type from Mabel Cove, Rottnest I., W.Aust., 0–1 m deep (*Woelkerling*, 9.ii.1978); holotype in LTB (10851); depicted, in part, in Woelkerling & Ducker (1987, figs 1–24).

Distribution: Kalbarri, W. Aust., to Urquhart Bluff, Vic.

Selected specimens: Kalbarri, W. Aust., 1–2 m deep (*Woelkerling*, 22.ii.1978; LTB, 10819). Flat Rocks, W. Aust., drift (*Woelkerling*, 25.ii.1978; LTB, 10769). North Point Reef, Rottnest I., W. Aust., 1–2 m deep (*Woelkerling*, 10.ii.1978; LTB, 10760). Sarge Bay, Cape Leeuwin, W. Aust. (*Parsons*, 16.xi.1968; AD, A56880). Point Malcolm, SW of Israelite Bay, W. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 7.ii.1984; LTB, 14203). Eucla, W. Aust. (*Womersley*, 2.ii.1954; AD, A56884). Wilson Bluff, S. Aust., drift (*Woelkerling*, 26.i.1978; LTB, 10814). Tiparra Reef, Spencer Gulf, S. Aust. (*Shepherd*, 20.viii.1971; AD, A56881). Vivonne Bay, Kangaroo I., S. Aust., upper sublittoral (*Woelkerling*, 23.ii.1979; LTB, 11650). Urquhart Bluff, Vic., drift (*Woelkerling & Woelkerling*, 22.i.1986; LTB, 15318).

Lesueuria minderiana has been found only on genicula of *Metagoniolithon chara* growing in tide pools and to depths of 8 m. Specimens are most easily detected by examining host genicula with a stereomicroscope; the conceptacles of *Lesueuria minderiana* commonly occur in small clusters and are readily recognised. Gametangial and tetrasporangial thalli usually occur within single populations.

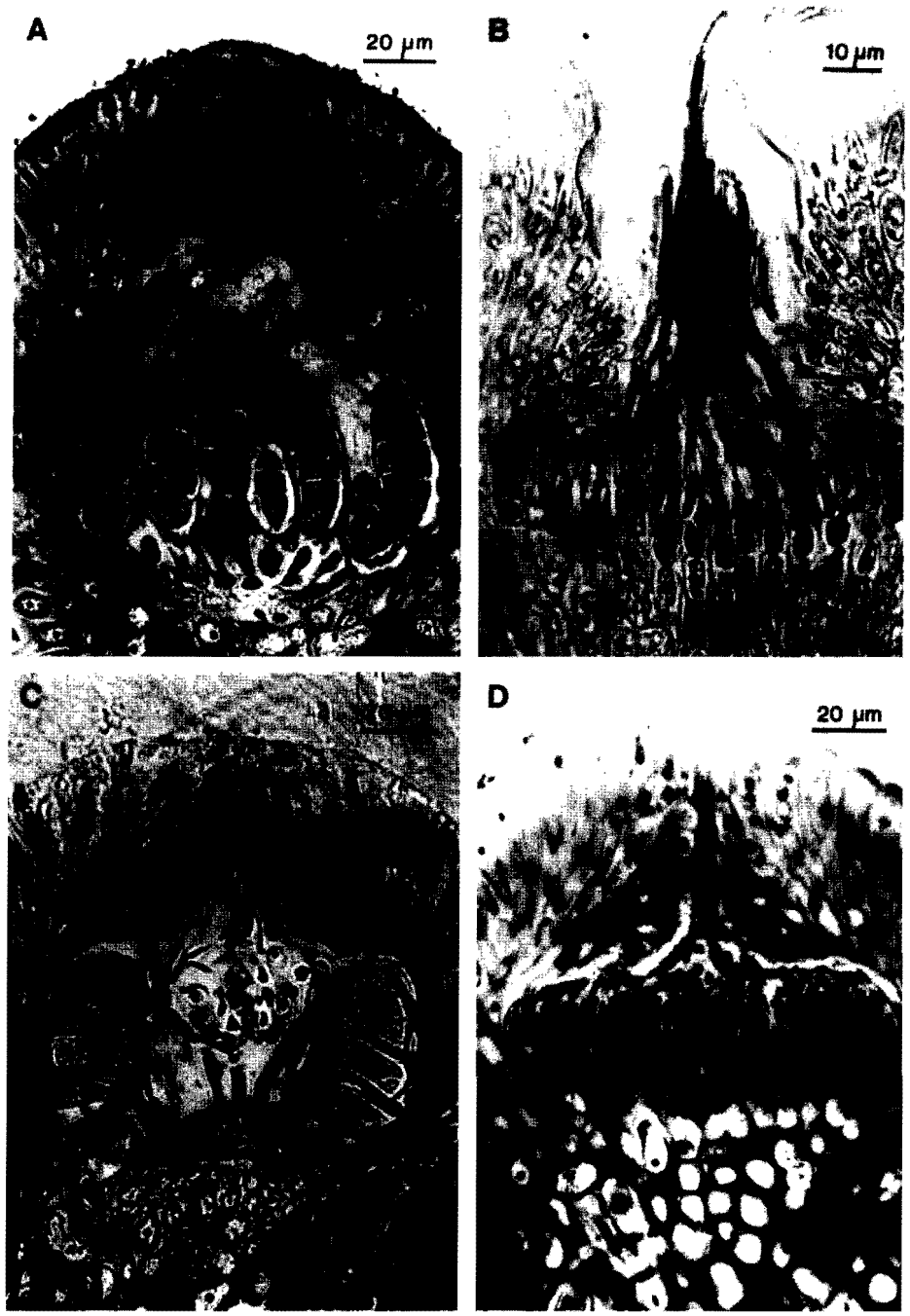


Fig. 107. *Lesueuria minderiana* (**A, C, D,** LTB, 10851; **B,** LTB, 10760). **A.** Section of most of a mature tetrasporangial conceptacle. **B.** Section of part of a female-carposporangial conceptacle with mature carpogonial filaments. **C.** Section of part of a female-carposporangial conceptacle with mature carposporophyte; g = gonimoblast filament; C = carposporangium. **D.** Section of most of a male conceptacle with unbranched spermatangial filaments arising from chamber floor.

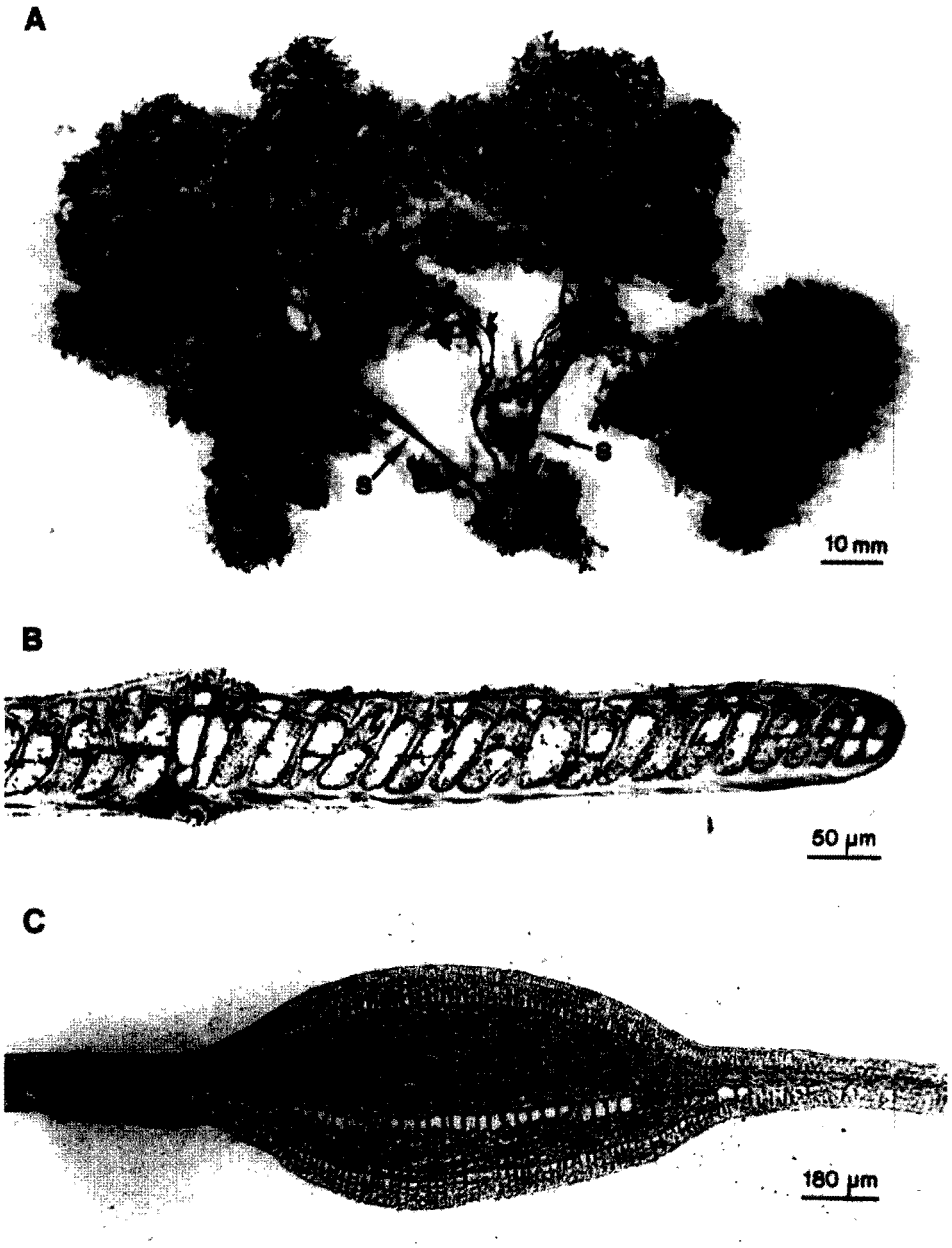


Fig. 108. *Metamastophora flabellata* (**A, C,** LTB, 10457; **B,** LTB, 14048). **A.** Arborescent thallus with holdfast (H), stipes (arrow-S) and expanded, flattened, ribbon like branches. **B.** Longitudinal section of branch tip showing a unistratose ventral layer of palisade cells each bearing a unicellular filament (epithallial cell) dorsally. Note that cell fusions are not evident between cells of the same filament. **C.** Section of older portion of a branch and stipe. Note how palisade layer (arrow) has become internal and branches have become a number of cells thick.

Genus METAMASTOPHORA Setchell 1943: 130

Thallus arborescent, composed of a basal holdfast and erect stipes bearing flattened, branched, flexible ribbon like branches; genicula absent. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, consisting of two distinct groups of filaments: a unistratose layer that is ventral in younger portions but becomes internal in older portions and in which each filament is composed of palisade cells, and secondly epithallial cells or filaments terminating in epithallial cells arising dorsally (and in older portions also ventrally) and more or less perpendicularly from cells of the unistratose palisade layer; cell elongation characteristics uncertain; cells of adjacent filaments joined by cell-fusions, secondary pit-connections very occasional in older part of thallus; epithallial cells with distal walls rounded or flattened but not flared; haustoria unknown; trichocytes uncommon, occurring singly or in horizontal rows or fields.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia and tetrasporangia borne in uniporate conceptacles; gametangia and carposporangia formed on separate thalli from tetrasporangia; conceptacles borne only on dorsal surface of branches. Bisporangia unknown.

Gametangial thalli dioecious or rarely monoecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Carposporophytes arising within female conceptacles after karyogamy, composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, produced on the floor of male conceptacle chambers.

Tetrasporangia formed peripheral to a central columella, roofs formed only by filaments peripheral to sporangial initials, each mature sporangium lacking an apical plug and containing four zonately arranged tetraspores.

Type species: *M. flabellata* (Sonder)Setchell 1943: 132. Basionym: *Melobesia flabellata* Sonder 1845: 55.

Five species were ascribed to *Metamastophora* by Setchell (1943); Woelkerling (1978) transferred one to *Mastophoropsis* and then (Woelkerling 1980b) reduced the remaining four to a single species. Details relating to generic etymology, nomenclature, synonymy, *etc.* are provided by Woelkerling (1988, pp. 133–139). The following species account constitutes an update of Woelkerling (1980a, 1980b).

Metamastophora flabellata (Sonder)Setchell 1943: 131. Huisman & Walker 1990: 413. Shepherd 1981: 460. Shepherd & Womersley 1970: 133; 1981: 165. Woelkerling 1980a: 201, figs 1–33; 1980b: 227, figs 1–5. Womersley 1953: 38.
Melobesia flabellata Sonder 1845: 55. Sonder 1848: 188.
Mastophora flabellata (Sonder)Harvey 1849: 108. Kützing 1849: 697. Womersley 1950: 167.
Melobesia plana Sonder 1845: 55.
Metamastophora plana (Sonder)Setchell 1943: 133.
Melobesia stelligera Endlicher et Diesing 1845: 290.
Metamastophora stelligera (Endlicher et Diesing)Setchell 1943: 132.
Peyssonelia caulescens Kützing 1849: 694.
Mastophora hypoleuca Harvey 1849: 108, pl. 41 figs 1–3.
Mastophora lamourouxii Decaisne *ex* Harvey 1849: 108, pl. 41 figs 1–5.
Metamastophora lamourouxii (Decaisne *ex* Harvey)Setchell 1943: 131.
Lichenella brentii J.E. Gray 1858: 322.
Additional references involving these binomials and further information on synonymy are provided by Woelkerling (1980b).

FIGS 108–110

Thallus normally pinkish to dull red, arborescent, mostly 5–23 cm tall, attached by a basal holdfast that produces 1–several erect stipes with flattened, branched, ribbon like branches that commonly have vein-like thickenings in older portions; branching mostly in one plane, pseudodichotomous to pseudopolychotomous. *Structure* pseudoparenchymatous

with dorsiventral organisation throughout; construction dimerous, consisting of a single layer of branched, laterally cohering, filaments occurring ventrally in younger portions but internally in older portions, each composed of palisade cells (10-) 15–40(-46) µm long and (30-) 35–85 µm high, and additionally of epithallial cells or of filaments terminating in epithallial cells and composed of cells that arise dorsally and in older portions ventrally and more or less perpendicularly from most cells of the unistratose palisade layer and are mostly 5–20 µm in diameter and 19–85 (-109) µm long; epithallial cells 11–49 µm in diameter and (8-) 11–25 µm long with distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell fusions, secondary pit-connections very occasional in older parts of thalli; haustoria unknown; trichocytes uncommon, occurring singly or in horizontal rows or fields.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia and tetrasporangia produced in uniporate conceptacles; gametangia and carposporangia formed on thalli separate to those bearing tetrasporangia, conceptacles borne only on dorsal surface of branches. Bisporangia unknown.

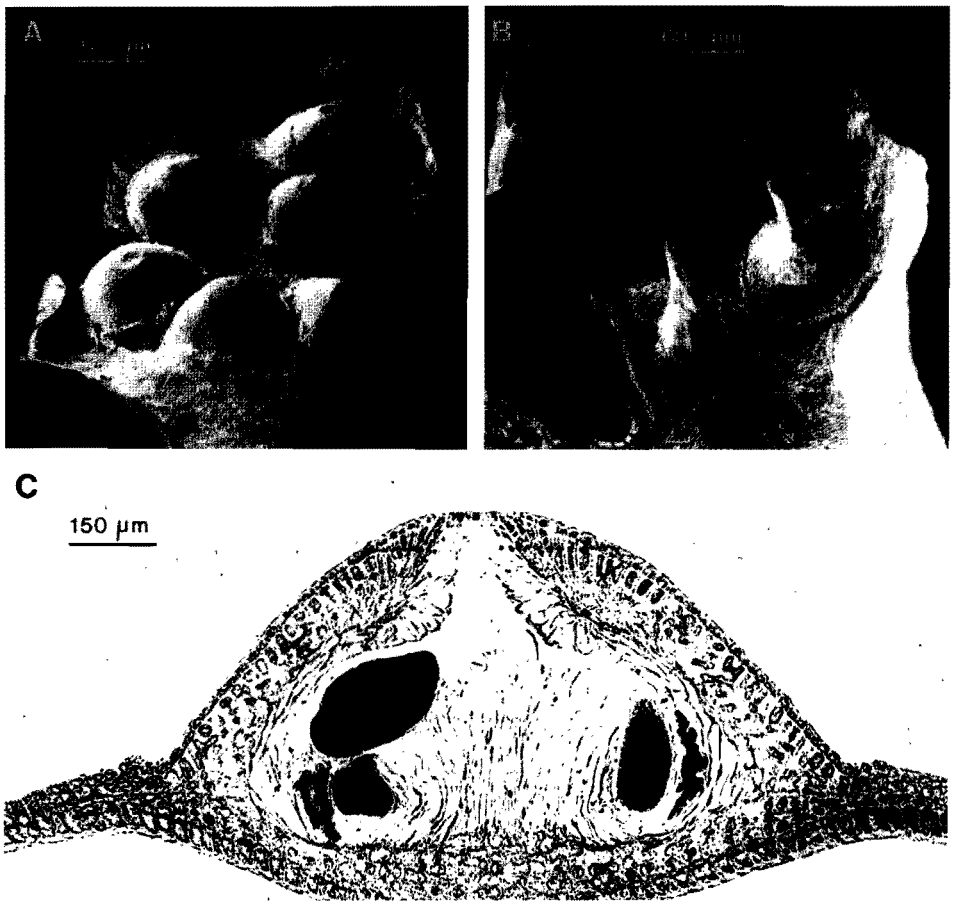


Fig. 109. *Metamastophora flabellata* (**A, B,** LTB, 10426; **C,** LTB, 10457). **A.** Surface view of dome like roofs characteristic of female/carposporangial and tetrasporangial conceptacles. **B.** Surface view of rostrate roofs characteristic of most male conceptacles. **C.** Section of mature tetrasporangial conceptacle.

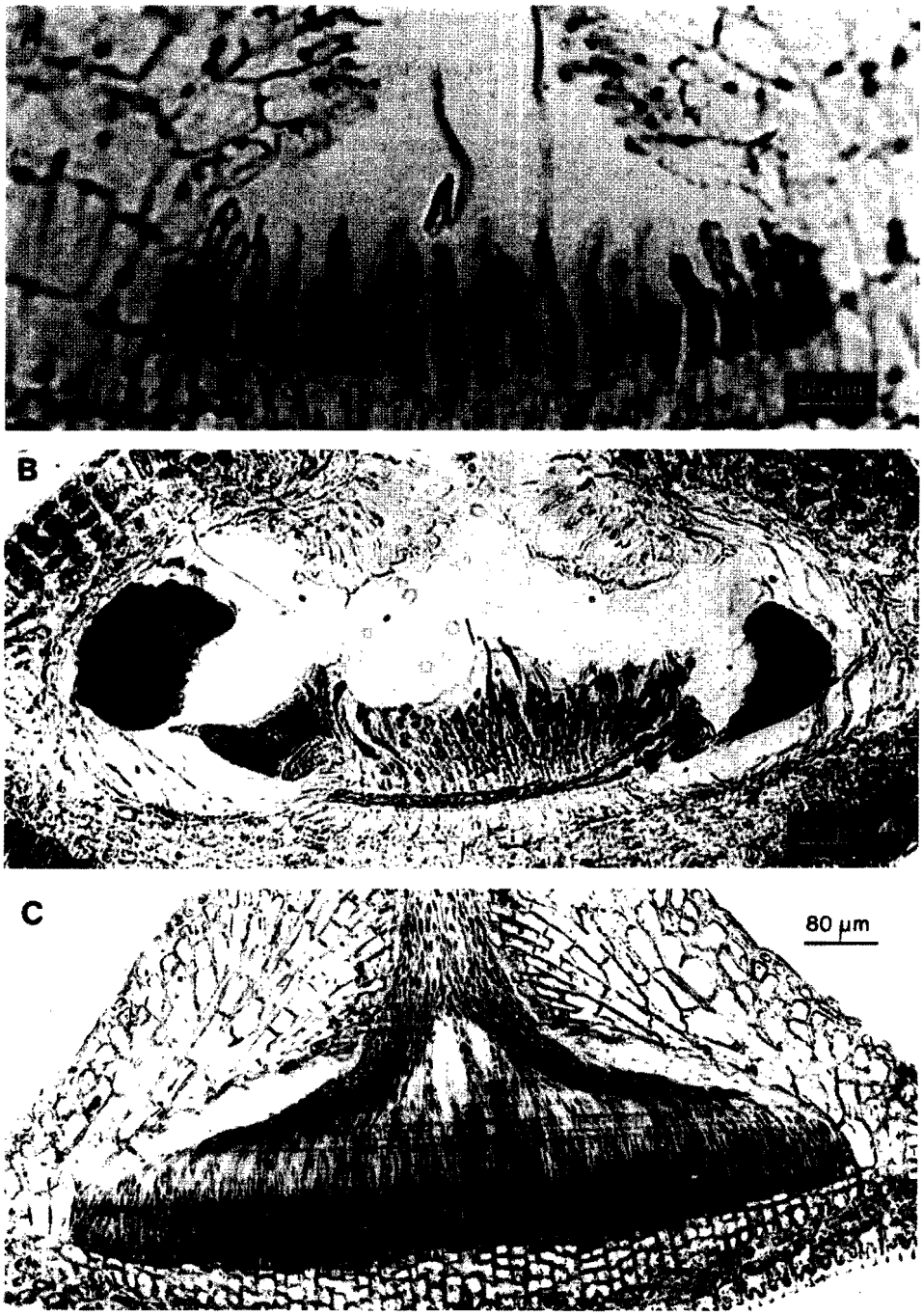


Fig. 110. *Metamastophora flabellata* (LTB, 10457). **A.** Section of part of a female-carposporangial conceptacle with mature carpogonial filaments. **B.** Section of part of a female-carposporangial conceptacle with mature carposporophyte. **C.** Section of part of male conceptacle with unbranched spermatangial filaments arising from chamber floor.

Gametangial thalli dioecious or rarely monoecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs normally dome-like, protruding above surrounding thallus surface, 110–160 μm thick, composed of 3–6 layers of cells above the chamber, conceptacle chambers 760–1075 μm in diameter and 145–435 μm high. Carposporophytes developing within female conceptacles after karyogamy, composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia 110–190 μm in diameter. Spermatangial filaments unbranched, borne across the male conceptacle chamber floor, mature male conceptacle roofs dome-like or more commonly rostrate, protruding above surrounding thallus surface, 370–960 μm thick, composed of 13–26 layers of cells above the chamber, male conceptacle chambers 850–950 μm in diameter and 200–370 μm high excluding the pore canal 900–1500 (-2000) μm long.

Tetrasporangial conceptacle roofs dome-like, protruding above surrounding surface, 110–260 μm thick above the chamber and composed of 3–7 layers of cells, pore canals lined by cells that are orientated more or less parallel to the roof surface and protrude slightly into the canal, conceptacle chambers 625–900 (-1000) μm in diameter and 230–510 μm high; tetrasporangia peripheral to a central columella, each mature sporangium 90–240 μm in diameter and 175–340 μm long, containing zonately arranged tetraspores.

Type from W. Aust.; lectotype in MEL (516739), designated by Woelkerling (1980b: 238), depicted in Woelkerling (1980b, fig. 1).

Distribution: Southern Africa. Woelkerling (1980b: 239) summarises incorrect and questionable records from elsewhere.

In Australia, Kalbarri, W. Aust., to Waterloo Bay, Wilsons Prom., Vic. and from Currie, King I., Tasmania.

Selected specimens: Kalbarri, W. Aust., 2–3 m deep (*Woelkerling*, 22.ii.1978; LTB, 11081, 12703). Flat Rocks (N of Dongara), W. Aust., drift (*Woelkerling*, 25.ii.1978; LTB, 10426). Cape Vlaming, Rottnest I., W. Aust., 0–3 m deep (*Woelkerling*, 8.ii.1978; LTB, 10457). Israelite Bay, W. Aust., drift (*Wells*, 10.xii.1974; AD, A46086). Twilight Cove, W. Aust., 1–3 m deep (*Woelkerling, Platt & Jones*, 2.ii.1984; LTB, 14048). Eucla, W. Aust., drift (*Womersley*, 2.ii.1954; AD, A19351). Point Sinclair, S. Aust., upper sublittoral, shaded (*Womersley*, 9.ii.1954; AD, A19600). Pearson I., S. Aust., 48 m deep (*Shepherd*, 9.i.1969; AD, A33722). Pondalowie Bay, S. Aust., 5–8 m deep (*Shepherd*, 14.iv.1963; AD, A26603). Young Rocks, S of Kangaroo I., S. Aust., 16–30 m deep (*Branden*, 18.vi.1991; AD, A61456). Toad Head, West I., S. Aust., 13 m deep (*Shepherd*, 24.x.1966; AD, A31553). Robe, S. Aust., shaded pool (*Womersley*, 27.viii.1949; AD, A11076). Beachport, S. Aust., 3–6 m deep (*Campbell & Penrose*, 26.ii.1988; LTB, 15688). Lady Julia Percy I., Vic., 3–6 m deep (*Shepherd*, 4.i.1968; AD, A32438). Peterborough, Vic., drift (*Womersley*, 17.viii.1949; AD, A12158). Point Roadknight, Vic., drift (*Sinkora*, 29.xi.1971; MEL, 516787 = AD, A43184). Point Lonsdale, Vic. (*Hallam*, 24.ii.1965; MELU, 2079). Cape Patterson, Vic., drift (*MacRaild*, 18.v.1972; MELU, 21423). Waterloo Bay, Wilsons Prom., Vic., 10 m deep (*Leach*, 21.x.1977; LTB, 10264). Currie, King I., Tas., upper sublittoral (*King*, 29.v.1971; MELU, 20994).

Metamastophora flabellata has been found on rock in intertidal pools and to depths of 48 m in southern Australia. At Rottnest I., W. Aust., dense populations dominate the flora of many subtidal vertical rock faces, and often tetrasporangial and gametangial thalli occur intermixed, although male thalli are far less common than either female-carposporangial or tetrasporangial thalli.

Genus **MASTOPHORA** Decaisne 1842a: 365

Thallus encrusting to layered, foliose or ribbon like, epigenous and partially or completely affixed by cell adhesion or rhizoids, or growing unattached and free living; genicula absent. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, consisting of two distinct groups of filaments/cells: a unistratose ventral layer in which each filament is composed of palisade cells, and secondly epithallial cells or occasionally filaments 2–3 (-5) cells long terminating in epithallial cells arising dorsally and more or less perpendicularly from cells of the unistratose palisade layer; cell elongation characteristics uncertain; cells of adjacent filaments joined by cell-fusions,

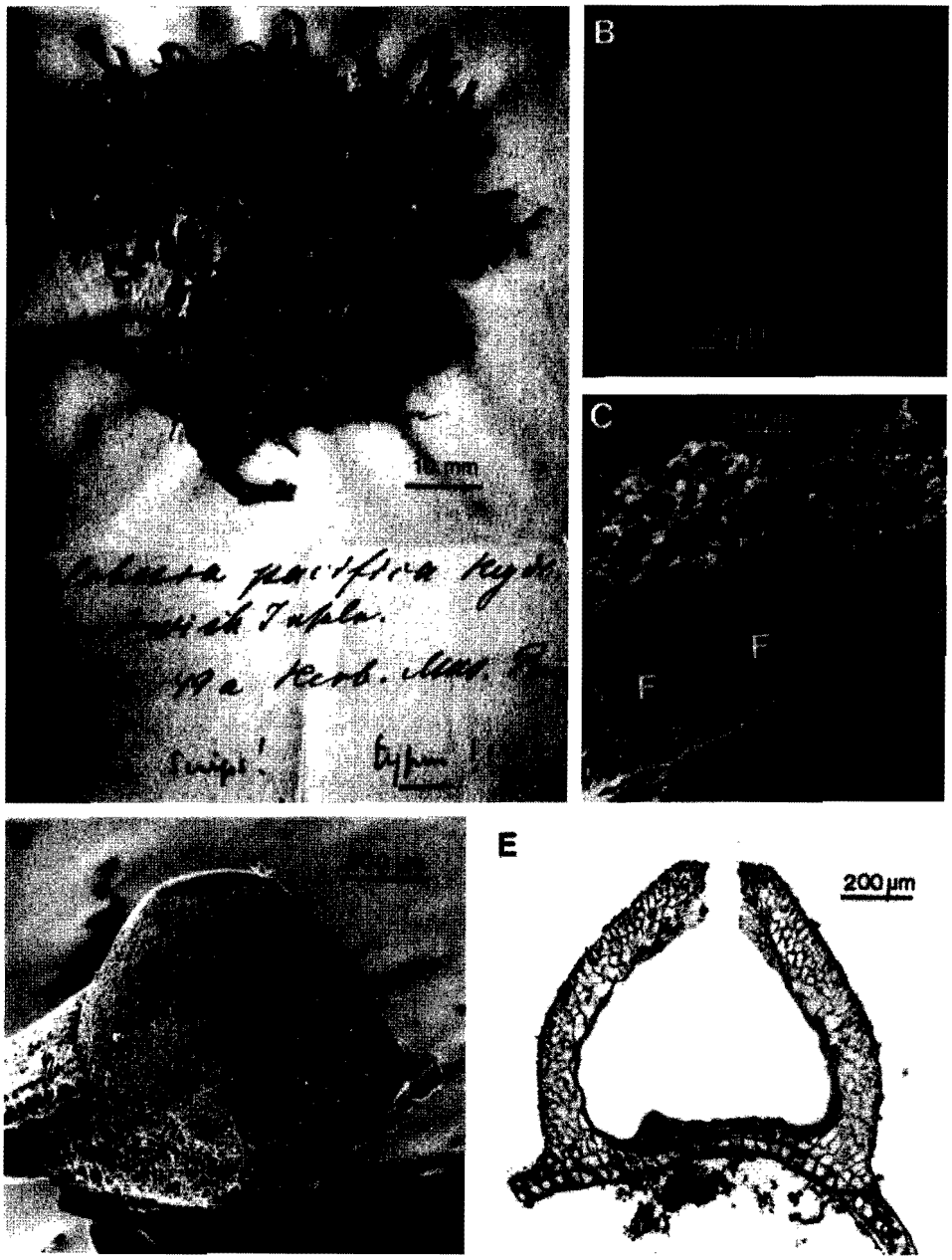


Fig. 111. *Mastophora pacifica* (**A–E,** Holotype, PC, Heydrich 49a, General Herbarium box collection). **A.** Holotype collection, consisting of *Gelidium*-like host material with fragments of *M. pacifica*. **B.** Longitudinal fracture of holotype showing palisade cells along a vegetative filament. **C.** Transverse fracture of holotype showing fusions (F) between palisade cells of contiguous filaments and epithallial cells (arrows). **D.** Surface view of an intact conceptacle. **E.** Section of a mature conceptacle devoid of contents but possibly once tetrasporangial. Remnants of a presumed columella occur on the conceptacle floor.

secondary pit-connections absent; epithallial cells with distal walls rounded or flattened but not flared; haustoria unknown; trichocytes sometimes present, occurring singly or in horizontal rows or fields and occasionally dividing transversely or obliquely to form two cells.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia, carposporangia and tetrasporangia borne in uniporate conceptacles, gametangia and carposporangia formed on separate thalli from tetrasporangia, conceptacles borne only on dorsal surfaces. Bisporangia unknown.

Gametangial thalli apparently dioecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Carposporophytes arising within female conceptacles after karyogamy, composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, produced on the floor of male conceptacle chambers.

Tetrasporangia formed peripheral to a central columella, roofs formed only by filaments peripheral to sporangial initials, each mature sporangium lacking an apical plug and containing four zonately arranged tetraspores.

Type species: *M. licheniformis* Decaisne 1842a: 359, 365.

At least 35 species and infraspecific taxa have been ascribed to *Mastophora* (Woelkerling 1988, p. 133). Setchell (1943), however, included only three species in a review of the genus. Species concepts require clarification in a modern context, and thus the number of true species is presently uncertain. Details relating to generic etymology, nomenclature, synonymy infrageneric classification, *etc.* are provided by Woelkerling (1988, pp. 129–133). The type species, *M. licheniformis*, a heterotypic synonym of *M. rosea* (C. Agardh)Setchell, has been studied by Turner & Woelkerling (1982a, 1982b). *Mastophora* is represented in southern Australia by one species, *M. pacifica* (Heydrich)Foslie, the most recent study of which was undertaken by Verheij (1993b, 1994).

Mastophora pacifica (Heydrich)Foslie 1901b: 19. Verheij 1993b: 50, figs 39–41; 1994: 110, figs 39–41; Woelkerling 1988: figs 120, 122–124.

Melobesia pacifica Heydrich 1901: 529. De Toni 1905: 1771. Woelkerling 1993: 167.

Lithoporella pacifica (Heydrich)Foslie 1909: 59. Dawson 1954: 428, fig. 40b. Gordon *et al.* 1976: 259, pl. IV fig. 6, pl. V figs 2–5. Lemoine 1976: 779. Pham Hoang Ho 1969: 155, fig. 2.82. Tseng 1983: 80, pl. 43 fig. 1.

FIGS 111–113

Thallus normally pinkish, encrusting to layered or foliose, mostly 15–70 mm across, epigenous and affixed by local cell adhesion or by unicellular rhizoids; lamellate branches applanate and inconspicuous. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, consisting of a single ventral layer of branched, laterally cohering, filaments each usually composed of palisade cells 16–32 µm long and 48–80 µm high, and additionally of epithallial cells or occasionally of small groups of filaments terminating in epithallial cells and arising dorsally and more or less perpendicularly from cells of the unistratose palisade layer, cells 8–27 µm in diameter and 27–50 µm long; epithallial cells 5–11 µm in diameter and 16–30 µm long with distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell fusions, secondary pit-connections and haustoria unknown; trichocytes sometimes present, occurring singly or in horizontal rows or fields and occasionally dividing transversely or obliquely to form two cells.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia and tetrasporangia produced in uniporate conceptacles, gametangia and carposporangia formed on thalli separate to those bearing tetrasporangia, conceptacles borne only on dorsal thallus surfaces. Bisporangia unknown.

Gametangial thalli dioecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above surrounding thallus surface, 80–110 µm thick, composed of 2–4 layers of cells above the chamber, conceptacle chambers 555–1330 µm in diameter and

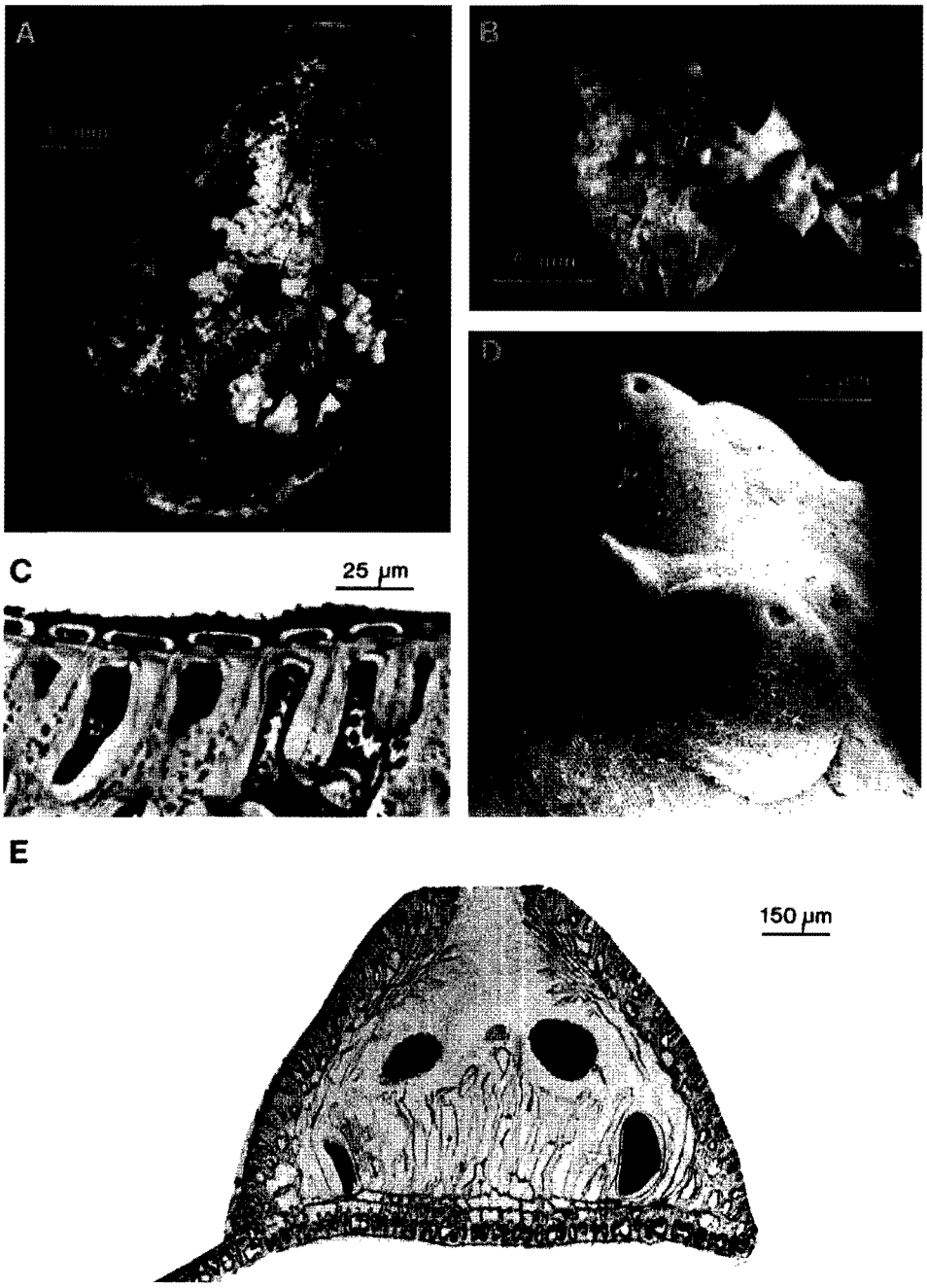


Fig. 112. *Mastophora pacifica* (**A, C,** LTB, 14288; **B,** LTB, 10948; **D, E,** LTB, 11053). **A.** Encrusting plants on a sponge. **B.** Encrusting plants on *Eucheuma*. **C.** Section of vegetative thallus showing a unistratose ventral layer of palisade cells each bearing a unicellular filament (epithallial cell) dorsally. **D.** Surface view of tetrasporangial conceptacles. **E.** Section of mature tetrasporangial conceptacle. Note conspicuous, central columella arising from the conceptacle chamber floor.

300–520 μm high. Carposporophytes developing within female conceptacles after karyogamy, composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia 95–215 μm in diameter. Spermatangial filaments unbranched, borne across the male conceptacle chamber floor, mature male conceptacle roofs protruding above surrounding thallus surface, 190–280 μm thick, composed of 5–9 layers of cells above the chamber; male conceptacle chambers 24–375 μm in diameter and 80–125 μm high.

Tetrasporangial conceptacle roofs protruding above surrounding surface, 95–190 μm thick above the chamber and composed of (2-) 4–8 layers of cells, pore canals lined by cells that are orientated more or less parallel to the roof surface and protrude slightly into the canal, conceptacle chambers 630–835 μm in diameter and 555–630 μm high; tetrasporangia peripheral to a central columella, each sporangium 130–210 μm in diameter and 220–300 μm long, containing four zonately arranged tetraspores.

Type from the Hawaiian Islands; holotype in PC (Heydrich 49a, General Herbarium box collection); depicted in this account, Fig. 110; additional data provided by Woelkerling (1993: 167).

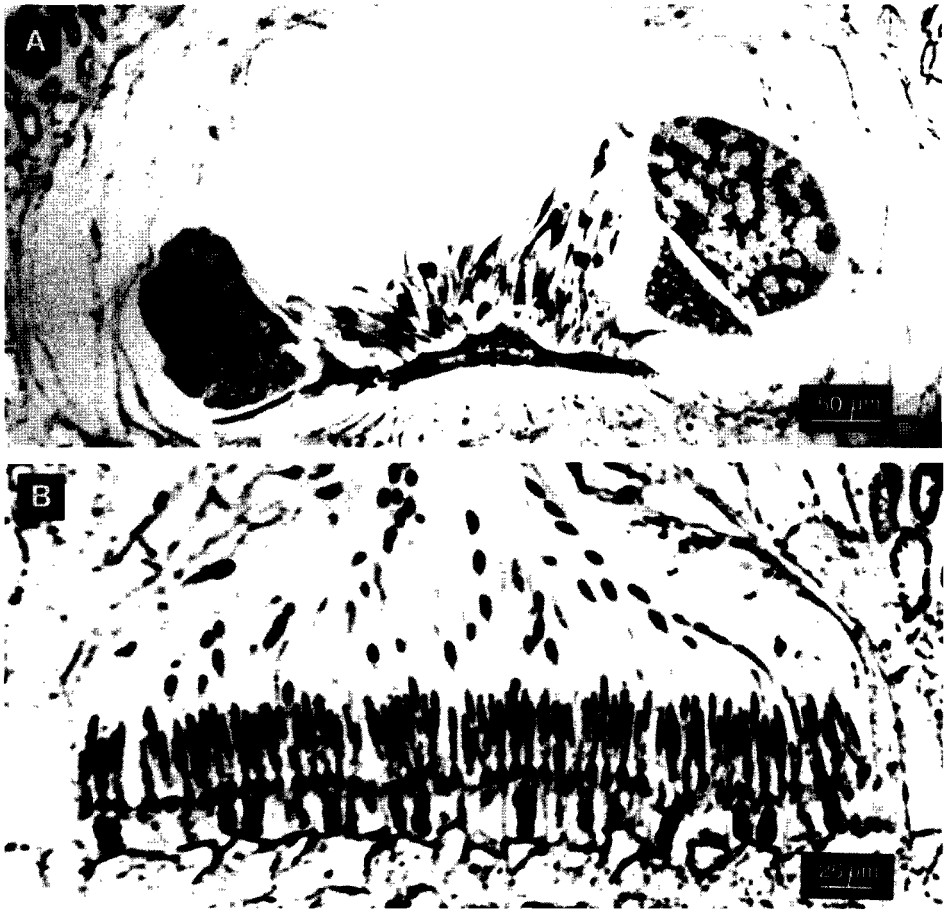


Fig. 113. *Mastophora pacifica* (**A, B,** LTB, 11053). **A.** Section of part of a female-carposporangial conceptacle with mature carposporophyte; F = fusion cell; g = gonimoblast filament; C = carposporangium. **B.** Section of part of a male conceptacle with unbranched spermatangial filaments arising from chamber floor.

Distribution: China (Tseng 1983: 80); Vietnam (Dawson 1954; Pham Hoang Ho 1969); Indonesia (Verheij 1993b, 1994); Guam (Gordon *et al.* 1976); Hawaiian Islands (Heydrich 1901).

In Australia, North Point Reef, Rottnest I., W. Aust., to Rye, Vic.

Known specimens: North Point Reef, Rottnest I., W. Aust., 1–2 m deep (*Woelkerling*, 10.ii.1978; LTB, 11053, 11057). Jeannie's Lookout, Rottnest I., W. Aust., 1–3 m deep (*Woelkerling*, 11.ii.1978; LTB, 10922, 10930 and 12.ii.1978; LTB, 10948, 10939, 10944). Lucky Bay, Cape Le Grand National Park, W. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 9.ii.1984; LTB, 14288). Rye (Number Sixteen reef), Vic., upper sublittoral (*Woelkerling*, 6.i.1978; LTB, 12495).

Mastophora pacifica has been found in southern Australia only on a dead abalone shell in a tide pool in Victoria and on a sponge growing at 2–3m deep in Western Australia. Specimens from Rottnest I. are epiphytic on fleshy red algae, while the type (Fig. 110), not previously studied in detail in a modern context, occurs on a *Gelidium*-like alga from the Hawaiian Islands. Dawson (1954, p. 428) and Gordon *et al.* (1976, p. 259) recorded specimens growing under corals at depths of 2–7 m.

Genus **LITHOPORELLA** Foslie 1909: 58

Thallus encrusting to layered or foliose, epigenous and partially or completely affixed by cell adhesion or envelopment of host axes; genicula absent. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, consisting of two distinct groups of filaments: a unistratose ventral layer in which each filament is composed of palisade cells, and secondly epithallial cells or occasionally filaments 2–3 (-5) cells long terminating in epithallial cells and arising dorsally and more or less perpendicularly from cells of the unistratose palisade layer; cell elongation characteristics uncertain; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; epithallial cells with distal walls rounded or flattened but not flared; haustoria unknown; trichocytes sometimes present, occurring singly or in horizontal rows or fields and occasionally dividing transversely or obliquely to form two cells.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia, carposporangia and tetrasporangia borne in uniporate conceptacles, gametangia and carposporangia formed on separate thalli from tetrasporangia, conceptacles borne only on dorsal surface of branches. Bisporangia unknown.

Gametangial thalli dioecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Carposporophytes arising within female conceptacles after karyogamy, composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, produced on the floor of male conceptacle chambers.

Tetrasporangia scattered across the conceptacle chamber floor, roofs formed by filaments peripheral to and interspersed amongst sporangial initials, each mature sporangium lacking an apical plug and containing four zonately arranged tetraspores.

Type species: *L. melobesioides* (Foslie)Foslie 1909: 59.

At least 21 species and infraspecific taxa have been referred to *Lithoporella*, including at least 10 fossil species, but a world monograph has not been produced and species concepts are uncertain (Woelkerling 1988, p. 128). Details relating to generic etymology, nomenclature, synonymy, infrageneric classification, *etc.* are provided by Woelkerling (1988, pp. 124–128). The only species known from southern Australia is the type species, *L. melobesioides*; Turner & Woelkerling (1982a, 1982b) provided morphological-anatomical data on southern Australian populations, and this forms the basis for the present taxonomic account.

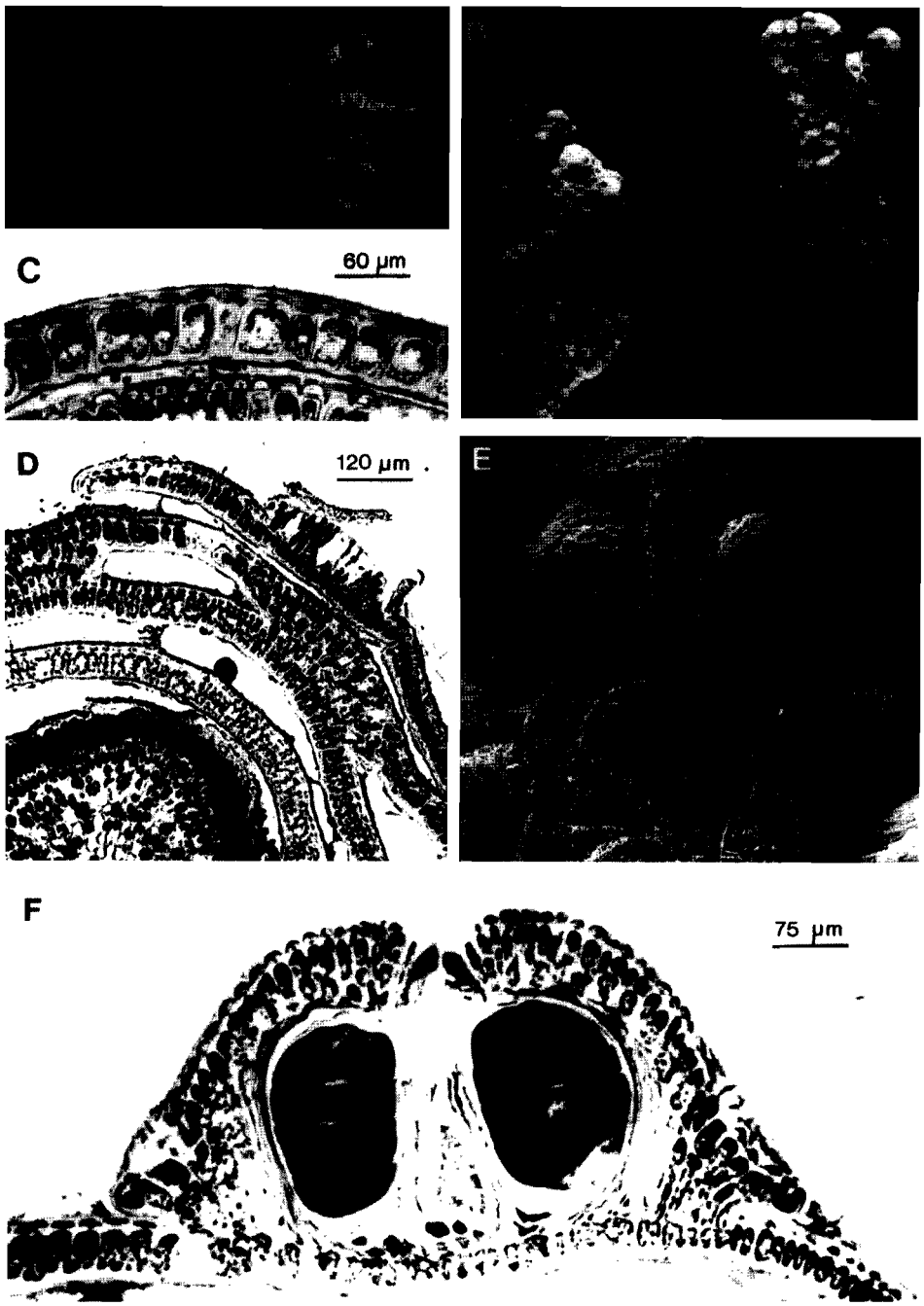


Fig. 114. *Lithoporella melobesioides* (**A,** LTB, 15587; **B,** LTB, 11526; **C, E, F,** LTB, 11466; **D,** LTB, 11811). **A, B.** Inconspicuously layered thalli growing on the brown alga *Xiphophora.* Note how host branch tips become enveloped (A). **C.** Section of thallus showing palisade cells and epithallial cells. **D.** Section of thallus showing layered, applanate branching. **E.** Surface view of thallus showing layered branching. **F.** Section of mature tetrasporangial conceptacle.

Lithoporella melobesioides (Foslie)Foslie 1909: 59. Adey *et al.* 1982: 34, fig. 20. Gordon *et al.* 1976: 257, pl. IV figs 4, 5, pl. V fig. 1. John *et al.* 1994: 66. Lemoine 1970a: 2645, pl. 1 figs 1–5; 1974: 32, pls 4–6; 1976: 773, pls 1, 2. Masaki 1968: 55, pl. 38, pl. 79 figs 1–5. Nelson & Adams 1984: 18. Tseng 1983: 78, pl. 42 fig. 4. Turner & Woelkerling 1982a: 204, figs 2–4, 9, 10, 12, 13, 16–25, 29, 30, 36; 1982b: 219, figs 2, 4, 6–11, 15–17, 20–22, 25–27. Womersley & Bailey 1970: 310. Zhang & Zhou 1980: 72, pl. II figs 1–3.

Mastophora melobesioides Foslie 1903a: 24; 1904a: 74, figs 30–32. Woelkerling 1993: 148.

Melobesia melobesioides (Foslie)Lemoine 1927: 196; 1939: 108, fig. 79.

Litholepis melobesioides (Foslie)Weber-van Bosse 1932: 21.

FIGS 114, 115

Thallus normally pinkish, encrusting to foliose, mostly 4–15 mm across, epigenous and affixed by localised cell adhesion or envelopment of host axes; lamellate branches common, applanate and often forming a number of layers that may or may not be conspicuous. *Structure* pseudoparenchymatous with dorsiventral organisation throughout; construction dimerous, each branch consisting of a single ventral layer of branched, laterally cohering, filaments each usually composed of palisade cells 10–35 (-69) µm long and 25–70 µm high, and additionally of epithallial cells or in areas of branching filaments 2–3(-5) cells long terminating in epithallial cells and arising perpendicularly from cells of the ventral filaments, cells 10–35 µm in diameter and 14–60 (-80) µm long; epithallial cells (5-) 10–38 µm in diameter and 5–20 µm long with distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell fusions, secondary pit-connections and haustoria unknown; trichocytes sometimes present, occurring singly or in horizontal rows or fields and occasionally dividing transversely or obliquely to form two cells.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia and tetrasporangia produced in uniporate conceptacles, gametangia and carposporangia formed on thalli separate to those bearing tetrasporangia, conceptacles borne only on dorsal thallus surfaces. Bisporangia unknown.

Gametangial thalli dioecious. Carpogonia terminating 2- or 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above surrounding thallus surface, 50–120 µm thick, composed of 2–4 layers of cells above the chamber, conceptacle chambers 230–555 µm in diameter and 80–300 µm high. Carposporophytes developing within female conceptacles after karyogamy, composed of a conspicuous central fusion cell and several-celled gonimoblast filaments bearing terminal carposporangia 65–150 µm in diameter. Spermatangial filaments unbranched, borne across the male conceptacle chamber floor, mature male conceptacle roofs protruding above surrounding thallus surface, 100–235 µm thick, composed of 3–7 layers of cells above the chamber, male conceptacle chambers 210–315 µm in diameter and 60–90 (-125) µm high.

Tetrasporangial conceptacle roofs protruding above surrounding surface, 70–95 µm thick above the chamber and composed of 2–4 layers of cells, pore canals lined by cells that are orientated more or less perpendicularly to the roof surface and do not protrude into the canal, conceptacle chambers (225-) 260–445 µm in diameter and (160-) 210–270 µm high; tetrasporangia scattered across the conceptacle chamber floor, each mature sporangium 50–90 (-110) µm in diameter and 120–220 µm long, containing zonately arranged spores.

Type from South Nilandu, Maldive Islands; lectotype in TRH (unnumbered), designated by Foslie (1904a: 74), depicted in Foslie (1904a, text figs 30a, 31a), Printz (1929: pl. 73 fig. 1), Turner & Woelkerling (1982a: fig. 2); additional data provided by Woelkerling (1993: 148).

Distribution: Reported from various islands in the tropical Atlantic, Indian and Pacific Oceans (Adey *et al.* 1982; John *et al* 1994; Masaki 1968; Womersley & Bailey 1970) and from the Red Sea; China; Japan and the Kermadec Is (New Zealand); most records require confirmation. In southern Australia, South West River, Hansen Bay, Kangaroo I., S. Aust., to Bear Gully (Maitland Beach), Vic., and Curries River, Tasmania.

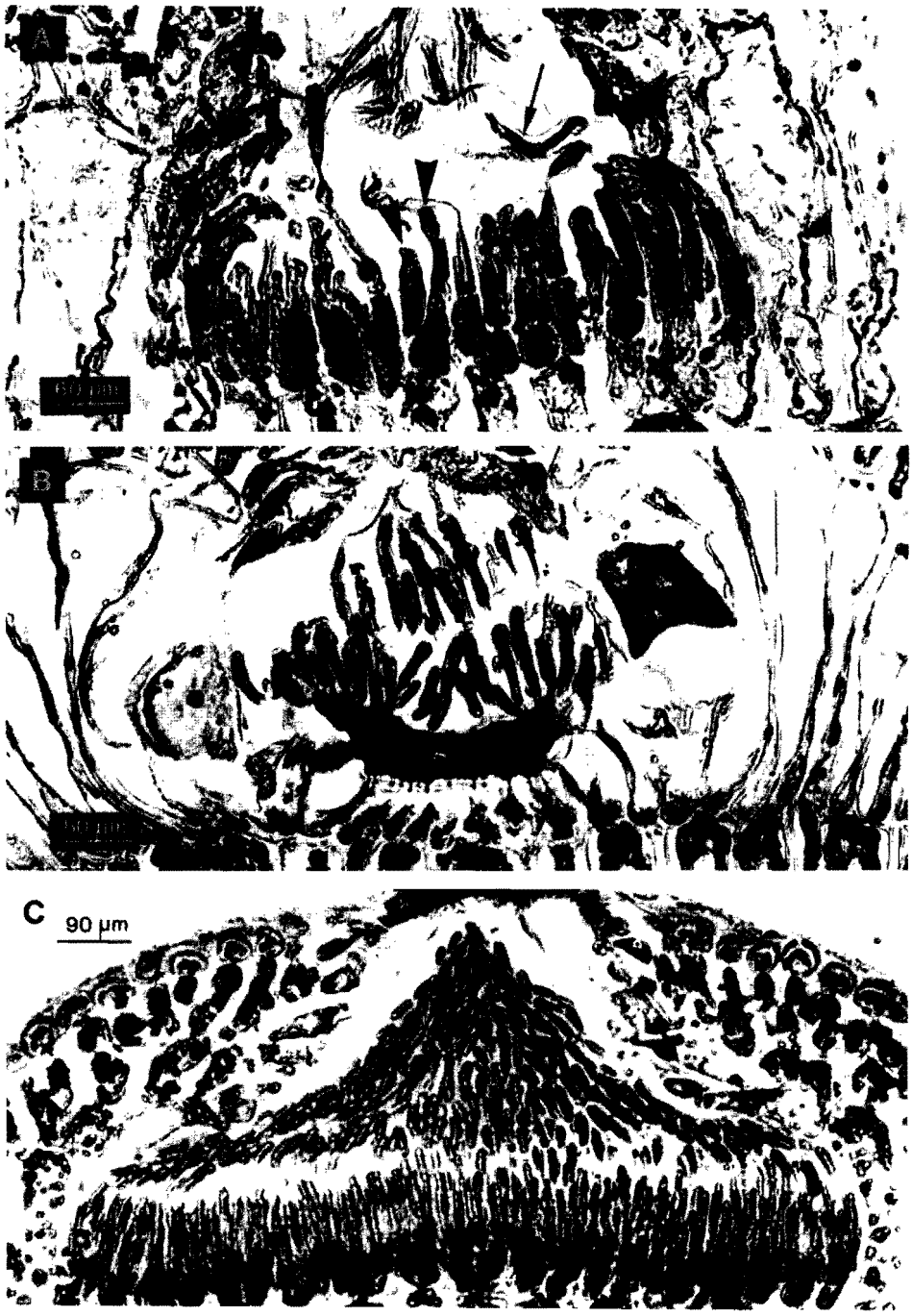


Fig. 115. *Lithoporella melobesioides* (**A–C**, LTB, 11811). **A.** Section of part of a female-carposporangial conceptacle with mature carpogonial filaments with carpogonia with (arrows) and without (arrowheads) trichogynes. **B.** Section of part of a female-carposporangial conceptacle with mature carposporophyte. **C.** Section of male conceptacle with unbranched spermatangial filaments arising from chamber floor.

Selected specimens: South West River, Hansen Bay, Kangaroo I., S. Aust., upper sublittoral (*Woelkerling*, 21.ii.1979; LTB, 11631). Seal Bay, Kangaroo I., S. Aust., upper sublittoral (*Woelkerling*, 22.ii.1979; LTB, 11787). Cape Willoughby, Kangaroo I., S. Aust., on *Xiphophora*, sublittoral fringe (*Womersley*, 25.i.1948; AD, A48115 = LTB, 13753; *Woelkerling*, 25.ii.1979; LTB, 11565) and 0–2 m deep (*Campbell & Penrose*, 6.iv.1988; LTB, 15587). Kitty Miller Bay, Phillip I., Vic., 1–2 m deep (*Woelkerling*, 18.vi.1983; LTB, 13579) and in lower eulittoral tidepools on *Xiphophora* (*Turner*, 24.i.1979; LTB, 11466). Cunningham Bay, Phillip I., Vic., in pools (*Turner*, 15.vi.1979; LTB, 11788 and 29.vii.1979; LTB, 11811). Bear Gully (Maitland Beach), Vic., upper sublittoral (*Turner*, 24.xii.1978; LTB, 11526 and 30.v.1979; LTB, 11786). Curries River mouth, Tas., lower eulittoral pools (*Womersley*, 28.i.1949; AD, A10315 = LTB, 13752).

Lithoporella melobesioides has been found in southern Australia as an epiphyte on the brown alga *Xiphophora chondrophylla* and on the geniculate coralline algae *Corallina* and *Jania* in intertidal tide pools and subtidally at depths of 0.5–2 m. Both gametangial and tetrasporangial thalli occur within single populations. Adey *et al.* (1982, p. 35) reported the species from the intertidal to depths of 85m in the Hawaiian Is. The type collection (Woelkerling 1993, p. 148) from the Maldive Is and specimens from the Solomon Is (Womersley & Bailey 1970) occur on coral rubble, while Foslie (1904a, p. 73) records collections on a variety of other substrata. Lemoine (1976) provides an account of a number of fossil collections.

Genus **HYDROLITHON** (Foslie)Foslie 1909: 55

by D.L. Penrose

Goniolithon Foslie (1900b) subg. *Hydrolithon* Foslie 1905: 7.

Thallus encrusting, warty or lumpy, epilithic, epiphytic or epizoic and affixed by cell adhesion, or unattached and free-living as rhodoliths; genicula absent. *Structure* pseudoparenchymatous; organisation dorsiventral; construction dimerous or monomerous, dimerous portions consisting of a single ventral layer of branched filaments composed of non-palisade cells, and unicellular or multicellular simple or branched filaments that arise more or less perpendicularly from cells of ventral layer filaments, monomerous portions consisting of a single system of branched filaments that collectively contribute to a ventrally or centrally situated core, and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; epithallial cells terminating filaments at the thallus surface, distal walls rounded or flattened but not flared; trichocytes present or absent, if present appearing, in section, arranged in horizontal fields, horizontal rows, vertical rows, or occurring singly at the thallus surface, sometimes becoming buried within the thallus.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia, carposporangia, tetrasporangia and bisporangia borne in uniporate conceptacles; gametangia and carposporangia usually formed on separate plants from tetrasporangia and bisporangia.

Gametangial plants monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Carposporophytes developing within female conceptacles after karyogamy, composed of a large central fusion cell and gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, formed on the chamber floor.

Tetrasporangia and bisporangia formed across the chamber floor or peripheral to a central columella, conceptacle roofs formed by filaments surrounding and interspersed amongst sporangial initials, each mature sporangium lacking an apical plug, usually regularly zonately divided.

Type species: Hydrolithon reinboldii (W.-van Bosse & Foslie)Foslie 1909: 55.

Hydrolithon includes six species on southern Australian coasts. The following account is based mainly on data in Penrose (1990, 1992a) and Penrose & Chamberlain (1993).

KEY TO SPECIES OF *HYDROLITHON*

1. Tetrasporangial conceptacles usually containing a single sporangium lying horizontally within the chamber (occasionally containing two upright sporangia); carposporangial conceptacles containing a single carposporangium in the chamber, pore canals formed obliquely to the surrounding thallus surface ..... 1. *H. cymodoceae*
1. Tetrasporangial conceptacles containing two or more upright sporangia within the chamber, carposporangial conceptacles containing more than one carposporangium peripherally in the chamber, pore canals formed perpendicularly to the surrounding thallus surface..... 2

    2. Thallus commonly composed of a number of applanate branches that overgrow one another and are attached to one another by cell adhesion and rhizoids ..... 2. *H. improcerum*
    2. Thallus rarely with applanate branches that overgrow one another and are attached to one another by cell adhesion and rhizoids..... 3

3. Thallus epiphytic, 2–5 cells high when reproductively mature ..... 3. *H. farinosum*
3. Thallus epilithic or epizoic, >10 cells high when reproductively mature..... 4

    4. Thallus commonly with horizontal rows of trichocytes occurring at the surface and buried within the thallus..... 4. *H. onkodes*
    4. Thallus occasionally with horizontal rows of trichocytes at the surface, lacking such rows buried within the thallus 5

5. Tetrasporangial conceptacles usually containing sporangia across the chamber floor and lacking a central columella, chambers usually >150 μm in diameter..... 5. *H. munitum*
5. Tetrasporangial conceptacles usually containing sporangia peripherally in the chamber and lacking a central columella, chambers usually <110 μm in diameter ..... 6. *H. rupestris*

1. **Hydrolithon cymodoceae** (Foslie)Penrose 1992a: 89, figs 1–30.
    Melobesia cymodoceae Foslie 1901: 23. Wilks & Woelkerling 1991: 528.
    Heteroderma cymodoceae (Foslie)Adey 1970: 16.
    Fosliella cymodoceae (Foslie)Jones & Woelkerling 1984: 184, figs 3, 6–13.

FIG. 116

Thallus encrusting, up to 1 mm thick, epiphytic and affixed by cell adhesion. *Structure* pseudoparenchymatous; organisation dorsiventral; construction dimerous or monomerous, dimerous portions consisting of a single ventral layer of branched filaments composed of non-palisade cells, and unicellular or multicellular simple or branched filaments that arise more or less perpendicularly from cells of ventral layer filaments, monomerous portions consisting of a single system of branched filaments that collectively contribute to a ventrally or centrally situated core, and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 5–20 μm in diameter and 5–30 μm long; epithallial cells terminating filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes occurring commonly in horizontal rows and singly at thallus surface, not becoming buried within thallus.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia, tetrasporangia and bisporangia produced in uniporate conceptacles.

Gametangial plants monoecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above or flush with surrounding thallus surface, composed of 2–4 cells above the chamber, pores orientated obliquely to surrounding thallus surface; conceptacle chambers 90–150 μm in diameter and 65–150 μm high. Carposporophytes developing within older female conceptacles after karyogamy, when mature composed of a large central fusion cell and gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, arising from the floor of male conceptacle chambers, mature male conceptacle roofs protruding above or flush with

surrounding thallus surface, conceptacle chambers 90–105 μm in diameter and 50–85 μm high.

Tetrasporangial and bisporangial conceptacle roofs protruding above or flush with surrounding thallus surface, 2–4 cells thick above the chamber, pore canals lined with non-protruding cells, conceptacle chambers 30–260 μm in diameter and 80–160 μm high; a single sporangium usually formed in the conceptacle chamber, sometimes 2 sporangia formed across the conceptacle chamber floor, each mature sporangium 45–135 μm in diameter and 80–185 μm long, usually zonately divided, sometimes irregularly divided.

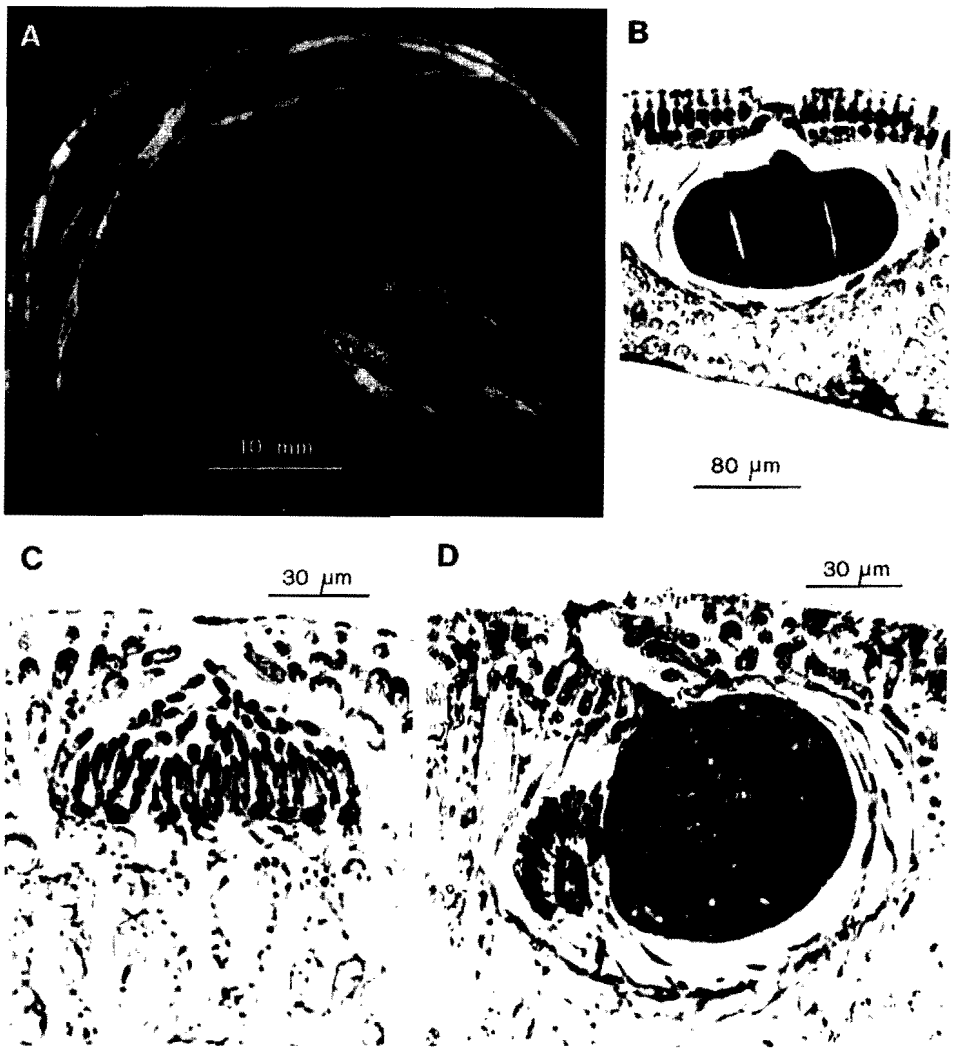


Fig. 116. *Hydrolithon cymodoceae* (**A**, LTB, 14489; **B**, LTB, 14254; **C**, LTB, 14388; **D**, LTB, 13893). **A**. Plants epiphytic on leaves and stems of the seagrass *Amphibolis antarctica*. **B**. Section of tetrasporangial conceptacle with a single sporangium lying horizontally in the chamber and distinctive cells lining the pore canal. **C**. Section of spermatangial conceptacle with initials formed across the chamber floor bearing spermatangia. **D**. Section of carposporangial conceptacle with a more or less ovoid fusion cell, a large carposporangium and a pore canal that is orientated obliquely to the thallus surface.

Type from Port Phillip Bay, Vic. (*F. v. Mueller*, 1862); lectotype in TRH (unnumbered), designated by Adey & Lebednik (1967: 32); illustrated by Penrose (1992a, figs 1,2).

Distribution: Shark Bay, W. Aust. (Harlin *et al.* 1985; Penrose 1992a) to Walkerville, Vic.

Selected specimens: Observatory Point, Esperance, W. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 5.ii.1984; LTB, 14152). Dempster Point, Israelite Bay, W. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 8.ii.1984; LTB 14254). 7 km E of Twilight Cove, Eyre, W. Aust., 0–3 m deep (*Woelkerling, Platt & Jones*, 2.ii. 1984; LTB, 14067). Point Fowler (E shore), S. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 14.ii.1984; LTB, 14388). Point Sinclair, S. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 15.ii.1984; LTB, 14489). Vivonne Bay, Kangaroo I., S. Aust., upper sublittoral (*Woelkerling*, 23.ii.1979; LTB, 11646, 11648). Apollo Bay, Vic., upper subtidal (*Bramwell*, 30.xii.1981; LTB, 14658). Torquay, Vic. (*Bramwell*, 14.i.1982; LTB, 15266). Flinders, Vic., intertidal pools (*Woelkerling*, 19.xi.1983; LTB, 13893). Rye, Vic., intertidal pools (*Kay*, 10.viii.1978; LTB, 11104). Kitty Miller Bay, Phillip I., Vic., upper subtidal (*Woelkerling, Campbell & Penrose*, 2.xii.1985; LTB, 15231). Walkerville North, Vic. (*Woelkerling*, 26.xi.1976; LTB, 11195).

H. cymodoceae occurs commonly in southern Australia and is found predominantly growing on the leaves and stems of the seagrass, *Amphibolis antarctica* (Penrose 1992a). The species is readily distinguished from others by the presence of a single tetrasporangium within the conceptacle chamber. Additional information on the species has been provided by Penrose (1990, 1992a).

2. **Hydrolithon improcerum** (Foslie & Howe *in* Foslie)Foslie 1909: 55.
Goniolithon improcerum Foslie & Howe *in* Foslie 1907b: 24. Townsend & Adey 1990: 99, figs 1–41.
Porolithon improcerum (Foslie & Howe *in* Foslie)Howe 1920: 587.

FIG. 117

Thallus encrusting, composed of a number of applanate branches that overgrow one another and that are attached to each other by cell adhesion and sometimes by rhizoids; epiphytic, epilithic or epizoic and affixed by cell adhesion. *Structure* pseudoparenchymatous; organisation dorsiventral; construction dimerous, consisting of a single ventral layer of branched filaments composed of non-palisade cells, and unicellular filaments that arise more or less perpendicularly from cells of ventral layer filaments, each filament composed of cells 5–22 µm in diameter and 5–35 µm long; epithallial cells terminating filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes occurring commonly in horizontal rows and singly at thallus surface, not becoming buried within thallus.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia, tetrasporangia and bisporangia produced in uniporate conceptacles.

Gametangial plants monoecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above or flush with surrounding thallus surface, composed of 2–4 cells above the chamber, conceptacle chambers 110–125 µm in diameter and 95–130 µm high. Carposporophytes developing within older female conceptacles after karyogamy, when mature composed of a large central fusion cell and gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, arising from the floor of male conceptacle chambers, mature male conceptacle roofs protruding above or flush with surrounding thallus surface, conceptacle chambers 58–88 µm in diameter and 42–64 µm high.

Tetrasporangial and bisporangial conceptacle roofs protruding above or flush with surrounding thallus surface, 2–4 cells thick above the chamber, pore canals lined with non-protruding cells, conceptacle chambers 98–145 µm in diameter and 86–110 µm high; tetrasporangia and bisporangia peripheral to a central columella, each mature sporangium zonately divided.

Type from Montego Bay, Jamaica; (*Howe*, 5.i.1907); holotype in TRH (Howe no. 4760b); illustrated by Townsend & Adey (1990).

Distribution: Bahamas; Caribbean; Jamaica.

In southern Australia, known from Kangaroo I. and Beachport, S. Aust. growing on *Botryocladia*, *Cladostephus*, *Caulocystis* sp., and *Dictyota* sp., and from Norfolk Point, Tasman Pen., Tasmania growing on rock.

Selected specimens: Point Tinline, Kangaroo I., S. Aust., drift (*Campbell & Penrose*, 10.iv.1988; LTB, 15745). Point Tinline, Kangaroo I., S. Aust., drift (*Campbell & Penrose*, 10.iv.1988; LTB, 15736). Seal Bay, Kangaroo I., S. Aust., 0–0.5 m deep (*Campbell & Penrose*, 8.iv.1988; LTB, 15701). Schnapper Point, Beachport, S. Aust., 1–3 m deep (*Campbell, Penrose & Woelkerling*, 26.ii.1988; LTB, 15864). Beachport, S. Aust., drift (*Campbell & Penrose*, 26.ii.1988; LTB, 15768). Norfolk Point, Tasman Pen., Tas., 0–2 m deep (*Platt & Woelkerling*, 27.ii.1983; LTB, 13322, 13343).

H. improcerum appears to be closely related to *Lithoporella melobesiodes* and further studies are needed to evaluate this.

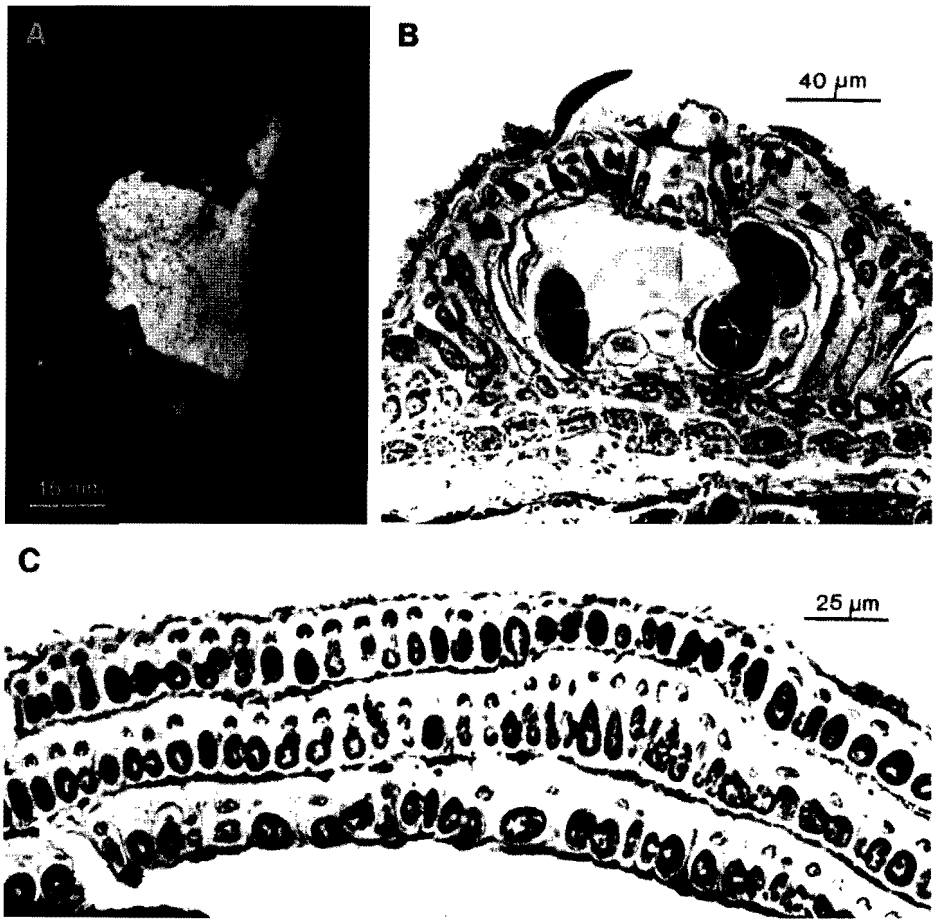


Fig. 117. *Hydrolithon improcerum* (**A**, LTB, 13343; **B, C**, LTB, 15701). **A**. Plants growing on rock. **B**. Section of conceptacle containing bisporangia peripherally in the chamber. **C**. Section of thallus showing applanate branches overgrowing one another.

3. **Hydrolithon farinosum** (Lamouroux)Penrose & Chamberlain 1993: 295. Chamberlain 1994b: 123, figs 3A, 54, 55.
Melobesia farinosa Lamouroux 1816: 315. Wilks &Woelkerling 1991: 528.
Fosliella farinosa (Lamouroux)Howe 1920: 587. Gordon *et al.* 1976: 255. Chamberlain 1983: 343.
Fosliella cruciata Bressan *et al.* 1977: 27. Jones & Woelkerling 1983: 449, figs 1, 2.

FIG. 118

Thallus encrusting, epiphytic and affixed by cell adhesion. *Structure* pseudoparenchymatous; organisation dorsiventral; construction dimerous, consisting of a single ventral layer of branched filaments composed of non-palisade cells, and unicellular or multicellular simple or branched filaments that arise more or less perpendicularly from cells of ventral layer filaments, each filament composed of cells 5–20 μm in diameter and 5–30 μm long; epithallial cells terminating most filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions,

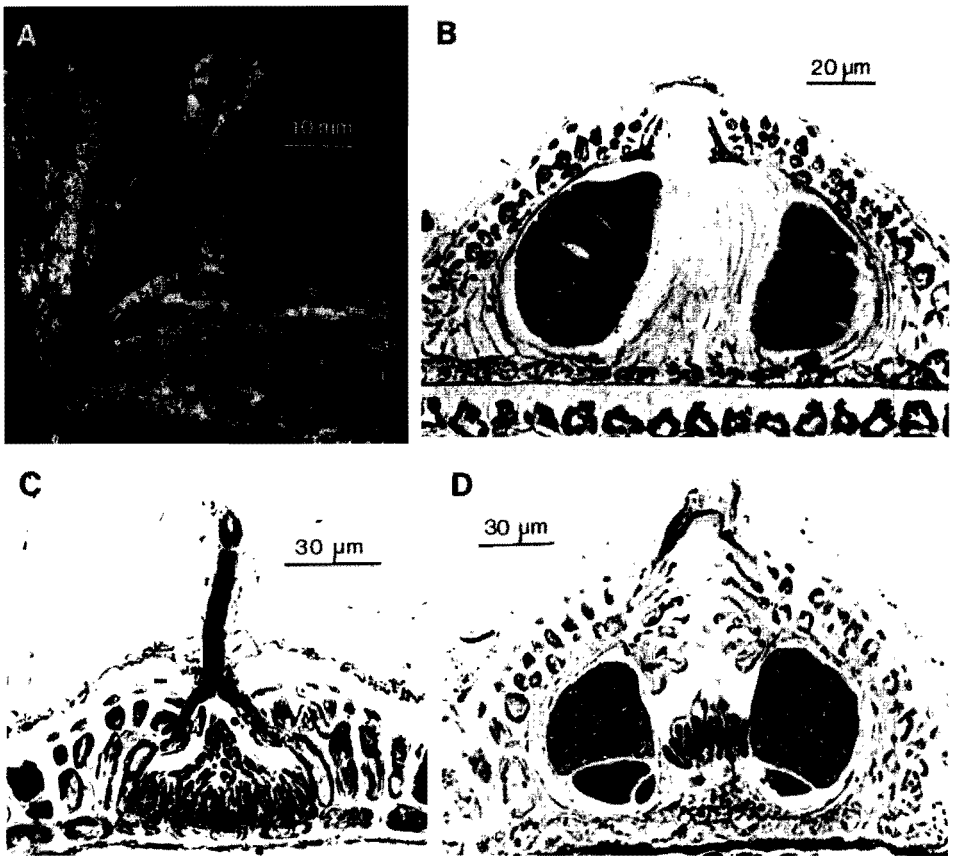


Fig. 118. *Hydrolithon farinosum* (**A, B,** LTB, 12528; **C, D,** LTB, 12700). **A.** Plants epiphytic on the seagrass *Amphibolis antarctica*. **B.** Section of tetrasporangial conceptacle containing sporangia peripherally in the chamber and a columella centrally, and with distinctive cells lining the pore canal. **C.** Section of spermatangial conceptacle with initials bearing spermatangia formed across the chamber floor and pore with an elongate spout. **D.** Section of conceptacle containing a carposporophyte with a fusion cell present in the centre of the chamber floor, gonimoblast filaments borne peripherally in the chamber at the margins of the fusion cell and bearing terminal carposporangia.

secondary pit-connections absent; trichocytes present or absent, if present, usually occurring singly at thallus surface, not becoming buried within thallus.

Reproduction. Vegetative reproduction by propagules. Gametangia, carposporangia, tetrasporangia and bisporangia produced in uniporate conceptacles.

Gametangial plants monoecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above or flush with surrounding thallus surface, composed of 2 or 3 cells above the chamber, conceptacle chambers 110–125 μm in diameter and 100–120 μm high. Carposporophytes developing within older female conceptacles after karyogamy, when mature composed of a large central fusion cell and gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, arising from the floor of male conceptacle chambers, mature male conceptacle roofs protruding above surrounding thallus surface, conceptacle chambers 60–85 μm in diameter and 40–55 μm high.

Tetrasporangial and bisporangial conceptacle roofs protruding above surrounding thallus surface, 2 or 3 cells thick above the chamber, pore canals lined with non-protruding cells, conceptacle chambers 100–140 μm in diameter and 85–105 μm high; tetrasporangia and bisporangia usually peripheral to a central columella, sometimes scattered across the conceptacle chamber floor, mature sporangia zonately divided.

Type from the Mediterranean Sea; lectotype in CN (unnumbered); accounts of the collection have been provided by Chamberlain (1983, p. 341, fig. 19) and Penrose & Chamberlain 1993, pp. 296, 297, figs 1–4).

Distribution: British Isles; France; Greece; Florida; Indonesia; Kenya; the Persian Gulf; the Red Sea; South Africa; Spain and tropical W. Aust. (see Penrose & Chamberlain 1993, p. 296).

In southern Australia, Point Westall, S. Aust. to Sorrento, Vic.

Selected specimens: Mabel Cove, Rottnest I., W. Aust., reef pools (*Woelkerling*, 9.ii.1978; LTB, 12700). Point Westall (S shore), S. Aust., intertidal (*Woelkerling*, 16.ii.1984; LTB, 14634). Brown Beach, Kangaroo I., S. Aust., drift (*Campbell & Penrose*, 6.iv.1988; LTB, 15748). Vivonne Bay, Kangaroo I., S. Aust., 0–1.5 m deep (*Campbell & Penrose*, 8.iv.1988; LTB, 15711). Sorrento (ocean beach), Vic., reef pools (*Jones*, 5.iv.1982; LTB 12528).

H. farinosum is a cosmopoliton species that is found commonly in southern Australian waters on various algae and on the seagrass *Amphibolis antarctica* (see Penrose & Chamberlain (1993). Detailed accounts of the species have been provided by Gordon *et al.* (1976) and Penrose & Chamberlain (1993). *Fosliella cruciata* is considered conspecific with *H. farinosum* (Penrose unpubl.). Further references to synonymy have been provided by Chamberlain (1983, p. 343).

4. **Hydrolithon onkodes** (Heydrich)Penrose & Woelkerling 1992a: 81, figs 4, 5. Verheij 1993b: 47, figs 31–35; 1994: 107, figs 31–35.
Lithothamnion onkodes Heydrich 1897c: 6, pl. 1 fig. 11a,b.
Goniolithon onkodes (Heydrich)Foslie 1898b: 8.
Lithophyllum onkodes (Heydrich)Heydrich 1901: 533.
Porolithon onkodes (Heydrich)Foslie 1909: 57.
Spongites onkodes (Heydrich)Penrose & Woelkerling 1988: 159, figs 10–14. Penrose 1990: 134, figs 44–49.

FIG. 119

Thallus encrusting, warty or lumpy 0.1–25 mm thick, epilithic or epizoic and affixed by cell adhesion. *Structure* pseudoparenchymatous; organisation dorsiventral; construction dimerous or monomerous, dimerous portions consisting of a single ventral layer of branched filaments composed of non-palisade cells, and multicellular simple or branched filaments that arise more or less perpendicularly from cells of ventral layer filaments, monomerous portions consisting of a single system of branched filaments that collectively contribute to a ventrally or centrally situated core, and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of

cells 5–15 μm in diameter and 5–22 μm long; 1–4 epithallial cells terminating filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes occurring commonly at thallus surface, arranged in horizontal rows, horizontal fields and singly, commonly becoming buried within thallus.

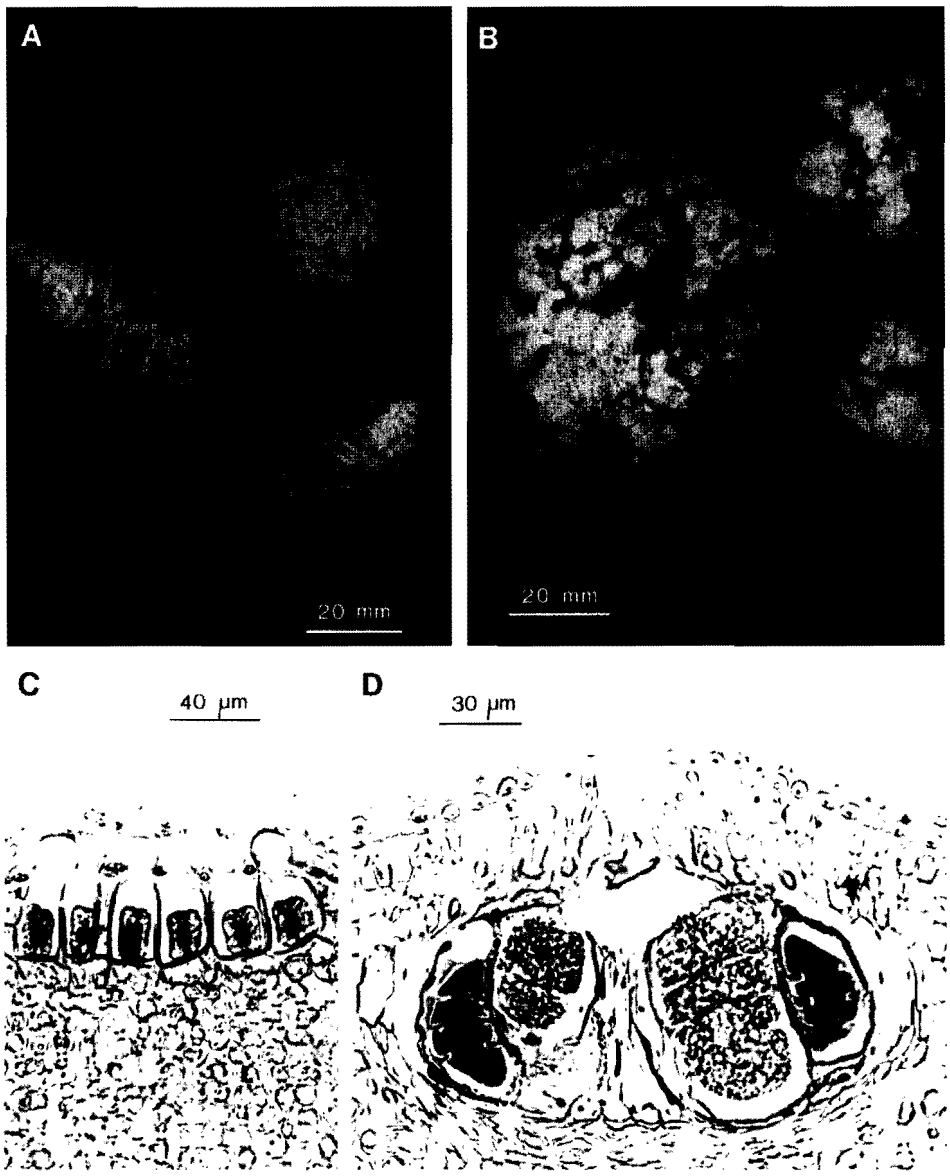


Fig. 119. *Hydrolithon onkodes* (**A**, LTB, 10617; **B**, LTB, 10722; **C**, **D**, LTB, 10647). **A**. Epizoic plants. **B**. Epilithic plants. **C**. Section of thallus showing a horizontal row of trichocytes. **D**. Section of tetrasporangial conceptacle with sporangia occurring peripherally in the chamber and a columella centrally, and large cells lining the pore canal.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia and tetrasporangia produced in uniporate conceptacles; bisporangia unknown.

Gametangial plants monoecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs flush with surrounding thallus surface, composed of 6–8 cells above the chamber, conceptacle chambers 136–191 μm in diameter and (74-) 123–150 μm high. Carposporophytes developing within older female conceptacles after karyogamy, when mature composed of a large central fusion cell and gonimoblast filaments bearing terminal carposporangia, pore canals formed perpendicularly to thallus surface. Spermatangial filaments unbranched, arising from the floor of male conceptacle chambers, mature male conceptacle roofs flush with surrounding thallus surface, composed of 2 or 3 cells, conceptacle chambers 69–82 μm in diameter and 55–61 μm high.

Tetrasporangial conceptacle roofs flush with surrounding thallus surface, 3–6 cells thick above the chamber, pore canals lined with non-protruding cells, conceptacle chambers 164–250 μm in diameter and 109–150 μm high; tetrasporangia usually occurring peripheral to a central columella, occasionally occurring across chamber floor, each mature sporangium 15–40 μm in diameter and 25–75 μm long, zonately divided.

Type from Tami I., north-west edge of Huon Gulf, New Guinea (Heydrich 97, *Bambler*, 1894); lectotype in TRH, designated by Adey *et al.* (1982); illustrated by Penrose & Woelkerling (1988, figs 10–14) and Penrose (1990, fig. 44A–D).

Distribution: Known from numerous subtropical and tropical localities including, Bikini Atoll, Canary Islands, Sri Lanka, Chile, China, Clipperton Island and Costa Rica, Cuba, Ellice Islands, Hawaii, Indian Ocean, Kenya, New Guinea, North Atlantic Ocean, northern Australia, Phillipines, Red Sea, Solomon Islands, Tahiti, West Africa, subtropical and tropical W. Aust. (see Penrose 1990).

In southern Australia, known only from Point Valliant, W. Aust.

Selected specimens: Pelsart I., Houtman Abrolhos, W. Aust., outer reef (*Womersley*, 2.ix.1947; LTB, 13633). Port Gregory, W. Aust., reef pools (*Woelkerling*, 23.ii.1978; LTB, 10717, 10718, 10719). Cape Vlaming, Rottnest I., W. Aust., reef edge or pools (*Woelkerling*, 8.ii.1978; LTB, 10617, and 10.ii.1978, LTB, 10605, 10606, 10609, 10613, 10616). Jeannies Lookout, Rottnest I., W. Aust., 1–3 m deep (*Woelkerling*, 12.ii.1978; LTB, 10630, 10635). North Point Reef, Rottnest I., W. Aust., reef edge or pools (*Woelkerling*, 10.ii.1978; LTB, 10663, 10667). Mabel Cove, Rottnest I., W. Aust., reef top in surf (*Woelkerling*, 9.ii.1978; LTB, 10647). Radar Reef, Rottnest I., W. Aust., reef pools (*Woelkerling*, 9.ii.1978; LTB, 10656, 10657, 10660). Point Valliant, Two People Bay, W. Aust., 0.5 m deep (*Woelkerling*, 2.ii.1978; LTB, 10722).

H. onkodes is essentially a tropical species and has been collected at only one locality within the southern Australian region. Additional data on the species have been provided by Penrose (1990).

5. **Hydrolithon munitum** (Foslie & Howe)Penrose, *comb. nov.*

Lithophyllum munitum Foslie & Howe 1906: 132, pls 86, 88, 89.

Neogoniolithon munitum (Foslie & Howe)Adey 1970: 9.

FIG. 120

Thallus encrusting or warty, up to 20 mm thick, epilithic or epizoic and affixed by cell adhesion. *Structure* pseudoparenchymatous; organisation dorsiventral; construction monomerous, consisting of a single system of branched filaments that collectively contribute to a ventrally situated core, and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; each filament composed of cells 2–11 μm in diameter and 2–25 (-35) μm long; a single epithallial cell terminating most filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes occurring commonly at thallus surface, arranged in vertical rows, horizontal fields or singly, not commonly becoming buried within the thallus.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia and tetrasporangia produced in uniporate conceptacles; bisporangia unknown.

Gametangial plants dioecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs flush with surrounding thallus surface, composed of 4–6 cells above the chamber, conceptacle chambers 164–178 µm in diameter and 104–115 µm high. Carposporophytes developing within older female conceptacles after karyogamy, when mature composed of a large central fusion cell and gonimoblast filaments bearing terminal carposporangia, pore canals formed perpendicularly to thallus surface. Spermatangial filaments unbranched, arising from the floor of male conceptacle chambers, mature male conceptacle roofs flush with surrounding thallus surface, composed of 8–10 cells, conceptacle chambers 312–352 µm in diameter and 121–140 µm high.

Tetrasporangial conceptacle roofs flush with surrounding thallus surface, 4–6 cells thick above the chamber, pore canals lined with non-protruding cells, conceptacle chambers 178–232 µm in diameter and 117–164 µm high; tetrasporangia usually occurring peripheral to a central columella, occasionally occurring across chamber floor, each mature sporangium (15-) 27–61 µm in diameter and 45–85 µm long, zonately divided.

Type from Cave Cays, Exuma Chain, Bahamas (*Howe*, 19.ii.1905); lectotype in TRH (no. 4023); designated by Adey in Adey & Lebednik 1967, p. 20; illustrated by Penrose (1990, fig. 37A–E).

Distribution: Bahamas; Jamaica; various localities in the tropical and subtropical Western Atlantic and tropical W. Aust.

In southern Australia, Lucky Bay, Cape Le Grand, W. Aust., to Point Westall, S. Aust.

Selected specimens: Lucky Bay, Cape Le Grand, W. Aust., 0–3 m deep (*Woelkerling, Platt & Jones*, 9.ii.1984; LTB, 14351). Dempster Point, Israelite Bay, W. Aust., intertidal (*Woelkerling, Platt & Jones*, 8.ii.1984; LTB, 14261). Point Malcolm, SW of Israelite Bay, W. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 7.ii.1984; LTB, 14227). Point Fowler (E shore), S. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 14.ii.1984; LTB, 14421). Point Sinclair, S. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 15.ii.1984; LTB, 14517). Point Westall (S shore), S. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 16.ii.1984; LTB, 14583).

Southern Australian plants of *H. munitum* closely resemble plants in the type collection (see Penrose 1990). The species appears to be closely related to *H. onkodes* and is distinguished by the lack of buried horizontal rows of trichocytes.

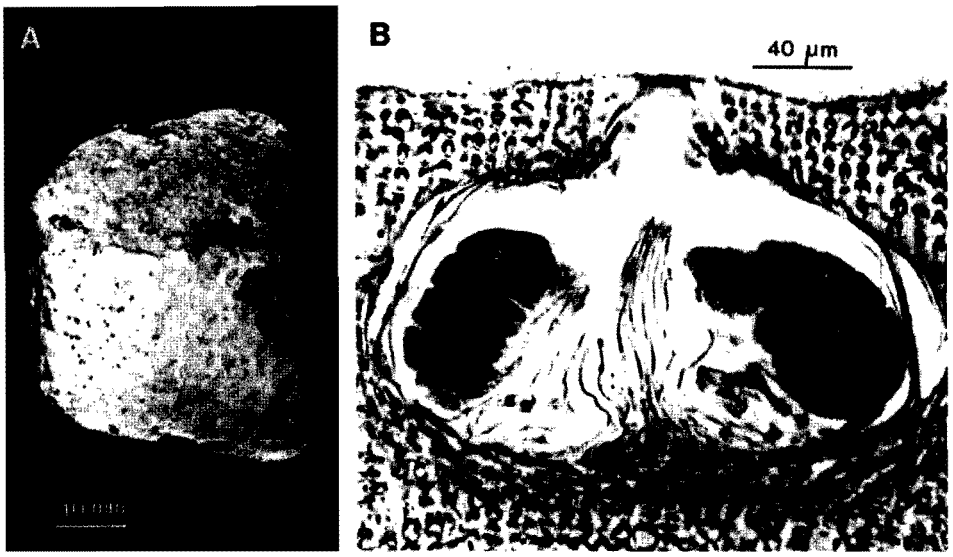


Fig. 120. *Hydrolithon munitum* (**A**, LTB, 14261; **B**, LTB, 14421). **A**. Epilithic plants. **B**. Section of tetrasporangial conceptacle with sporangia occurring peripherally in the chamber and a columella centrally, and darkly staining cells lining the pore canal.

6. **Hydrolithon rupestris** (Foslie)Penrose, *comb. nov.*
Lithophyllum rupestre Foslie 1907a: 26. Woelkerling & Campbell 1992: 100.
Mesophyllum rupestre (Foslie)Adey 1970: 26.

FIG. 121

Thallus encrusting or warty, 0.15–4 mm thick, epilithic or epizoic and affixed by cell adhesion. *Structure* pseudoparenchymatous; organisation dorsiventral; construction monomerous, consisting of a single system of branched filaments that collectively contribute

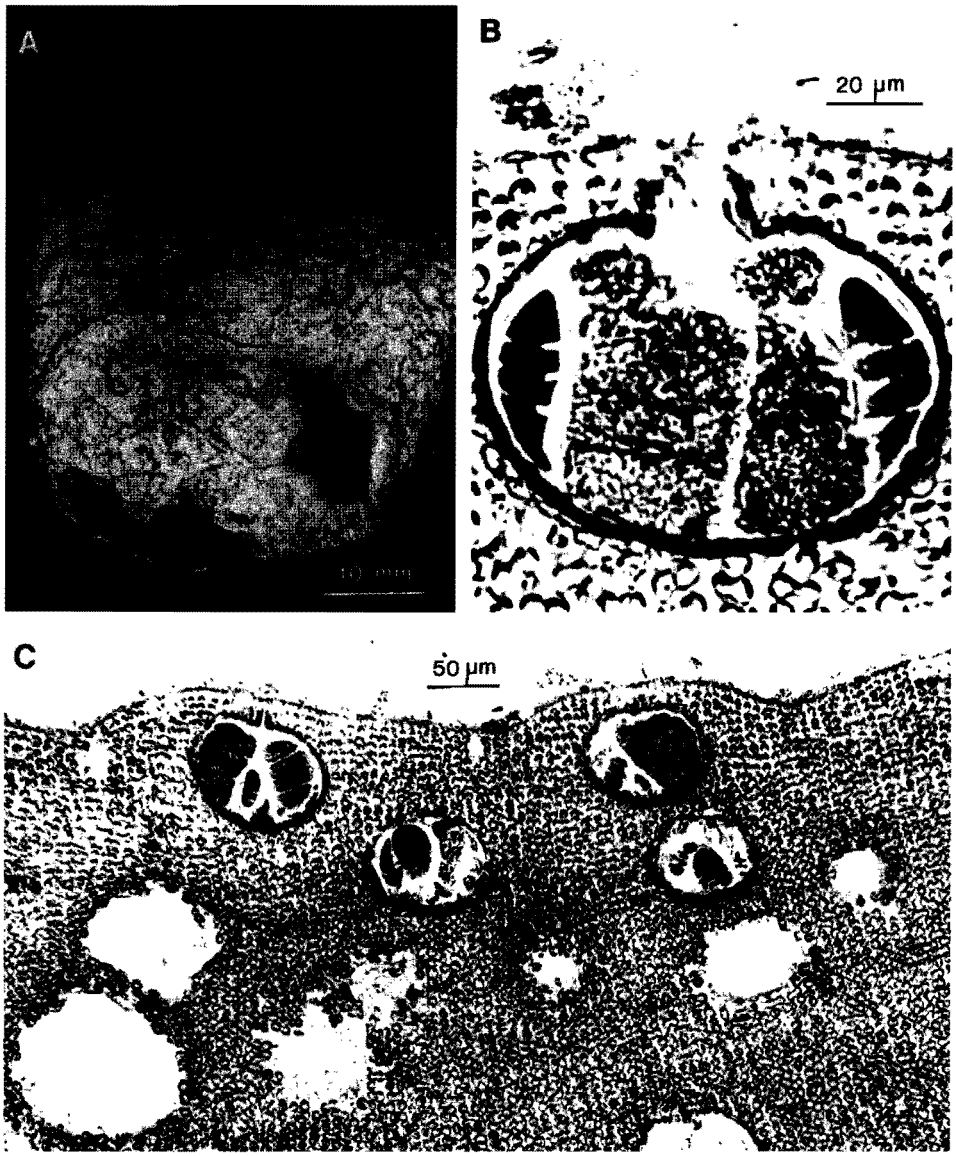


Fig. 121. *Hydrolithon rupestris* (**A**, LTB, 15603; **B, C**, LTB, 14564). **A**. Epilithic plants. **B**. Section of tetrasporangial conceptacle with sporangia across the chamber floor and elongate cells lining the pore canal. **C**. Section of thallus showing scattered tetrasporangial conceptacles and the regularity in the shape and size of cells.

to a ventrally situated core, and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 2–6 μm in diameter and 2–17 μm long; a single epithallial cell terminating most filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes occurring commonly at thallus surface, arranged in horizontal fields or singly, not becoming buried within the thallus.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia and tetrasporangia produced in uniporate conceptacles; bisporangia unknown.

Gametangial plants monoecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs flush with surrounding thallus surface, usually composed of 3 cells above the chamber, conceptacle chambers 77–104 μm in diameter and 63–90 μm high. Carposporophytes developing within older female conceptacles after karyogamy, when mature composed of a large central fusion cell and gonimoblast filaments bearing terminal carposporangia, pore canals formed perpendicularly to thallus surface. Spermatangial filaments unbranched, arising from the floor of male conceptacle chambers, mature male conceptacle roofs flush with surrounding thallus surface, composed of 3 or 4 cells, conceptacle chambers 49–55 μm in diameter and 41–49 μm high.

Tetrasporangial conceptacle roofs flush with surrounding thallus surface, 3 or 4 cells thick above the chamber, pore canals lined with non-protruding cells, conceptacle chambers 82–96 μm in diameter and 82–77 μm high; tetrasporangia scattered across chamber floor, each mature sporangium 15–35 μm in diameter and 40–55 μm long, zonately divided.

Type from Phillip I., Vic. (*C. J. Gabriel*, iv 1905); holotype in TRH; illustrated by Penrose (1990, fig. 54A–D).

Distribution: Lucky Bay, W. Aust., eastwards to Phillip I., Vic., and from Cape Green, southern N.S.W.

Selected specimens: Lucky Bay, Cape Le Grand, W. Aust., 0–3 m deep (*Woelkerling, Platt & Jones*, 9.ii.1984; LTB, 14344). Dempster Point, Israelite Bay, W. Aust., intertidal (*Woelkerling, Platt & Jones*, 8.ii.1984; LTB, 14259, 14262). 10 km E of Eyre, W. Aust., 0–1.2 m deep (*Woelkerling, Platt & Jones*, 9.ii.1984; LTB, 14127). Point Fowler (E shore), S. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 14.ii.1984; LTB, 14465). Point Westall, S. Aust. (*Platt & Jones*, 16.ii.1984; LTB, 14564). Elliston, S. Aust. (*Turner*, 2.xi.1986; LTB, 15412). Beachport (Post Office Rock), S. Aust., 0–3 m deep (*Campbell & Penrose*, 6.xi.1987; LTB, 15844). Cape Cassini, Kangaroo I., S. Aust., 0–2 m deep (*Penrose*, 3.iv.1988; LTB, 15612). Stokes Bay, Kangaroo I., S. Aust., 0–2 m deep (*Campbell & Penrose*, 4.iv.1988; LTB, 15603). Vivonne Bay, Kangaroo I., S. Aust., 0–1.5 m deep (*Campbell & Penrose*, 8.iv.1988; LTB, 15714). Rye (ocean beach), Vic., tide pools (*Woelkerling*, 14.ii.1977; LTB, 12488). Sorrento (ocean beach), Vic., reef pools (*Woelkerling*, 5.xii.1976; LTB, 12507).

H. rupestris occurs commonly on intertidal rock platforms in southern Australia. Additional information on the species has been provided by Penrose (1990).

Genus **PNEOPHYLLUM** Kützing 1843: 385

by D.L. Penrose

Thallus encrusting, epiphytic and affixed by cell adhesion. *Structure* pseudoparenchymatous; organisation dorsiventral; construction dimerous, consisting of a single ventral layer of branched filaments composed of non-palisade cells, and unicellular or multicellular simple or branched filaments that arise more or less perpendicularly from cells of ventral layer filaments; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; epithallial cells terminating filaments at the thallus surface, distal walls rounded or flattened but not flared; trichocytes present or absent, if present usually occurring singly at the thallus surface, not becoming buried within the thallus.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia, tetrasporangia and bisporangia borne in uniporate conceptacles; gametangia and carposporangia usually formed on separate plants from tetrasporangia and bisporangia.

Gametangial plants monoecious; carpogonia and spermatangia produced in separate conceptacles or rarely in the same conceptacle. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Carposporophytes developing within older female conceptacles after karyogamy, when mature composed of a large central fusion cell and short gonimoblast filaments bearing terminal carposporangia, conceptacle pores surrounded by or lacking coronas of filaments and flush with or sunken below the surrounding thallus surface. Spermatangial filaments unbranched, borne on the floor of male conceptacle chambers.

Tetrasporangia and bisporangia formed across the chamber floor or peripheral to a central columella, conceptacle roofs formed by filaments either surrounding sporangial initials or surrounding and interspersed amongst sporangial initials, pores surrounded by or lacking coronas of filaments and flush with or sunken below the surrounding thallus surface; each mature sporangium lacking an apical plug, zonately divided.

Type species: *Pneophyllum fragile* Kützing 1843: 385

The genus was established by Kützing (1843) for a single species, *P. fragile*, but generally was not recognised until Chamberlain (1983) provided an account of the type specimen and the species in the British Isles. *Pneophyllum* has been distinguished from *Spongites* by the mode of tetrasporangial conceptacle roof development (Penrose & Woelkerling 1992b). Recent data (Penrose, unpubl.) have shown that this character may be unreliable in distinguishing the two genera, and further studies are needed to evaluate this.

KEY TO SPECIES OF *PNEOPHYLLUM*

1. Tetrasporangial and carposporangial conceptacles with pores surrounded by coronas of filaments ..... 1. *P. coronatum*
1. Tetrasporangial and carposporangial conceptacles with pores lacking coronas of filaments 2

    2. Tetrasporangial and carposporangial conceptacles with pores that are flush with the surrounding thallus surface ..... 2. *P. fragile*
    2. Tetrasporangial and carposporangial conceptacles with pores that are sunken below the surrounding thallus surface ..... 3. *P. submersiporum*

1. **Pneophyllum coronatum** (Rosanoff)Penrose *in* Chamberlain 1994a: 141.
    Melobesia coronata Rosanoff 1866: 64, pl. 4 fig. 9.
    Heteroderma coronata (Rosanoff)Foslie 1909: 56.
    Melobesia caulerpae Foslie 1906: 16.
    Heteroderma caulerpae (Foslie)Adey 1970: 16.
    Pneophyllum caulerpae (Foslie)Jones & Woelkerling 1984: 184, fig. 18.

FIG. 122

Thallus encrusting, epiphytic and affixed by cell adhesion. *Structure* pseudoparenchymatous; organisation dorsiventral; construction dimerous, consisting of a single ventral layer of branched filaments composed of non-palisade cells, and unicellular or multicellular simple or branched filaments that arise more or less perpendicularly from cells of ventral layer filaments, each filament composed of cells 2–15 µm in diameter and 2–20 µm long; epithallial cells terminating most filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes present or absent, if present, usually occurring singly or in pairs at the thallus surface, not becoming buried within the thallus.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia, tetrasporangia and bisporangia produced in uniporate conceptacles.

Gametangial plants monoecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above or flush with surrounding thallus surface, composed of 4–6 cells above the chamber, pores surrounded by coronas of filaments, conceptacle chambers 135–250 µm in diameter and

135–180 μm high. Carposporophytes developing within older female conceptacles after karyogamy, when mature composed of a large central fusion cell and with gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, arising from the floor of male conceptacle chambers, mature male conceptacle roofs protruding above or flush with surrounding thallus surface, conceptacle chambers 50–70 μm in diameter and 30–55 μm high.

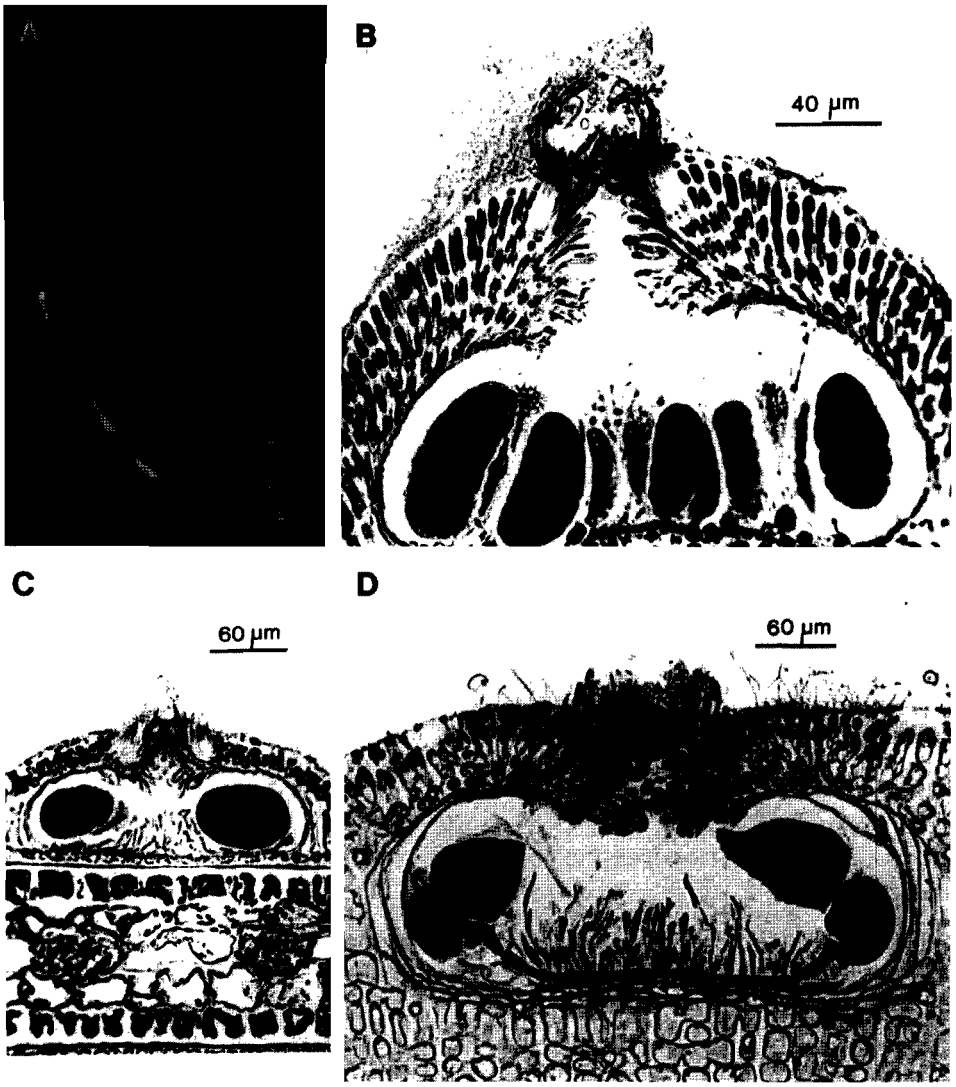


Fig. 122. *Pneophyllum coronatum* (**A,** LTB, 13402; **B,** LTB, 13038; **C,** LTB, 12527; **D,** LTB, 14486). **A.** Plants epiphytic on stems of the seagrass *Amphibolis antarctica*. **B.** Section of tetrasporangial conceptacle with sporangia occurring across the chamber floor. **C.** Section of thallus that is 4 cells high in vegetative regions with tetrasporangial conceptacles containing sporangia peripherally in the chamber and a columella centrally. **D.** Section of conceptacle containing a carposporophyte with a fusion cell present across the chamber floor, gonimoblast filaments borne peripherally in the chamber at the margins of the fusion cell and bearing terminal carposporangia.

Tetrasporangial and bisporangial conceptacle roofs protruding above or flush with surrounding thallus surface, 3–6 cells thick above the chamber, pore canals lined with protruding cells, pores surrounded by coronas of filaments, conceptacle chambers 135–235 μm in diameter and 85–185 μm high; tetrasporangia and bisporangia scattered across the conceptacle chamber floor or peripheral to a central columella, each mature sporangium 15–45 μm in diameter and 40–80 μm long, zonately divided.

Type from Port Phillip Bay, Vic. (collector and date unknown); holotype in CN (unnumbered); illustrated by Penrose (1990, fig. 18A–C).

Distribution: The Malay Archipelago; New Zealand; tropical W. Aust.

In southern Australia, Point Sinclair, S. Aust. eastwards to Sorrento, Vic., and around Tasmania.

Selected specimens: Point Sinclair, S. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 15.ii.1984; LTB, 14486). Nine Mile Reef, 15 km W of Eyre, W. Aust., 0–3 m deep (*Woelkerling, Platt & Jones*, 1.i.1984; LTB, 13997). Cape Willoughby, Kangaroo I., S. Aust. (*Campbell & Penrose*, 6.iv.1988; LTB, 15615). Point Tinline, Kangaroo I., S. Aust., 0–1 m deep (*Campbell & Penrose*, 10.iv.1988; LTB, 15723). Point Lonsdale, Vic., tide pools (*Jones*, 25.viii.1982; LTB, 12527). Sorrento, Vic. (*Jones*, 23.iii.1981; LTB, 12530). Greens Beach, Tas., 1 m deep (*Platt*, 2.iii.1983; LTB, 13402). Bluestone Bay, Freycinet Pen., Tas., 0–4 m deep (*Platt & Woelkerling*, 21.ii.1983; LTB, 13038). Snug Cove, SW end of Clarke I., Tas., 6–7 m deep (*Leach*, 28.ii.1979; LTB, 11597).

P. coronatum commonly grows intermixed with *P. fragile* on various algae and on the seagrass *Amphibolis antarctica* (Penrose 1990). An examination of the type of *P. caulerpae* has shown that it is conspecific with *P. coronatum*. Additional data have been provided by Penrose (1990).

2. **Pneophyllum fragile** Kützing 1843: 385. Chamberlain 1983: 300, 356–359, figs 24–27; 1994b: 141, figs 64, 65. Penrose & Woelkerling 1991: 495, figs 1–27.
Melobesia pruinosa Kützing 1845: 295 (see Chamberlain 1983: 359).
Pneophyllum lejolisii (Rosanoff)Chamberlain 1983: 359.

FIG. 123

Thallus encrusting, epiphytic and affixed by cell adhesion. *Structure* pseudoparenchymatous; organisation dorsiventral; construction dimerous, consisting of a single ventral layer of branched filaments composed of non-palisade cells, and unicellular or multicellular simple or branched filaments that arise more or less perpendicularly from cells of ventral layer filaments, each filament composed of cells 5–14 μm in diameter and 3–11 μm long; epithallial cells terminating filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes present or absent, if present, usually occurring singly at thallus surface, not becoming buried within thallus.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia, tetrasporangia and bisporangia produced in uniporate conceptacles.

Gametangial plants monoecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above or flush with surrounding thallus surface, composed of 4–6 cells above the chamber, pores lacking coronas of filaments and flush with surrounding thallus surface, conceptacle chambers 196–218 μm in diameter and 49–150 μm high. Carposporophytes developing within older female conceptacles after karyogamy, when mature composed of a large central fusion cell and with gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, arising from the floor of male conceptacle chambers, mature male conceptacle roofs protruding above or flush with surrounding thallus surface, conceptacle chambers 82–109 μm in diameter and 49–91 μm high.

Tetrasporangial and bisporangial conceptacle roofs protruding above or flush with surrounding thallus surface, 2–10 cells thick above the chamber, pore canals lined with protruding cells, pores lacking coronas of filaments and flush with surrounding thallus surface, conceptacle chambers 80–265 μm in diameter and 55–195 μm high; tetrasporangia

and bisporangia usually peripheral to a central columella, sometimes scattered across the conceptacle chamber floor, each mature sporangium 15–45 μm in diameter and 20–85 μm long, zonately divided.

Type from an unknown locality in the Mediterranean Sea; holotype in L (941.241–152); illustrated by Chamberlain (1983, figs 24–27) and Penrose & Woelkerling (1991, figs 1–8).

Distribution: British Isles; Canada; Caribbean; Europe; Mediterranean Sea; Pacific Mexico; subtropical and tropical W. Aust.; USA; USSR (see Chamberlain 1983, pp. 359, 360; Penrose & Woelkerling 1991, p. 501).

In southern Australia, Bunbury, W. Aust., eastwards to Sealers Cove, Wilsons Prom., Vic., and around Tasmania.

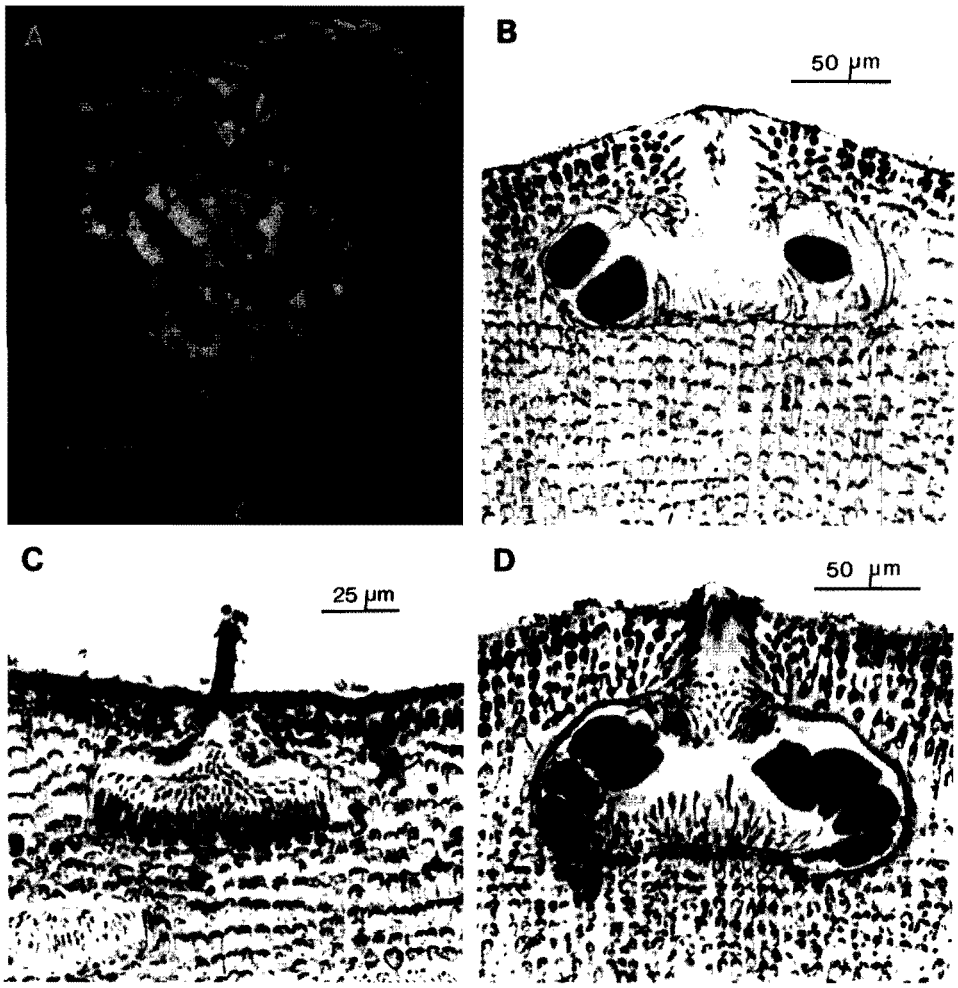


Fig. 123. *Pneophyllum fragile* (**A**, LTB, 10848; **B**, LTB, 13930; **C**, LTB, 13036; **D**, LTB, 13931). **A**. Plants epiphytic on *Laurencia* sp. **B**. Section of tetrasporangial conceptacle containing sporangia peripherally in the chamber and a columella centrally. **C**. Section of conceptacle containing spermatangia that have arisen from initials formed across the chamber floor. Note the pore has an elongate mucilaginous spout. **D**. Section of conceptacle containing a carposporophyte with a fusion cell present across the chamber floor, gonimoblast filaments borne peripherally in the chamber at the margins of the fusion cell and bearing terminal carposporangia.

Selected specimens: Mabel Cove, Rottnest I., W. Aust., reef edge on *Laurencia* (*Woelkerling*, 9.ii.1978; LTB, 10848). Bunbury, W. Aust., 0–1 m deep (*Woelkerling*, 5.ii.1978; LTB, 10570). Lucky Bay, Cape Le Grand, W. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 9.ii.1984; LTB, 14331). Point Malcolm, SW of Israelite Bay, W. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 7.ii.1984, LTB, 14201). Nine Mile Reef, W of Eyre, W. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 1.ii.1984; LTB, 13946). Point Sinclair, S. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 15.ii.1984; LTB, 14474). Penneshaw, Kangaroo I., S. Aust., 0–2 m deep (*Campbell & Penrose*, 13.iv.1988; LTB, 15675). Beachport, S. Aust., 3–6 m deep (*Campbell & Penrose*, 26.ii.1988; LTB, 15689). Marengo, Apollo Bay, Vic., reef edge (*Woelkerling*, 11.i.1984; LTB, 13930, 13931). Blanket Bay, Otway National Park, Vic., 4 m deep (*Campbell, May & Penrose*, 14.xi.1985; LTB, 15244). Rye (ocean beach), Vic., tide pools (*Kay*, 6.i.1978; LTB, 11130). Sealers Cove, Wilsons Prom., Vic., upper subtidal (*Leach*, 19.vii.1977; LTB, 10131). Snug Cove, Clarke I., Bass Strait, Tas., 6–7 m deep (*Leach*, 28.ii.1979; LTB, 11599). Bluestone Bay, Freycinet Pen., Tas., 0–4 m deep (*Platt & Woelkerling*, 21.ii.1983; LTB, 13036). Sister Bay, Southport, Tas., 3–4 m deep (*Platt, Woelkerling & Thomas*, 16.ii.1983; LTB, 12875). Safety Cove (N shore), Port Arthur, Tas., 0–2 m deep (*Platt & Woelkerling*, 25.ii.1983; LTB, 12835).

P. fragile is a variable species (see Penrose & Woelkerling 1991) that occurs commonly on *Acrocarpia* spp., *Laurencia* spp., and on the seagrass *Amphibolis antarctica*. Additional data on the species have been provided by Penrose & Woelkerling (1991).

3. **Pneophyllum submersiporum** Penrose, *sp. nov.*

FIG. 124

Thallus encrusting, epiphytic and affixed by cell adhesion. *Structure* pseudoparenchymatous; organisation dorsiventral; construction dimerous, consisting of a single ventral layer of branched filaments composed of non-palisade cells, and unicellular or multicellular simple or branched filaments that arise more or less perpendicularly from cells of ventral layer filaments, each filament composed of cells 2–14 μm in diameter and 2–18 μm long; epithallial cells terminating filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes present or absent, if present, usually occurring singly at thallus surface, not becoming buried within thallus.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia, tetrasporangia and bisporangia produced in uniporate conceptacles.

Gametangial plants monoecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above or flush with surrounding thallus surface, composed of 4–6 cells above the chamber, pores lacking coronas of filaments and submersed below surrounding thallus surface, conceptacle chambers 130–240 μm in diameter and 135–150 μm high. Carposporophytes developing within older female conceptacles after karyogamy, when mature composed of a large central fusion cell and gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, arising from the floor of male conceptacle chambers, mature male conceptacle roofs protruding above or flush with surrounding thallus surface, conceptacle chambers 40–55 μm in diameter and 30–45 μm high.

Tetrasporangial and bisporangial conceptacle roofs protruding above or flush with surrounding thallus surface, 4–6 cells thick above the chamber, pore canals lined with protruding cells, pores lacking coronas of filaments and submersed below surrounding thallus surface, conceptacle chambers 135–220 μm in diameter and 90–150 μm high; tetrasporangia and bisporangia usually peripheral to a central columella, sometimes scattered across the conceptacle chamber floor, mature sporangia zonately divided.

Diagnosis. Pneophyllum submersiporum characteribus generis *Pnophylli* a speciebus affinibus conceptaculis tetrasporangiorum et carposporangiorum poris submersis, filamentis 2–5 cellulis compositis circumcintus distinguitur.

Type from Safety Cove, Port Arthur, Tas. (*Platt & Woelkerling*, 25.ii.1983); holotype in LTB (12808).

Distribution: Known from Lucky Bay, Cape Le Grand, W. Aust., Point Sinclair, S. Aust., Phillip Island, Vic. and SE Tasmania.

Known specimens: Lucky Bay, Cape Le Grand, W. Aust., 0–3 m deep (*Woelkerling, Platt & Jones*, 9.ii.1984; LTB, 14325, 15015). Point Sinclair, S. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 15.ii.1984; LTB, 14476). Kitty Miller Bay, Phillip Island, Vic., upper subtidal (*Turner*, 24.1.1979; LTB, 11474). The Gap, Cunningham Bay, Phillip Island, Vic., reef pools (*Kemp*, iv.1982; LTB, 12580). Bluestone Bay, Freycinet Pen., Tas., 0–4 m deep (*Platt & Woelkerling*, 21.ii.1983; LTB, 13044). Safety Cove, Port Arthur, Tas., intertidal (*Platt & Woelkerling*, 25.ii.1983; LTB, 12808).

P. submersiporum occurs on *Sargassum* spp. and *Zonaria* spp. The species appears to be closely related to *P. coronatum* and is distinguished from it by the sunken pores of the tetrasporangial and carposporangial conceptacles and the lack of coronas of filaments surrounding the pores.

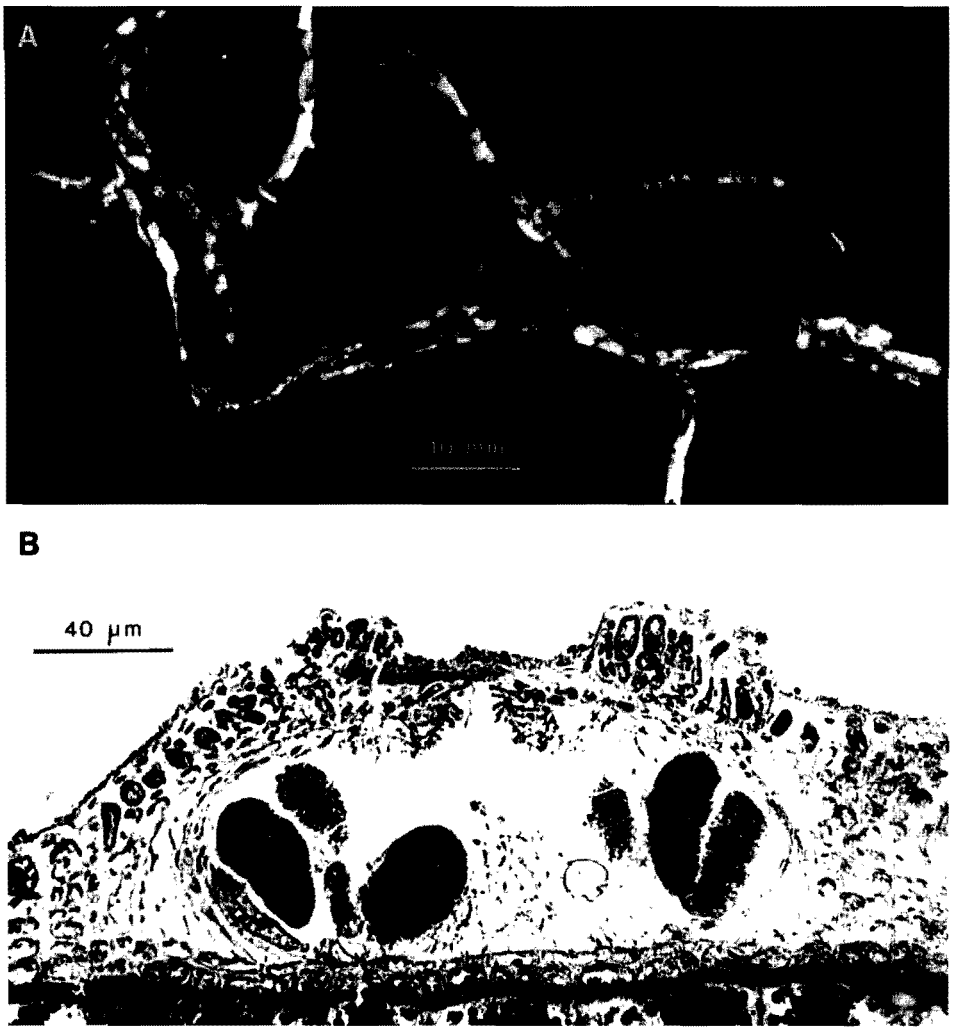


Fig. 124. *Pneophyllum submersiporum* (**A**, LTB, 13044; **B**, LTB, 12808). **A**. Plants epiphytic on *Sargassum* sp. **B**. Section of tetrasporangial conceptacle showing roof cells and submersed pore.

Genus SPONGITES Kützing, 1841: 30

by D.L. Penrose

Melobesia Lamouroux sect. *Spongites* (Kützing)Decaisne 1842b: 126.
Paraspora Heydrich 1900: 315, a later homonym of *Paraspora* Grove 1884: 196.

Thallus encrusting, warty, lumpy, fruticose, epilithic or epizoic and affixed by cell adhesion, or unattached and free-living as rhodoliths; genicula absent. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions and radial in protuberant branches; construction monomerous, consisting of a single system of branched filaments that collectively contribute to a ventrally or centrally situated core, and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; 1–7 epithallial cells terminating most filaments at the thallus surface, distal walls rounded or flattened but not flared; trichocytes present or absent, if present appearing, in section, arranged in horizontal fields, horizontal rows, vertical rows, or occurring singly at the thallus surface, sometimes becoming buried within the thallus.

Reproduction. Vegetative reproduction, where known, by thallus fragmentation. Gametangia, carposporangia, tetrasporangia and bisporangia borne in uniporate conceptacles; gametangia and carposporangia usually formed on separate plants from tetrasporangia and bisporangia.

Gametangial plants monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Carposporophytes developing within female conceptacles after karyogamy, consisting of a large central fusion cell and gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, formed on the chamber floor only.

Tetrasporangia and bisporangia formed across the chamber floor or peripheral to a central columella, conceptacle roofs formed by filaments either surrounding sporangial initials or surrounding and interspersed amongst sporangial initials, pores either surrounded by a corona of filaments or lacking one, each mature sporangium lacking an apical plug, zonately divided.

Type species: *Spongites fruticulosus* Kützing 1841: 33.

Spongites has been distinguished from *Pneophyllum* by the mode of tetrasporangial conceptacle roof development (Penrose & Woelkerling 1992b). Recent data (Penrose, unpubl.) have shown that this character may be unreliable in distinguishing the two genera, and further studies are needed to evaluate this.

KEY TO SPECIES OF *SPONGITES*

1. Thallus composed of a cluster of branch-like protuberances; 2–7 layers of epithallial cells present at the thallus surface ..... 1. *S. hyperellus*
1. Thallus crustose, with a more or less flattened dorsal surface or with wart-like protuberances; a single layer of epithallial cells present at the thallus surface 2

    2. Tetrasporangial conceptacles >450 µm in diameter and >240 µm high ..... 2. *S. fruticulosus*
    2. Tetrasporangial conceptacles <250 µm in diameter and <200 µm high 3

3. Tetrasporangial conceptacles with pores surrounded by coronas of filaments; tetrasporangia occurring across the chamber floor ..... 3. *S. tunicatus*
3. Tetrasporangial conceptacles with pores lacking coronas of filaments; tetrasporangia occurring peripherally in the chamber and a columella occurring centrally ..... 4. *S. yendoi*

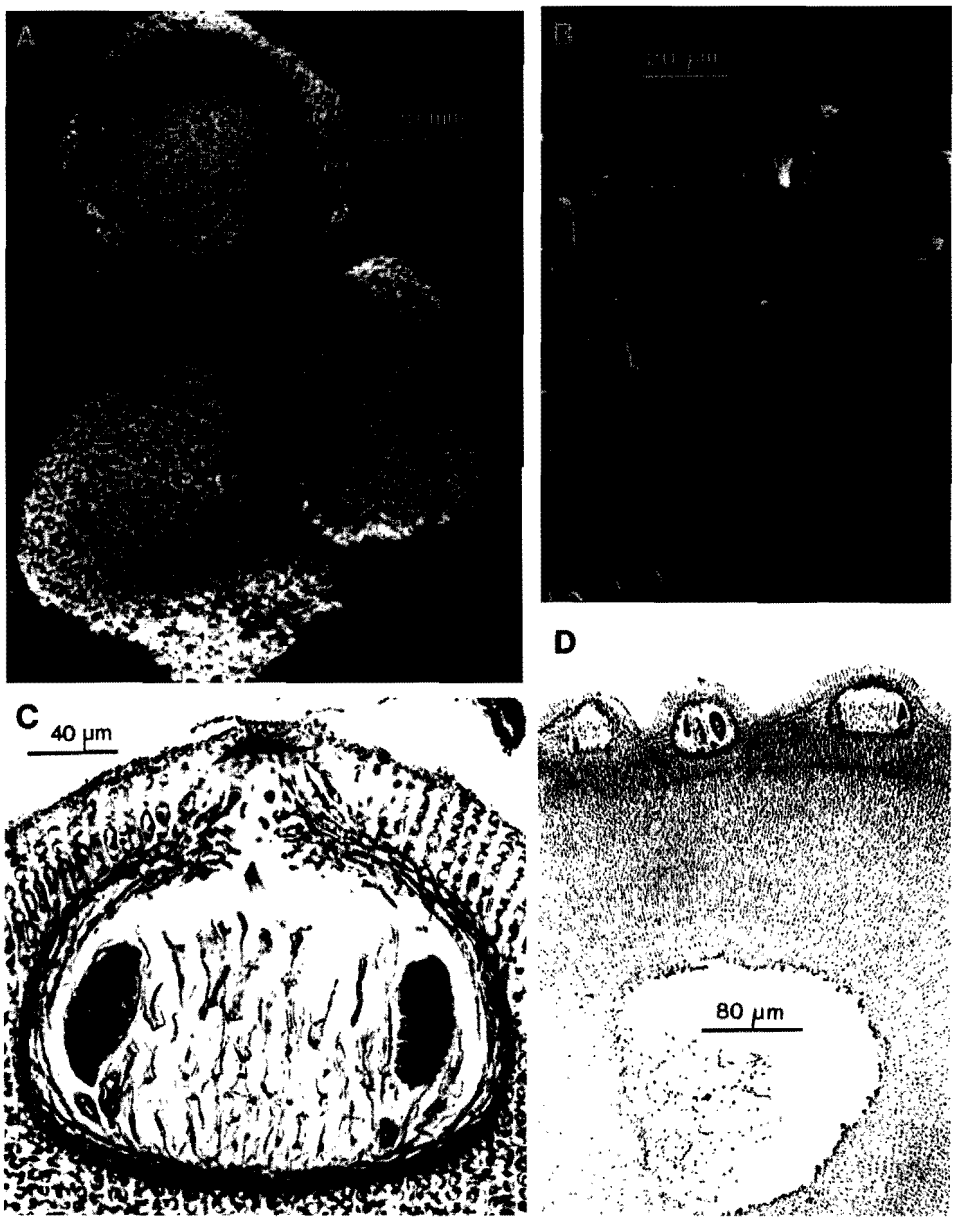


Fig. 125. *Spongites hyperellus* (**A, C,** LTB, 13258; **B,** LTB, 12805; **D,** LTB, 12819). **A.** Epilithic plants composed of clumps of anastomosed branch-like protuberances. **B.** SEM of piece of thallus showing parenchymatous structure and regularly aligned filaments connected laterally by cell fusions. **C.** Section of conceptacle with sporangia occurring peripherally in the chamber and a columella centrally, and elongate cells protruding laterally into the pore canal. **D.** Section of protuberance showing radial organisation and tetrasporangial conceptacles at thallus surface.

1. **Spongites hyperellus** (Foslie)Penrose, *comb. nov.*

Lithophyllum hyperellum Foslie 1900a: 27. Womersley 1959: 584; 1981: 227, 229; 1984: 47, 48, pl. 9 fig. 2.

Lithophyllum hyperellum f. *fastigiata* Foslie 1900a: 27. Woelkerling & Campbell 1992: 99.

Lithophyllum hyperellum f. *heteroidea* Foslie 1900a: 27.

Pseudolithophyllum hyperellum (Foslie)Adey 1970: 13.

PLATE 4 fig. 1; FIG. 125

Thallus fruticose, epilithic and affixed by cell adhesion, or unattached and free-living as rhodoliths. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions and radial in protuberant branches; construction monomerous, consisting of a single system of branched filaments that collectively contribute to a ventrally or centrally situated core, and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 2–8 µm in diameter and 2–14 µm long; 1–7 epithallial cells terminating most filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes present at thallus surface, occurring singly or in horizontal fields, not becoming buried within thallus.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia, carposporangia and tetrasporangia produced in uniporate conceptacles; bisporangia unknown.

Gametangial plants monoecious; carpogonia and spermatangia produced in separate conceptacles or in the same conceptacle. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above the surrounding thallus surface, composed of 3–7 cells above the chamber, conceptacle chambers 136–150 µm in diameter and 109–128 µm high. Carposporophytes developing within older female conceptacles after karyogamy, when mature consisting of a flattened central fusion cell and gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, arising from the floor of male conceptacle chambers, conceptacle chambers 109 µm in diameter and 55 µm high.

Tetrasporangial conceptacle roofs protruding above surrounding thallus surface, 3–7 cells thick above the chamber, pore canals lined with protruding cells, conceptacle chambers 141–186 µm in diameter and 136–163 µm high; tetrasporangia scattered across the conceptacle chamber floor, each mature sporangium 20–45 µm in diameter and 45–105 µm long, zonately divided.

Type from Western Port, Vic. (*J. Gabriel*, 1899); lectotype in TRH, designated by Adey in Adey & Lebednik (1967, p. 19); illustrated by Penrose (1990, fig. 33A–C).

Distribution: Known from the type collected in Western Port, Vic., and around Tasmania.

Selected specimens: Three Hummock I., Tas., lower eulittoral (*Bennett*, 17.i.1954; AD, A19679 = LTB, 13647). Curries River, Tas., upper sublittoral (*Cribb*, 17.ix.1950; AD, A16319 = LTB, 13691). Bicheno, Tas., lower eulittoral (*Womersley*, 4.xi.1982; AD, A56460). Clydes I., Eaglehawk Neck, Tas., intertidal (*Platt & Woelkerling*, 26.ii.1983; LTB, 13258). Safety Cove, Port Arthur, Tas., intertidal (*Platt & Woelkerling*, 25.ii.1983; LTB, 12805, 12819). Fluted Cape, Bruny I., Tas., uppermost sublittoral (*Shepherd*, 10.ii.1972; AD, A41765 = LTB, 13650). Sandy Cape, Tas., outer reef (*Bennett*, 15.i.1954; AD, A43936 = LTB, 13633). Maatsuyker I., Tas., lower eulittoral (*Bennett*, 26.vi.1954; AD, A19798 = LTB, 13681).

S. hyperellus is often readily distinguished by its external appearance. Womersley (1984, p. 47) considered the species to be a dominant alga in the lower intertidal zone along rocky Tasmanian coasts subject to strong wave action. Additional information on the species has been provided by Penrose (1990).

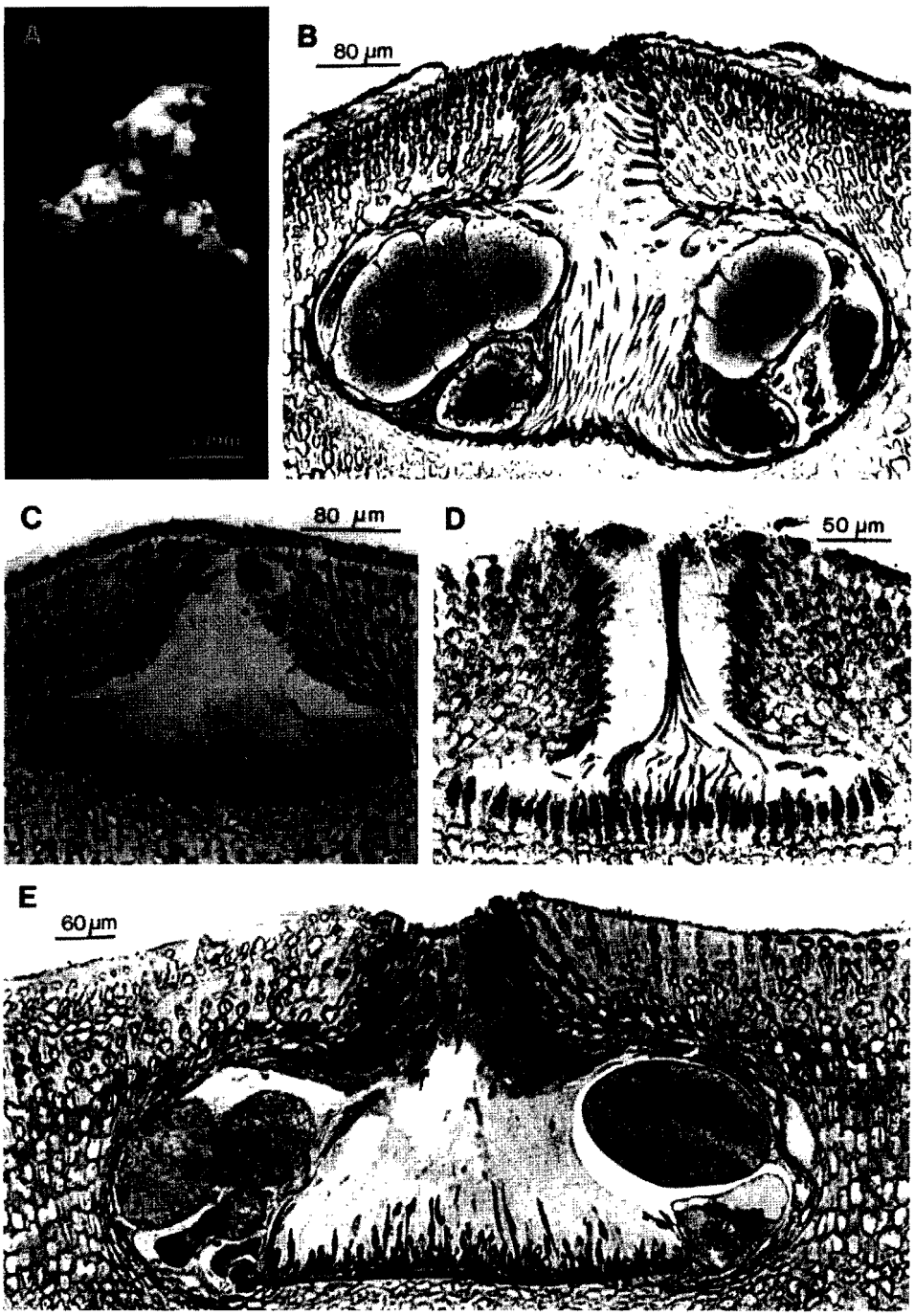


Fig. 126. *Spongites fruticulosus* (**A**, LTB, 14081; **B**, LTB, 14006; **C**, LTB, 14095; **D**, LTB, 14495; **E**, LTB, 14040). **A**. Epilithic plants. **B**. Section of conceptacle with sporangia occurring peripherally in the chamber and a columella centrally, and elongate cells protruding laterally into the pore canal. **C**. Section of conceptacle with initials bearing spermatangia occurring across the chamber floor.

2. **Spongites fruticulosus** Kützing 1841: 33. Woelkerling 1985: 135, 150, figs 23–32; Woelkerling & Penrose in Woelkerling 1988: 155, 157; Penrose 1991: 438, figs 1–24.
Lithothamnion fruticulosum (Kützing)Foslie 1895: 46.
Melobesia fruticulosa (Kützing)Decaisne 1842a: 126.
Paraspora fruticulosa (Kützing)Heydrich 1900: 315.
Lithothamnion fasciculatum § *fruticulosum* (Kützing)Hauck 1883: 274.
Goniolithon verrucosum Foslie 1900a: 24.

FIG. 126

Thallus encrusting or warty, 0.3–30 mm thick, epilithic and affixed by cell adhesion or growing unattached as rhodoliths. *Structure* pseudoparenchymatous; organisation dorsiventral; construction monomerous, consisting of a single system of branched filaments that collectively contribute to a ventrally situated core, and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 5–16 μm in diameter and 5–35 μm long; a single epithallial cell terminating filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes occurring present at thallus surface, arranged in horizontal fields or singly, not becoming buried within thallus.

Reproduction. Vegetative reproduction unknown. Gametangia, carposporangia and tetrasporangia produced in uniporate conceptacles; bisporangia unknown.

Gametangial plants dioecious; carpogonia and spermatangia produced in separate conceptacles. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above or flush with surrounding thallus surface, usually composed of 8–12 cells above the chamber, conceptacle chambers 575–595 μm in diameter and 295–320 μm high. Carposporophytes developing within older female conceptacles after karyogamy, when mature composed of a large central fusion cell and gonimoblast filaments bearing terminal carposporangia, pores not surrounded by coronas of filaments. Spermatangial filaments unbranched, arising from the floor of male conceptacle chambers, mature male conceptacle roofs flush with surrounding thallus surface, composed of 3 or 4 cells, conceptacle chambers 235–335 μm in diameter and 145–245 μm high.

Tetrasporangial conceptacle roofs protruding above or flush with surrounding thallus surface, 8–12 cells thick above the chamber, pore canals lined with protruding cells, conceptacle chambers 350–595 μm in diameter and 275–410 μm high; tetrasporangia peripheral to a central columella, each mature sporangium 65–130 μm in diameter and 85–225 μm long, zonately divided.

Type from the Mediterranean Sea; holotype in L (943, 8–134), illustrated by Woelkerling (1985, figs 23–32) and Penrose (1991, figs 1–3).

Distribution: Mediterranean Sea; Red Sea.
In southern Australia, Esperance, W. Aust. to Eagles Nest, Vic.

Selected specimens: Five Fathom Bank, 6 km W of Garden I., W. Aust., 12–15 m deep (*Cambridge*, 21.ii.1978; LTB, 11495). Observatory Point, Esperance, W. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 5.ii.1984; LTB, 14173). Nine Mile Reef, 15 km W of Eyre, W. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 1.ii.1984; LTB, 14006). 7 km E of Twilight Cove, Eyre, W. Aust., 0–3 m deep (*Woelkerling, Platt & Jones*, 2.ii.1984; LTB, 14040, 14081, 14095). Point Fowler (E shore), S. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 14.ii.1984; LTB, 14470). Point Sinclair, S. Aust., 0–2 m deep (*Woelkerling, Platt & Jones*, 15.ii.1984; LTB, 14495). Point Westall, S. Aust., 2–3 m deep (*Platt & Jones*, 16.ii.1984; LTB, 14570). Cape Jaffa, S. Aust., 1 m deep (*Campbell & Penrose*, 18.ii.1987; LTB, 15552). Potato Patch Reef, Anglesea, Vic., 8–9 m deep (*Beanland*, 31.viii.1982; LTB, 12723). Eagles Nest (E of Cape Patterson), Vic., intertidal pools (*Turner*, 10.i.1979; LTB, 11546).

D. Section of conceptacle containing carpogonial branches across the chamber floor. **E**. Section of conceptacle containing a fusion cell across the chamber floor with gonimoblast filaments occurring at the margins and bearing terminal carposporangia.

S. fruticulosus was known only from the type specimen until recently and is now known to occur commonly along the southern Australian coast (Penrose 1991). An examination of the type of *Goniolithon verrucosum* has shown that it is conspecific with *S. fruticulosus*. Additional information on the species has been provided by Penrose (1991).

3. **Spongites tunicatus** Penrose, *sp. nov.*

FIG. 127

Thallus encrusting or warty, epilithic or epizoic and affixed by cell adhesion. *Structure* pseudoparenchymatous; organisation dorsiventral; construction dimerous, consisting of a single ventral layer of branched filaments composed of non-palisade cells, and multicellular filaments that arise more or less perpendicularly from cells of ventral layer filaments, each

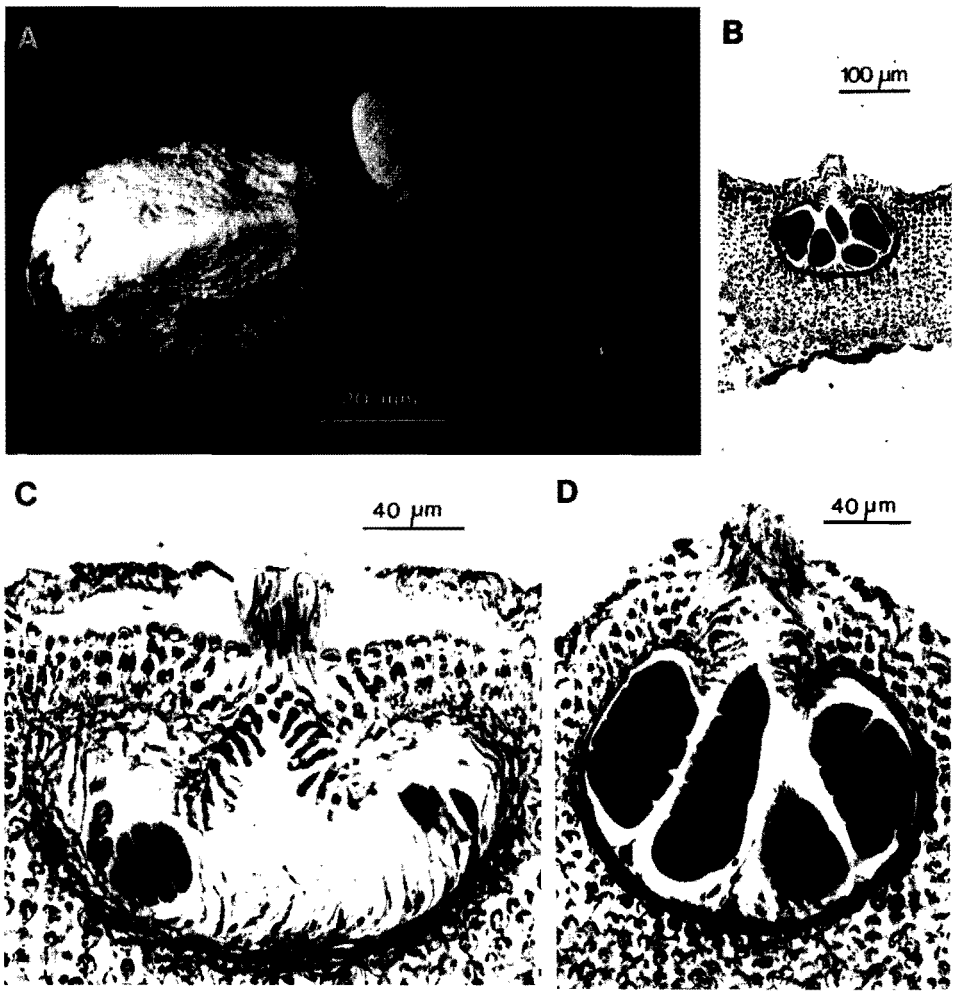


Fig. 127. *Spongites tunicatus* (**A**, LTB, 15259; **B–D**, LTB, 12980). **A.** Epilithic plants. **B.** Section of thallus showing tetrasporangial conceptacle at thallus surface, dorsiventral organisation and regularity in size and shape of cells. **C.** Section of immature tetrasporangial conceptacle containing sporangial initials in the chamber and with a corona of filaments surrounding the pore. **D.** Section of mature tetrasporangial conceptacle containing sporangia in the chamber and with a corona of filaments surrounding the pore.

filament composed of cells 2–9 μm in diameter and 2–11 μm long; single epithallial cells terminating filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes unknown.

Reproduction. Vegetative reproduction, gametangial plants and bisporangia unknown. Tetrasporangia produced in uniporate conceptacles.

Tetrasporangial conceptacle roofs flush with surrounding thallus surface, 3 or 4 cells thick above the chamber, pore canals lined with protruding cells, pores surrounded by coronas of filaments, conceptacle chambers 136–142 μm in diameter and 109–158 μm high; tetrasporangia occurring across chamber floor; each mature sporangium zonately divided.

Diagnosis. Spongites tunicatus a ceterus speciebus *Spongites* cognitis praesentiis coronarum filorum diagnoscendus.

Type from Variety Bay, Bruny I., Tas. (*Woelkerling, Platt & Brown*, 17.ii.1983); holotype in LTB (12980), illustrated in Fig. 13B–D and by Penrose (1990, figs 59, 60).

Distribution: Known from Otway National Park, Vic., and Bruny I., Tas.

Selected specimens: Crayfish Bay, Otway National Park, Vic., intertidal (*Campbell, May & Penrose*, 13.xi.1985; LTB, 15262). Blanket Bay, Otway National Park, Vic., intertidal (*Campbell, May & Penrose*, 13.xi.1985; LTB, 15259). Variety Bay, Bruny I., Tas., 2–4 m deep (*Woelkerling, Platt & Brown*, 17.ii.1983; LTB, 12980).

S. tunicatus appears to be most closely related to *S. yendoi* and is distinguished from this species by the presence of coronas of filaments.

4. **Spongites yendoi** (Foslie)Chamberlain 1993: 100.
Goniolithon yendoi Foslie 1900a: 25.
Lithophyllum yendoi (Foslie)Foslie 1900b: 20.
Pseudolithophyllum yendoi (Foslie)Adey 1970: 14.
Lithophyllum natalense Foslie 1907a: 27.

FIG. 128

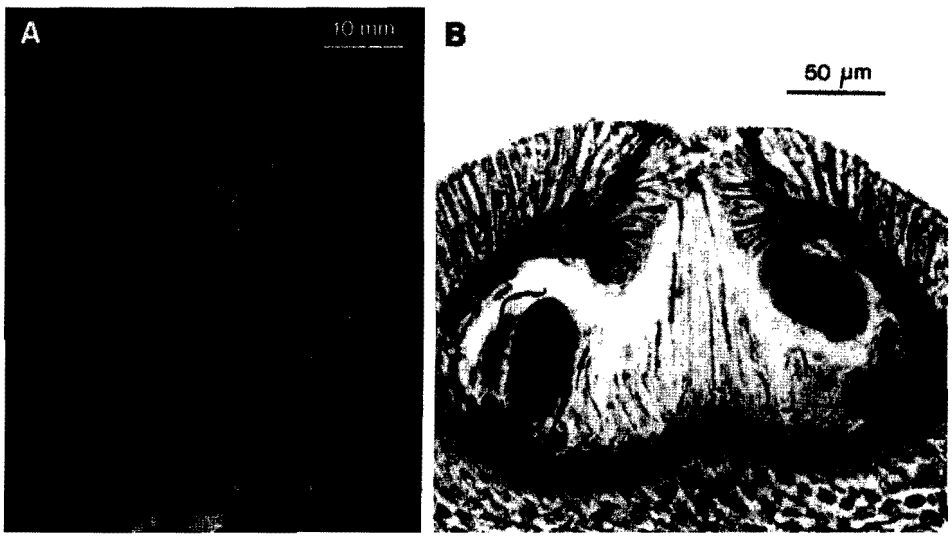


Fig. 128. *Spongites yendoi* (**A, B,** LTB, 11758). **A.** Plants epizoic on a tunicate. **B.** Section of tetrasporangial conceptacle showing sporangia peripherally in the chamber and elongate cells protruding into the pore canal.

Thallus encrusting or warty, epilithic and affixed by cell adhesion. *Structure* pseudoparenchymatous; organisation dorsiventral; construction monomerous, consisting of a single system of branched filaments that collectively contribute to a ventrally situated core, and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 2–6 μm in diameter and 5–22 μm long; a single epithallial cell terminating filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes occurring at thallus surface, arranged in horizontal fields or singly, not becoming buried within thallus.

Reproduction. Vegetative reproduction, gametangial plants and bisporangia unknown. Tetrasporangia produced in uniporate conceptacles.

Tetrasporangial conceptacle roofs flush with surrounding thallus surface, 3–5 cells thick above the chamber, pore canals lined with protruding cells, pores lacking coronas of filaments, conceptacle chambers 164–232 μm in diameter and 109–185 μm high; tetrasporangia peripheral to a central columella, each mature sporangium zonately divided.

Type from Shimoda Harbour, Izul, Japan (*K. Yendo*, April 1899); lectotype in TRH (Yendo no. 66), designated by Foslie (1904).

Distribution: Japan; South Africa.

In southern Australia, known from Lorne, Vic.

Known specimens: Big Hill Creek, Lorne, Vic., intertidal (*Wilks & Woelkerling*, 9.iv.1991; LTB, 16185). Lorne, Vic., upper subtidal (*Woelkerling*, 4.i.1979; LTB, 11758).

S. yendoi appears similar in vegetative portions of the thallus to *Phymatolithon repandum* and an examination of sections of tetrasporangial conceptacles is required to positively identify the species. The species occurs commonly in South Africa (Chamberlain 1993), and it is considered likely that with further examination of collections, the species also will be found to occur commonly in southern Australia.

Genus **NEOGONIOLITHON** Setchell & Mason 1943: 90

by D.L. Penrose

Thallus encrusting, warty, lumpy or fruticose; epilithic or epizoic and affixed by cell adhesion, or unattached and free-living as rhodoliths; genicula absent. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions and radial in protuberant branches; construction monomerous, consisting of a single system of branched filaments that collectively contribute to a ventrally or centrally situated core, and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; epithallial cells terminating filaments at the thallus surface, distal walls rounded or flattened but not flared; trichocytes present or absent, if present appearing, in section, arranged in horizontal fields, horizontal rows, vertical rows, or occurring singly at the thallus surface, sometimes becoming buried within the thallus.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia, carposporangia, tetrasporangia and bisporangia borne in uniporate conceptacles; gametangia and carposporangia usually formed on separate plants from tetrasporangia and bisporangia.

Gametangial plants monoecious or dioecious; carpogonia and spermatangia produced in separate conceptacles or rarely in the same conceptacle. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Carposporophytes developing within female conceptacles after karyogamy, lacking a large central fusion cell and with short gonimoblast filaments bearing terminal carposporangia. Spermatangial filaments unbranched, formed on the chamber floor, walls and roof.

Tetrasporangia and bisporangia formed across the chamber floor or peripheral to a central columella, conceptacle roofs formed by filaments either surrounding sporangial initials or surrounding and interspersed amongst sporangial initials, each mature sporangium lacking an apical plug, zonately divided.

Type species: *Neogoniolithon fosliei* (Heydrich)Setchell & Mason 1943: 90.

At least 62 species and infraspecific taxa have been ascribed to *Neogoniolithon* (Woelkerling 1988, p. 142). Recently, an emended description of the genus has been published (Penrose 1992b) and the number of true species of *Neogoniolithon* is unknown. Information on nomenclature and the historical background of the genus has been provided by Woelkerling (1988, pp. 141,142,145).

Neogoniolithon brassica-florida (Harvey)Setchell & Mason 1943: 91. Woelkerling *et al.* 1993: 323, figs 7–11. Verheij 1993b: 53, figs 51–57; 1994: 113, figs 51–57.
Melobesia brassica-florida Harvey 1849: 110.
Lithothamnion fosliei Heydrich 1897a: 58, pl. 3 figs 9–11, text fig. 1.
Lithophyllum fosliei (Heydrich)Heydrich 1897b: 410.
Archaeolithothamnion fosliei (Heydrich)Foslie 1898: 4.
Goniolithon fosliei (Heydrich)Foslie 1903: 470.
Neogoniolithon fosliei (Heydrich)Setchell & Mason 1943: 90. Penrose 1992b: 338, figs 1–29
Goniolithon finitimum Foslie 1908:8.
Neogoniolithon finitimum (Foslie)Setchell & Mason 1943: 91. Penrose 1990: 191.

FIG. 129

Thallus encrusting, warty, lumpy or fruticose, 0.2–40 mm thick, epilithic or epizoic and affixed by cell adhesion, or unattached and free-living as rhodoliths. *Structure* pseudoparenchymatous; organisation dorsiventral in crustose portions and radial in protuberant branches; construction monomerous, consisting of a single system of branched filaments that collectively contribute to a ventrally or centrally situated core, and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface, each filament composed of cells 10–20 µm in diameter and 10–40 µm long; epithallial cells terminating filaments at the thallus surface, distal walls rounded or flattened but not flared; cells of adjacent filaments joined by cell-fusions, secondary pit-connections absent; trichocytes present or absent, if present appearing, in section, arranged in horizontal fields, horizontal rows, vertical rows, or occurring singly at the thallus surface, sometimes becoming buried within the thallus.

Reproduction. Vegetative reproduction by thallus fragmentation. Gametangia, carposporangia, tetrasporangia and bisporangia produced in uniporate conceptacles.

Gametangial plants dioecious or monoecious; carpogonia and spermatangia produced in separate conceptacles or in the same conceptacle. Carpogonia terminating 3-celled filaments arising from the female conceptacle chamber floor. Mature female-carposporangial conceptacle roofs protruding above the surrounding thallus surface, composed of 10–25 cells above the chamber, conceptacle chambers 460–630 µm in diameter and 500–710 µm high. Carposporophytes developing within older female conceptacles after karyogamy, when mature lacking a large central fusion cell and with short gonimoblast filaments bearing terminal carposporangia 25–85 µm in diameter and 56–90 µm high. Spermatangial filaments unbranched, arising from the floor, walls and roof of male conceptacle chambers, mature male conceptacle roofs protruding above the surrounding thallus surface, composed of 10–25 cells, conceptacle chambers 295–335 µm in diameter and 350–380 µm high.

Tetrasporangial and bisporangial conceptacle roofs protruding above surrounding thallus surface, 10–25 cells thick above the chamber, pore canals lined with protruding cells, conceptacle chambers 590–820 µm in diameter and 370–820 µm high; tetrasporangia and bisporangia scattered across the conceptacle chamber floor; each mature sporangium 20–70 µm in diameter and 110–165 µm long, zonately divided.

Type from Algoa Bay, South Africa (*Bowerbank*); lectotype in BM (algal box collection no. 78), designated by Penrose & Chamberlain (in Woelkerling 1992, p. 43).

Distribution: Indian Ocean; Pacific Ocean; Red Sea; tropical W. Aust. and Queensland. In southern Australia, Rottnest I., W. Aust., to Walkerville, Vic.

Selected specimens: Jeannies Lookout, Rottnest I., W. Aust., 1–3 m deep (*Woelkerling*, 12.ii.1978; LTB, 10624). Point Valliant, Two People Bay, W. Aust., 0.5 m deep (*Woelkerling*, 2.ii.1978; LTB, 10724). Lucky Bay, Cape Le Grand, W. Aust., 0–3 m deep (*Woelkerling, Platt & Jones*, 9.ii.1984; LTB, 14343). Rossiter Bay, Esperance, W. Aust., 1–2 m deep (*Woelkerling*, 28.i.1978; LTB, 10740). 10 km E of Eyre, W. Aust., 1–2 m deep (*Woelkerling, Platt & Jones*, 3.ii.1984; LTB, 14135). Point Fowler (E shore), S. Aust., 2–3 m deep (*Woelkerling, Platt & Jones*, 14.ii.1984; LTB, 14457). Elliston, S. Aust., 6 m deep (*Turner*, 29.x.1981; LTB, 15366). Hansen Bay, Kangaroo I., S. Aust., 0–1.5 m deep (*Campbell & Penrose*, 9.iv.1988; LTB, 15702, 15707). Cape Jaffa, S. Aust.1 m deep (*Campbell & Penrose*, 18.ii.1987; LTB 15550). Beachport (W of Post Office Rock), S. Aust., 0–2 m deep

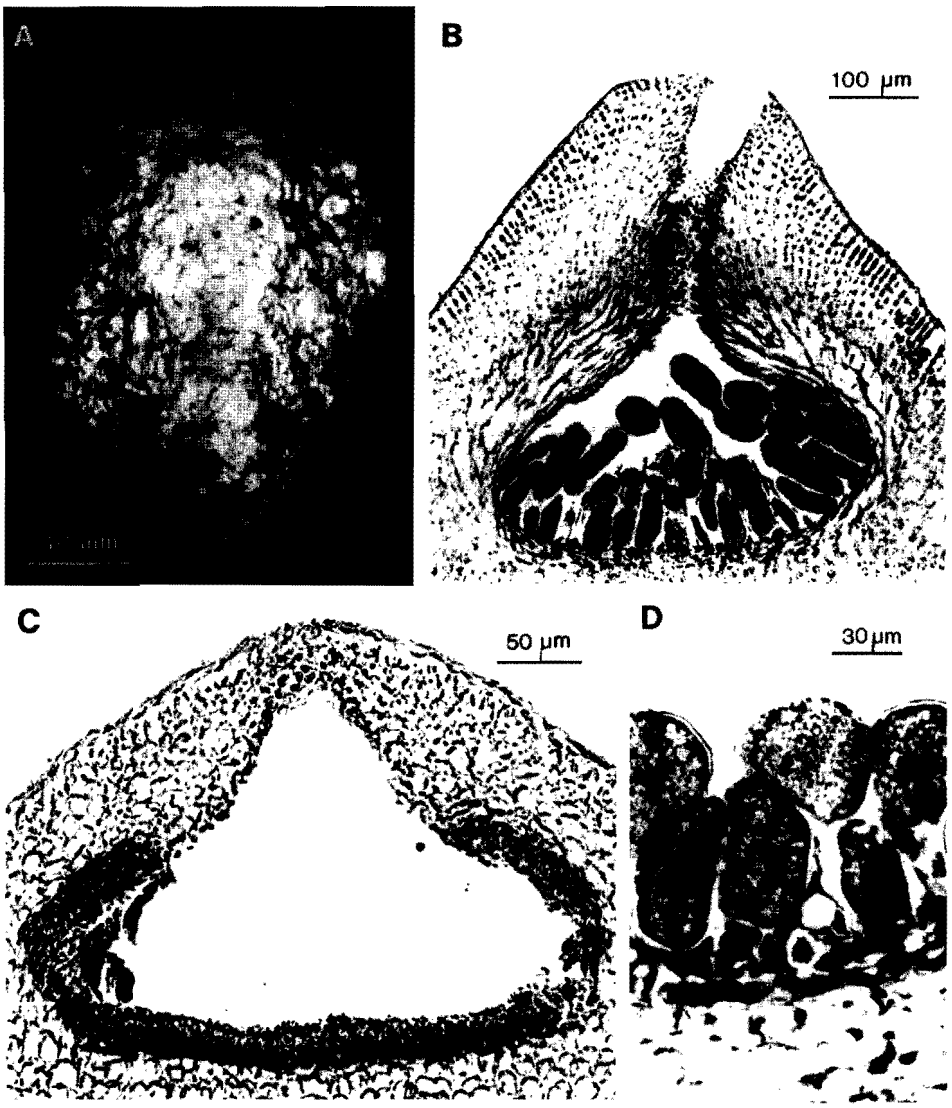


Fig. 129. *Neogoniolithon brassica-florida* (**A**, LTB, 14343; **B**, LTB, 15702; **C**, LTB, 10624; **D**, LTB, 15707). **A**. Epilithic plants with wart-like protuberances. **B**. Section of tetrasporangial conceptacle. **C**. Section of conceptacle containing spermatangia that have arisen from initials formed across the chamber floor and on the roof. **D**. Section of conceptacle showing part of a fusion cell with gonimoblast filaments formed at the dorsal surfaces of the fusion cell and bearing terminal carposporangia.

(*Campbell, Penrose & Woelkerling*, 26.ii.1988; LTB, 15786). Blanket Bay, Cape Otway National Park, Vic., 4 m deep (*Campbell, Penrose & May*, 14.xi.1985; LTB, 15234). Ingoldsby Reef, Anglesea, Vic., reef top (*Beanland*, 26.ii.1983; LTB, 13506). Eagles Nest (E of Cape Patterson), Vic., upper sublittoral (*Campbell*, iii.1988; LTB, 16040). Walkerville, Vic., intertidal pools (*Woelkerling*, 28.xii.1978; LTB, 11754)

N. brassica-florida occurs commonly throughout southern Australia and often can be recognised in the field by its large conceptacles which protrude conspicuously above the surrounding thallus surface. Additional data on the species (as *N. fosliei*) have been provided by Penrose (1992b).

SUBFAMILY AMPHIROIDEAE Johansen 1969: 47

by H.B.S. Womersley & H.W. Johansen

Thallus with an encrusting non-geniculate holdfast and erect, compressed or terete, dichotomous to whorled branches composed of alternating genicula and intergenicula. *Structure* of branches multiaxial; intergenicula with a medulla of cohering filaments in one to numerous tiers of cells, in *Amphiroa* with single tiers of shorter cells separated by 2–7 tiers of longer cells; genicula in *Amphiroa* of one to several tiers similar in structure to intergenicula (in *Lithothrix* of single long-celled tiers), not producing lateral branches. Apical cells with epithallial cells but without conspicuous mucilaginous caps. Secondary pit-connections formed laterally between medullary cells, often in arcs across the medulla; cell-fusions absent. Cortex of anticlinal filaments of isodiametric cells in both intergenicula and genicula.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli monoecious or (usually) dioecious, carpogonia and spermatangia produced in separate conceptacles. Carpogonial filaments usually 2-celled, arising on the chamber floor, carposporangia terminating short gonimoblast filaments arising from a basal fusion cell. Spermatangia on short unbranched filaments on the male chamber floor.

Tetrasporangia borne on separate thalli, conceptacle roofs connected to elongate cells arising from the chamber floor among the sporangia.

Type genus: *Amphiroa* Lamouroux 1812: 186.

The Amphiroideae contains two tribes, the Amphiroeae Cabioch (1972, p. 266) with *Amphiroa*, and the Lithotricheae Johansen & Silva (1978, p. 415), containing only the Pacific N. American genus *Lithothrix* Gray, which is characterised by alternating single tiers of long genicula cells and short intergenicula cells, and an intergenicular cortex extending down over the genicula.

TRIBE AMPHIROEAE Cabioch 1972: 266

Characters as for the subfamily Amphiroideae, with one to several medullary cell tiers in the genicula, several to many tiers in the intergenicula with tiers of shorter cells separated by 2–7 tiers of longer cells, and a cortex several cells thick in both genicula and intergenicula.

Genus AMPHIROA Lamouroux 1812: 186

Thallus with a crustose or endophytic base and erect to decumbent geniculate branches, with dichotomous, compressed branches or terete branches bearing clustered or whorled branches from the upper ends of many intergenicula; holdfast crustose or filamentous, endophytic, epilithic or epiphytic. *Structure* of branches with a 1– multi-tiered medulla of alternating short and one to several long-celled tiers, with lateral secondary pit-connections and a cortex several cells thick in both genicula and intergenicula, with epithallial cells; genicula formed by decalcification.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Conceptacles on the surfaces of intergenicula. Gametangial thalli usually dioecious, if monoecious with carpogonia and spermatangia in separate conceptacles. Carpogonial filaments usually 2-celled, arising on chamber floor, carposporangia terminating short gonimoblast filaments arising from a basal fusion cell. Spermatangia on short unbranched filaments on the chamber floor.

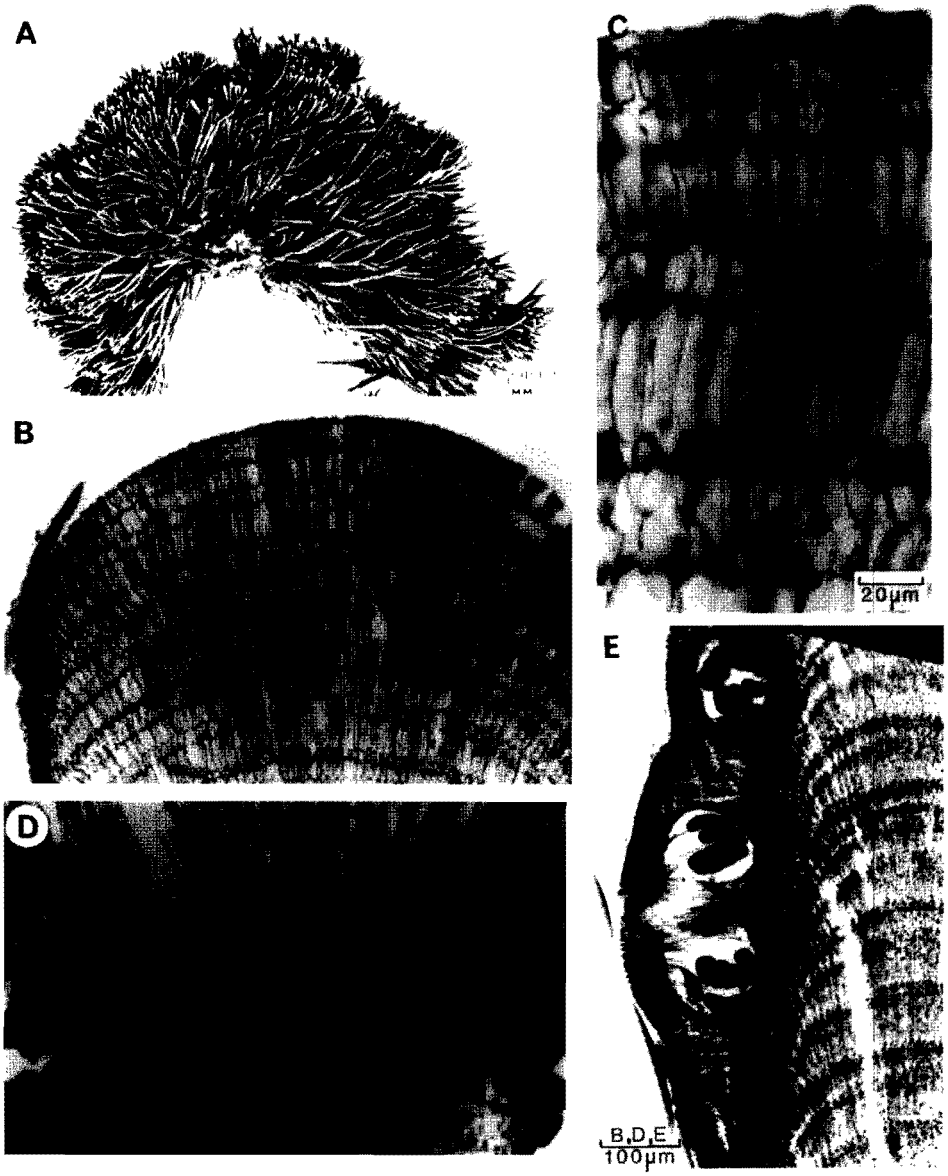


Fig. 130. *Amphiroa anceps* (**A**, AD, A64304; **B–D**, AD, A52701; **E**, AD, A13831). **A.** Habit. **B.** Longitudinal section of branch apex showing long and short tiers and arcs of lateral pit-connections. **C.** As for **B**, enlarged. **D.** Longitudinal section of intergeniculum (upper) and geniculum (lower) with boundary of decalcification lying across the cell tiers. **E.** Longitudinal section through tetrasporangial conceptacles.

Tetrasporangia borne on separate thalli, with the roofs of the conceptacles connected to elongate cells from the floor which are interspersed among and peripheral to the zonately divided sporangia.

Lectotype species: *A. tribulus* (Ellis & Solander)Lamouroux 1812: 186. (Hamel & Lemoine 1953: 40.)

Amphiroa contains numerous species, mainly tropical – subtropical in distribution, with two species on southern Australian coasts.

While only one species, *A. anceps*, is common in southern Australia (from Cape Naturaliste south), another species, *A. gracilis* Harvey (1855a, p. 547), which was described from "King George's Sound and Rottnest", occurs in scattered localities.

KEY TO SPECIES OF *AMPHIROA*

1. Branches compressed, 1–3 (-4) mm broad except near the base ..... 1. *A. anceps*
1. Branches terete, 1–2 mm in diameter near the base, 300–500 μm in diameter near the apices ..... 2. *A. gracilis*

1. **Amphiroa anceps** (Lamarck)Decaisne 1842b: 125. Adams 1994: 160, pl. 55 upper left. Areschoug 1852: 536. Chapman & Parkinson 1974: 172. De Toni 1905: 1815. Ganesan 1968: 7, figs 1, 2, 5–7, 12–20, pl. 1 figs 3, 4. Harvey 1849a: 98, pl. 37 lower. Huisman & Walker 1990: 411. Kützing 1849: 702; 1858: 24, pl. 49 fig. IV. May 1965: 357. Millar 1990: 315, fig. 9. Sonder 1881: 20. Weber-van Bosse 1904: 93, pl. 16 figs 6–8.
   Corallina anceps Lamarck 1815: 238.
   Amphiroa dilatata Lamouroux 1816: 299. Areschoug 1852: 536. De Toni 1905: 1815. Harvey 1849a: 97. Kützing 1849: 703; 1858: 25, pl. 50 fig. II. Sonder 1853: 687. Yendo 1902: 12, pl. 1 figs 17–21, pl. 5 fig. 4.
   Amphiroa galaxauroides Sonder 1848: 188; 1881: 20. Kützing 1849: 703; 1858: 25, pl. 51 fig. I.
   Amphiroa nobilis Kützing 1849: 703; 1858: 25, pl. 51 fig. II. Areschoug 1852: 541. De Toni 1905: 1821.
   Galaxaura versicolor Sonder 1845: 50.
   ?*Amphiroa beauvoisii* Lamouroux *sensu* King *et al.* 1971: 121. Woelkerling 1988: fig. 43.
   Amphiroa ephedraea (Lamarck)Decaisne *sensu* Harvey 1863, synop.: xxix. Lucas 1929b: 53. Saenger 1974: 80. Tisdall 1898: 507.

FIG. 130

Thallus (Fig. 130A) medium red-purple, often fading to grey-red in shallow-water plants, 2–10 (-15) cm high, often tufted and much branched dichotomously (rarely with small proliferations) from the upper end of each intergeniculum, branching essentially complanate, intergenicula more or less terete near the base, compressed to flat above and 4–10 (-15) mm long, (0.5-) 1–3 (-4) mm broad and (300-) 500–1000 μm thick centrally, edges thinner and more or less sharp-edged, margins parallel to slightly broader above, calcification over genicula closer near the margins. Holdfast crustose, 2–10 mm across, bearing numerous fronds; epilithic. *Structure* multiaxial. Intergenicula (Fig. 130B, C) consisting of numerous curved tiers of medullary cells with the filaments splaying laterally, with lateral secondary pit-connections between the medullary cells forming arcs across the intergenicula; medulla with tiers of shorter cells (10–25 μm long) separating every 2–5 tiers of longer cells (40–70 μm long), all 8–15 μm in diameter, ends rounded and separated when decalcified. Genicula (Fig. 130D) with the upper and lower margins not corresponding to the ends of cell tiers, of similar structure to intergenicula but cell walls more darkly staining. Cortex compact, extending from outer cells of the medullary filaments, cortical filaments of 3–8 isodiametric or slightly elongate cells 7–12 μm in diameter, with terminal epithallial cells; usually thicker near tetrasporangial conceptacles. Apices of branches (Fig. 130C) with meristematic cells surmounted with small epithallial cells. Rhodoplasts discoid.

Reproduction. Conceptacles uniporate, mostly on the surface of one side of the intergenicula. Gametangial thalli dioecious. Female conceptacles (Ganesan 1968, p. 12, fig. 19) 400–800 µm in external diameter and 128–160 µm high; carposporophyte with a broad, thin fusion cell bearing marginal short chains of ovoid carposporangia 25–30 µm in diameter. Male conceptacles (Ganesan 1968, p. 14, fig. 19) inconspicuous, 400–450 µm in external diameter, with spermatangia cut off from initials on the chamber floor, ovoid, 1.5–3 µm in diameter.

Tetrasporangial conceptacles (Fig. 130E) prominent, 250–500 µm in external diameter, with a central tuft of elongate cells and tetrasporangia lying between similar cells, elongate-ovoid, 20–50 µm in diameter, zonately divided or often as bisporangia.

Type from "Nouvelle-Hollande" (*Péron & Lesueur*); holotype in PC.

Distribution: All around Australia except for Tasmania, but less frequent in SE S. Aust. and Victoria.

Widespread in the Indo-Pacific.

Selected specimens: Off Hillarys Boat Harbour, Sorrento, W. Aust., 6 m deep (AIMS–NCI, Q66C 2614-I, 12.iii.1989; AD, A59759). Whitford Beach, Perth, W. Aust., 6 m deep (*Cook*, 20.viii.1979; AD, A50557). Strickland Bay, Rottnest I., W. Aust., 1–2 m deep (*Clarke & Engler*, 5.ix.1979; AD, A51114). Green I., Rottnest I., W. Aust., upper sublittoral (*Parsons*, 11.xi.1968; AD, A33339). Cowaramup Bay, W. Aust., 2–3 m deep (*Clarke & Engler*, 1.ix.1979; AD, A50647). Twin Rocks, Head of Great Australian Bight, S. Aust., 20–22 m deep (*Branden*, 19.i.1991; AD, A61131). Masillon I., Isles of St Francis, S. Aust., 13–18 m deep (*Shepherd*, 5.i.1971; AD, A38009). Smooth Pool, W of Streaky Bay, S. Aust., upper sublittoral (*Johansen* 81-10-14a, 25.x.1981; AD, A52755). Louth Bay, S. Aust., upper sublittoral (*Womersley*, 5.i.1951; AD, A13831). Port Noarlunga, S. Aust., on off-shore reef (*Womersley*, 21.x.1944; AD, A1681). Aldinga, S. Aust., upper sublittoral pools (*Clarke & Engler*, 29.x.1981; AD, A52701). Judith Cove, West I., S. Aust., 3–4 m deep (*Shepherd*, 19.vi.1995; AD, A64304). Cape du Couedic, Kangaroo I., S. Aust., sublittoral fringe (*Womersley*, 12.i.1948; AD, A7013). Between Knob Point and Cape Cassini, Kangaroo I., S. Aust., 8 m deep (AIMS–NCI, Q66C 2173-C, 29.i.1989; AD, A59689). Warrnambool, Vic., upper sublittoral (*Womersley*, 13.iv.1959; AD, A22892). Port Phillip Heads, Vic., in pools (*Sinkora* A942, 8.xi.1970; AD, A62565). Walkerville, Vic., in large pool (*Sinkora* A1776, 21.xi.1973; AD, A53478).

Amphiroa anceps, with its flat branches, is a distinctive species but plants vary considerably in width of the intergenicula. Broader branches (e.g. AD, A59759) appear to occur in deeper water (or shaded) habitats in Western Australia, with narrow ones in shallow water (e.g. AD, A52755).

While *A. anceps* is common in warmer waters, it extends along the southern Australian coast but has not been recorded from Tasmania. The European *A. beauvoisii* Lamouroux has been recorded from Port Phillip Heads, Vic., by King *et al.* (1971, p. 121) and from Port Fairy, Vic., 4.i.1979 (LTB, 11707) by Woelkerling (1988, fig. 43). These records probably apply to *A. anceps*. Records of the tropical *A. ephedraea* probably also apply to *A. anceps*; Weber van-Bosse (1904, p. 93) placed Harvey's record from N.S.W. as *A. anceps*.

The very regular tiers of cells, and the lateral pit-connections, indicate that both the cells and pit-connections are formed sequentially near the branch apices. Sexual thalli have not been recorded in southern Australian plants.

2. **Amphiroa gracilis** Harvey 1855a: 547; 1862: pl. 231; 1863, synop.: xxix. De Toni 1905: 1809. Huisman & Walker 1990: 411. Johansen 1969: 50 pl. 14C (as *Amphiroa* sp. but based on Harvey, Alg. Aust. Exsicc. 459A). Lucas & Perrin 1947: 394. Sonder 1881: 20.
Metagoniolithon gracile (Harvey)Yendo 1905: 12. Ducker 1979: 96, fig. 15B. Ganesan 1971: 248. Manza 1940: 311. May 1965: 356.

FIG. 131

Thallus (Fig. 131A) medium red-brown, fading to grey-red, 4–10 cm high, with several axes from the holdfast, branching usually fastigiate with 2–4 (-6) branches from each intergeniculum, not complanate, intergenicula terete, 4–6 mm long and (1-) 1.5–2 mm in diameter near the base, decreasing evenly to (3-) 4–6 mm long and 300–500 µm in diameter

above. Holdfasts crustose, 2–8 mm across, bearing several to numerous fronds; epilithic. *Structure* multiaxial. Intergenicula (Fig. 131B) of numerous arching tiers of medullary cells, with lateral pit-connections about three-quarters up the cells; single tiers of shorter cells (15–45 μm long) separating every 2–4 (-7) tiers of longer cells (60–90 μm long), all 9–16 μm in diameter, ends rounded. Genicula (Fig. 131C) ends not corresponding to tiers, similar in structure to intergenicula but cells narrower, thicker walled and darkly staining, with lateral pit-connections. Cortex compact, developed from larger, ovoid, outer medullary cells, consisting of anticlinal filaments of 5–10 ovoid cells (6-) 7–9 μm in diameter, with short epithallial cells, present but less well developed on genicula. Apices of branches with meristematic cells and small epithallial cells. Rhodoplasts discoid to laminate.

Reproduction. Gametangial thalli unknown.

Tetrasporangial conceptacles (Fig. 131D) prominent, 250–500 μm in external diameter, tetrasporangia among elongate cells, 70–110 μm long and 35–55 μm in diameter, zonately divided.

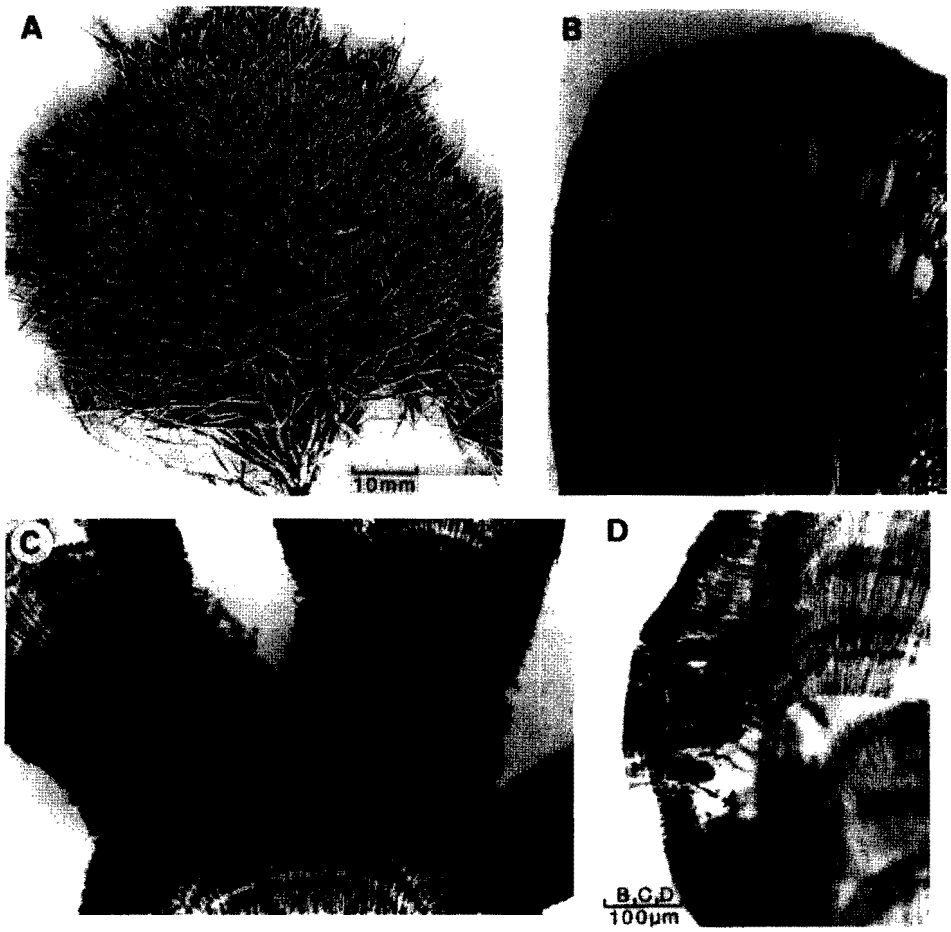


Fig. 131. *Amphiroa gracilis* (**A**, AD, A13829; **B–D**, AD, A64576). **A.** Habit. **B.** Longitudinal section of branch apex showing long and short tiers and arcs of lateral pit-connections; spaces due to processing. **C.** Longitudinal section of genicula and adjacent intergenicula. **D.** Longitudinal section (broken) of tetrasporangial conceptacle.

Type from "King George Sound and Rottnest", W. Aust. (*Harvey*, Trav. Set 218); lectotype (here designated) from Rottnest I, W. Aust.; in TCD.

Distribution: Kalbarri, W. Aust., to Troubridge Hill, Yorke Pen., S. Aust.

Selected specimens: Red Bluff, Kalbarri, W. Aust., upper sublittoral pools (*Womersley*, 15.ix.1979; AD, A51287 —"Marine Algae of southern Australia" No. 199). Port Denison, W. Aust., outer reef pools (*Gordon*, 8.xi.1968; AD, A33150). Fish Hook Bay, Rottnest I., W. Aust., upper sublittoral (*Gordon-Mills*, 6.xii.1984; AD, A56660). Fenelon I., Isles of St Francis, S. Aust., 5 m deep (*Edyvane*, 19.vi.1992; AD, A62134). The Gap, Thorny Passage, NW Thistle I., S. Aust., 4–5 m deep (*Branden*, 30.ix.1989; AD, A59932, A59933). Louth Bay, S. Aust., upper sublittoral (*Womersley*, 5.i.1951; AD, A13829). Cable Hut Bay, Yorke Pen., S. Aust., 5 m deep (*Edyvane*, 27.x.1993; AD, A64426). Troubridge Hill, S. Aust., 5 m deep (*Edyvane*, 30.x.1993; AD, A64576).

A. gracilis was described from "King George's Sound and Rottnest", based on Harvey's Trav. Set 218. No specimens from King George Sound were located in TCD in 1952, and Harvey's 218 from Rottnest I. (the lectotype) is in fragments. There are three good specimens from "Swan River" in TCD.

A. gracilis occurs on southern Australian coasts as far east as Troubridge Hill, Yorke Peninsula, but it is apparently not common. Structurally it is a typical *Amphiroa*, but it can superficially resemble slender *Metagoniolithon radiatum*. However, *A. gracilis* usually forms more erect, fastigiate tufts with several clustered fronds from the holdfast, the intergenicula decreasing fairly evenly in length from the base upwards.

Ducker (1979, p. 98) queried whether *A. gracilis* is not synonymous with *A. fragilissima*, but the latter differs in habit and in having collars at the ends of older intergenicula (Weber-van Bosse 1904, p. 91). Further comparisons with tropical species of *Amphiroa* are clearly needed.

Metagoniolithon gracile, as recorded in Womersley (1950, p. 167), is now referred to *M. chara*.

SUBFAMILY CORALLINOIDEAE (Areschoug)Foslie 1908: 19

by H.B.S. Womersley & H.W. Johansen

Thallus with an encrusting non-geniculate holdfast and erect to procumbent, terete to compressed, dichotomous to pinnate or radially branched, branches of alternating genicula and intergenicula; basal stolons present in some taxa. *Structure* of branches multiaxial, intergenicula with a medulla of cohering filaments in 1 to 25 (-40) tiers of cells, without lateral secondary pit-connections but with lateral cell-fusions; genicula with single tiers of non-calcified cells, cells usually longer than intergenicula cells. Cortex on intergenicula only, with epithallial cells on all calcified surfaces except branch apices and margins of crustose holdfasts.

Life history triphasic, with isomorphic gametophytes and tetrasporophytes.

Reproduction. Propagula present in a few taxa. Reproductive organs borne in uniporate conceptacles. Gametangial thalli monoecious or dioecious, with separate axial or lateral female and male conceptacles, usually urceolate. Carpogonial filaments usually 2-celled, arising on the chamber floor, carposporangia terminating short gonimoblast filaments from all over or from the margins of the basal fusion cell. Spermatangia on short filaments on the floor or sides of the male conceptacle chambers.

Tetrasporangia (or bisporangia) borne on separate thalli in urceolate or embedded conceptacles, roofs formed from peripheral filaments; sporangia zonately divided.

Type genus: *Corallina* Linnaeus 1759: 646, 805.

The Corallinoideae include twelve genera, five known from southern Australia. The doubtful reference to *Bossiella* in southern Australia (Johansen 1981, p. 123) is based on *Amphiroa tasmanica* Sonder (1853, p. 686), from "Van Diemensland (*Stuart*)", which Setchell & Gardner (1903, p. 360) suggested (as did Yendo 1902, p. 714) was a form of

Amphiroa cretacea (now *Bossiella*). The lectotype (47421) and isolectotype (47422) are in MEL, and were illustrated by Kützing (1858, p. 23, pl. 47, fig. II), who shows an irregularly branched plant with cylindrical intergenicula. The latter (apparently sterile) have single-tiered genicula and intergenicula which show centrally numerous short tiers surrounded by a rather loose and untiered outer medulla, the cells with lateral cell-fusions, and a thick cortex; this is very similar to *B. cretacea* from Japan (AD, A57512). No other specimens from southern Australia corresponding to these have been seen, and it seems most likely that the types are mis-labelled for locality. They agree well with *Bossiella cretacea* (Postels & Ruprecht)Johansen (1969, p. 59) from the northern Pacific. Until further collections are made, it seems best to eliminate "*Amphiroa tasmanica* Sonder" from the southern Australian flora. It has also been recorded from southern South America (see Pujals 1963, p. 19).

KEY TO TRIBES OF CORALLINOIDEAE

1. Intergenicula with 10–25 (-50) tiers of medullary cells; fusion cells thin and broad, with surface and marginal carposporangial filaments; male conceptacles with beaks and low ceilings; usually many (>30) tetrasporangia per conceptacle ..... Corallineae
1. Intergenicula with (1-) 3–6 (-25) tiers of medullary cells; fusion cells thick and compact, with marginal carposporangial filaments; male conceptacles without beaks and with high ceilings; few (<15) tetrasporangia per conceptacle ..... Janieae

TRIBE CORALLINEAE Areschoug 1852: 509

Thallus usually pinnately branched. Intergenicula with (8-) 10–25 (-50) tiers of medullary cells each 50–90 µm long. Fusion cells thin (6–12 µm) and broad (90–300 µm), with carposporangial filaments from margins and/or upper surface; male conceptacles with a broad chamber (350–450 µm), low ceilings and long canal (200–500 µm). Tetrasporangia relatively small, many (>30) per conceptacle, with interspersed paraphyses, conceptacles usually without branches.

KEY TO GENERA OF CORALLINEAE

1. Intergenicula with (8-) 10–20 (-25) tiers of medullary cells. Carposporangial filaments near the margin of fusion cells; male conceptacles with short beaks; tetrasporangial conceptacles seldom bearing branchlets; fertile intergenicula narrow ..... CORALLINA
1. Intergenicula with 20–50 tiers of medullary cells. Carposporangial filaments over the surface of fusion cells; male conceptacles usually with long beaks; all conceptacles usually bearing branchlets, fertile intergenicula broad ..... ARTHROCARDIA

Genus CORALLINA Linnaeus 1758: 646, 805

Thallus with few to numerous erect, pinnate, geniculate fronds, often with clustered to whorled branchlets, intergenicula usually compressed, cuneate above, elongate and subterete below; holdfast crustose, stolons rare or absent, usually epilithic, sometimes epiphytic. *Structure.* Intergenicula with (8-) 10–20 (-25) arching tiers of elongate medullary cells, with lateral cell-fusions but without lateral pit-connections. Genicula of single tiers of elongate, thicker walled, cells. Cortex present on intergenicula, of short splaying to anticlinal filaments, terminating in short epithallial cells.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Conceptacles usually axial and terminal, occasionally with short branchlets. Gametangial thalli dioecious. Carpogonial filaments 2-celled, arising on floor of female conceptacles, carposporangia in 2–6-celled filaments near the margins of a thin fusion cell. Male conceptacles with short beaks, without branchlets, spermatangia terminating short filaments on the floor and lower walls of chambers.

Tetrasporangia (or bisporangia) borne on separate thalli, conceptacles occasionally bearing branchlets, ovoid-urceolate, with several to numerous tetrasporangia arising from the

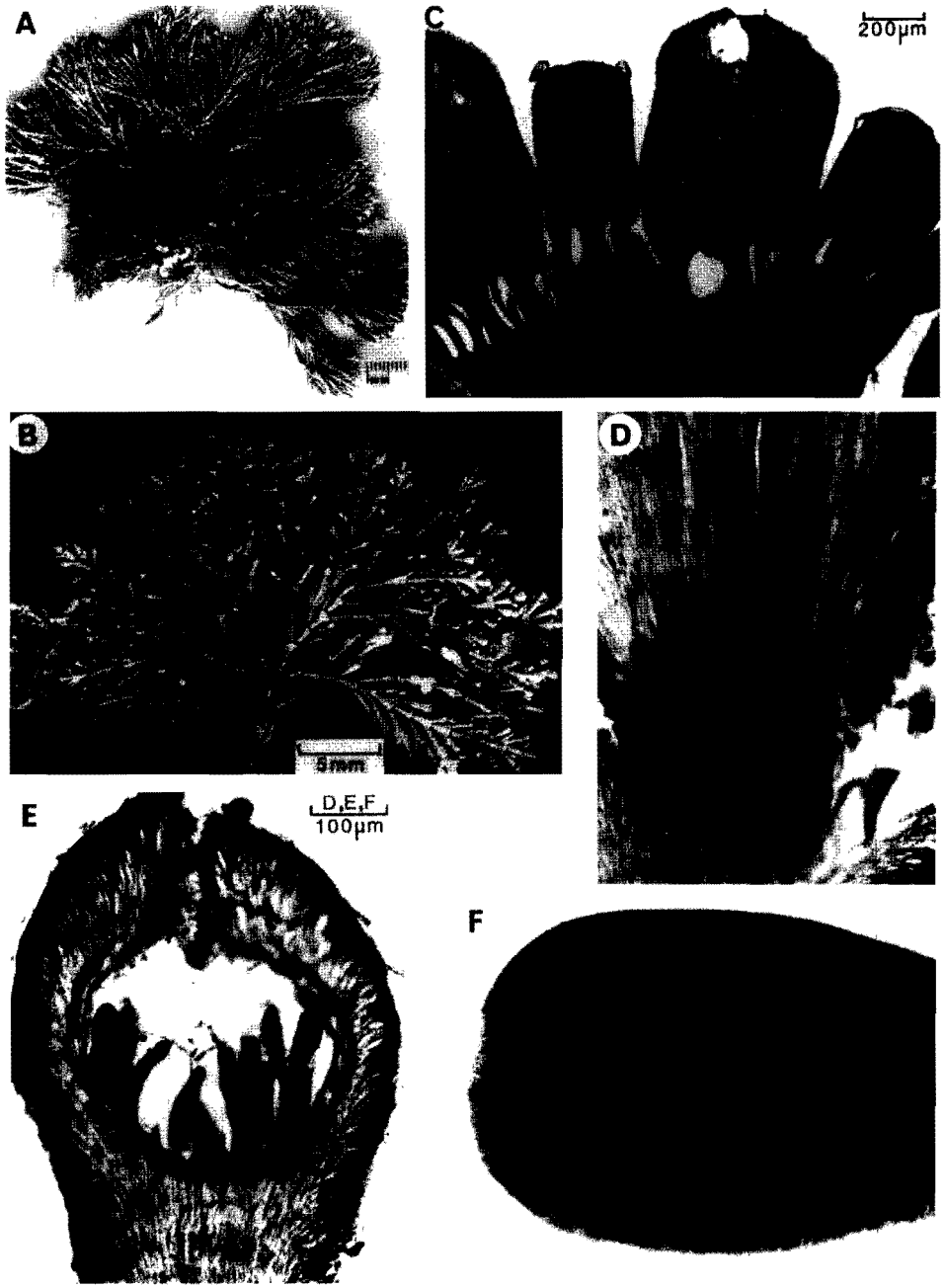


Fig. 132. *Corallina officinalis* (**A–D,** AD, A59915; **E, F,** AD, A52774). **A.** Habit. **B.** Habit, enlarged. **C.** Longitudinal section of apex with five branches. **D.** Longitudinal section of geniculum and intergenicula tiers. **E.** Longitudinal section of tetrasporangial conceptacle. **F.** Longitudinal section of conceptacle with mature tetrasporangia.

chamber floor, with interspersed paraphyses in young conceptacles; intergenicula narrow just below conceptacles.

Lectotype species: *Corallina officinalis* Linnaeus 1758: 805 (Schmitz 1889: 455).

Corallina contains numerous species, with the type species widely distributed in temperate waters, often forming mats near low water level. Although information on species delimitation in *Corallina* is limited, probably only a single species occurs in southern Australia.

Corallina officinalis Linnaeus 1758: 805. Borowitzka & Vesk 1978: 295, figs 1–5. Chapman & Parkinson 1974: 180, pl. 61b. De Toni 1905: 1840. Hamel & Lemoine 1953: 31, figs 1–3, pl. 1 fig. 1. Harvey 1849b: pl. 222; 1859b: 310. Irvine & Johansen 1994: 44, figs 12A, 13A, B, 14C, D, 15A, B, 18A. King *et al.* 1971: 121. Kylin 1944: 47, pl. 9 fig. 29. Manza 1940: 275, pl. 7. Suneson 1937: 29, figs 18–22, pl. 1. Womersley 1950: 1167; 1966: 146.
Corallina chilensis Decaisne *in* Harvey 1849a: 103 *sensu* Gepp & Gepp 1906: 261. Harvey 1863, synop.: xxviii. Millar & Kraft 1993: 13. Sonder 1881: 21.
Corallina pilulifera Postels & Ruprecht *sensu* Cribb 1954: 35.

PLATE 4 fig. 2; FIG. 132

Thallus (Fig. 132A, B) pink-grey to medium red-purple, fading to light grey, (1-) 2–6 cm high, usually in tufts of several to numerous erect fronds from a crustose base. Fronds pinnately and complanately branched for 2–3 orders, usually from each intergeniculum (Fig. 132C) with one or two lateral branches from each shoulder, commonly denuded below. Intergenicula subterete to slightly compressed near the base of axes, compressed above and broader apically, usually 500–1000 (-1500) µm long and 500–800 (-1500) µm broad, edges rounded in section. Lateral branches distinctly slenderer, simple or branched, terete and tapering to slightly broader above, 200–300 (-500) µm in diameter, intergenicula 700–1500 µm long; some terminal intergenicula flat and spathulate. Holdfast discoid, becoming crustose and (0.5-) 1–2 cm across; epilithic or on mollusc shells. *Structure* multiaxial, intergenicula (Fig. 132D) of (8-) 10–20 (-25) tiers of medullary cells 30–60 µm long and 6–10 µm in diameter, with frequent lateral cell-fusions; ends of tier cells usually not aligned. Cortex of splaying filaments from the outer medullary filaments, cells 4–10 µm in diameter and L/D (1-) 2–4, with small epithallial cells. Rhodoplasts discoid to laminate. Genicula (Fig. 132D) of single tiers of slender, cells 180–350 µm long and 4–7 µm in diameter, walls staining darkly.

Reproduction. Gametangial thalli dioecious. Conceptacles uniporate, axial, swollen, terminating lateral branchlets or occasionally (female and tetrasporangial) bearing short slender branchlets.

Carposporangial conceptacle chambers (Irvine & Johansen 1994, p. 45) 250–400 µm in diameter, 300–320 µm high, roofs 150–240 µm thick, fusion cells 90–200 µm in diameter and 6–11 µm thick; carposporangia 30–80 µm in diameter. Male conceptacle chambers 250–480 µm in diameter, 100–300 µm high, roofs 200–600 µm thick.

Tetrasporangial conceptacle chambers (Fig. 132E, F) 300–450 µm in diameter, 300–600 µm high, with neck canal 200–250 µm long through the thickened roof; tetrasporangia 180–240 µm long and 55–85 µm in diameter, zonately divided.

Type from Europe; lectotype (Schmitz 1889: 455) in LINN, 1293.9.

Distribution: Widespread in temperate seas.

Selected specimens: Frenchman Bay, King George Sound, W. Aust., lower eulittoral (*Womersley*, 29.viii.1979; AD, A51660). Point Sinclair, S. Aust., lower eulittoral (*Womersley*, 26.i.1951; AD, A15121). Just SE of Wanna, S. Aust., upper sublittoral (*Johansen* 81-11-1b, 2.xi.1981; AD, A52774). Gleeson Landing, Yorke Pen., S. Aust., lower eulittoral (*Womersley*, 15.x.1989; AD, A59915 — "Marine Algae of southern Australia" No. 335a). Port Noarlunga, S. Aust., reef pool edges (*Johansen* 81-10-12, 13.x.1981; AD, A52708 —"Marine Algae of southern Australia" No. 335). Judith Cove, West I., S. Aust., 2 m deep (*Shepherd*, 5.xi.1966; AD, A31593). Cape du Couedic, Kangaroo I., S. Aust., upper sublittoral (*Womersley*, 17.i.1950; AD, A12671). Redbanks, Kangaroo I., S. Aust., upper sublittoral (*Womersley*, 29.i.1956; AD, A20332). Robe, S. Aust., lower eulittoral (*Womersley*,

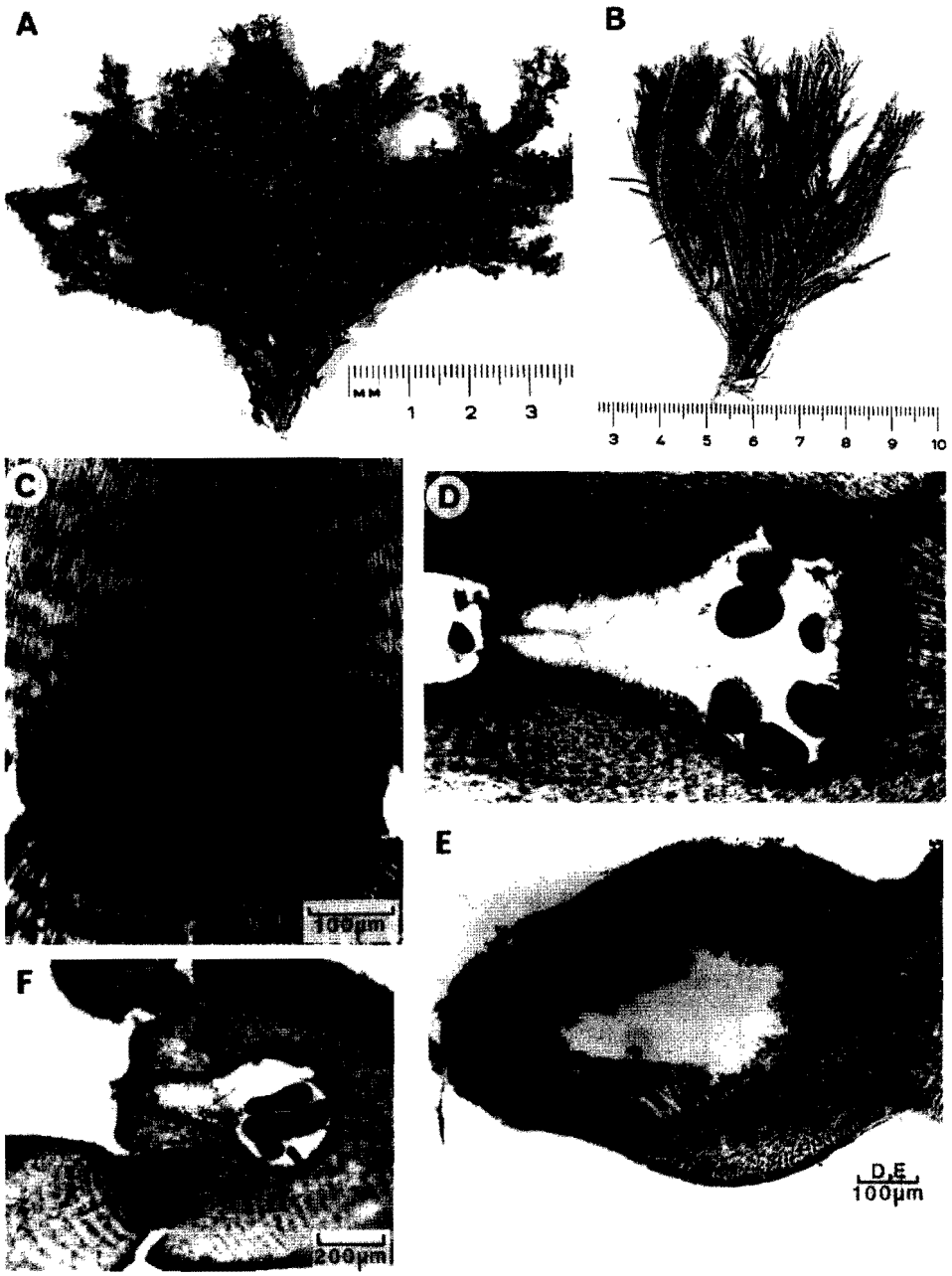


Fig. 133. *Arthrocardia wardii* (**A,** AD, A32317; **B,** AD, A32436; **C, E,** AD, A52798; **D, F,** AD, A64434). **A.** Habit of robust plant with proliferating adventitious branches. **B.** Habit of slender form. **C.** Longitudinal section of geniculum and part intergenicula. **D.** Longitudinal section of carposporangial conceptacle showing broad, thin fusion cell and peripheral carposporangia. **E.** Longitudinal section of male conceptacle. **F.** Longitudinal section of branch with a bisporangial conceptacle.

20.xii.1953; AD, A19134). Bridgewater Bay, Vic., lower eulittoral (*Womersley*, 29.xii.1981; AD, A52867). Rickett Point, Port Phillip, Vic., rock pools (*Sinkora* A388, 31.iii.1970; AD, A62593; MEL, 2010324). Queenscliff, Vic., upper sublittoral (*Johansen* 81-8-12a, 31.viii.1981; AD, A52610). Cape Sorell, W Tas., low eulittoral (*Bennett*, 4.ii.1955; AD, A20611). Shelter Point, Boat Harbour, N Tas., mid eulittoral pool (*Womersley*, 16.x.1982; AD, A55725). Bicheno, Tas. (*Perrin*, July 1940; AD, A61902). Canoe Bay, Fortescue Bay, Tasman Pen., Tas., 3–4 m deep (*Gowlett-Holmes*, 23.vi.1995; Ad, A64460). Fluted Cape, Bruny I., Tas., 19 m deep (*Shepherd*, 11.ii.1972; AD, A41842).

Corallina officinalis is the commonest geniculate coralline alga just above low tide level, often forming a distinct turf in the lower eulittoral zone. *Haliptilon roseum* also occurs frequently at this level, but is readily distinguished by having few medullary tiers compared to the many in *Corallina*.

Genus ARTHROCARDIA Decaisne 1842a: 365

Thallus with a crustose base bearing several to numerous erect, sparsely to densely pinnate fronds, largely complanately branched, intergenicula compressed, elongate to cuneate, broader above; holdfast crustose, epilithic. *Structure*. Intergenicula with 20–40 (-50) tiers of medullary cells, with lateral cell-fusions but without lateral pit-connections. Genicula of a single tier of elongate, thicker walled cells. Cortex present on intergenicula, of splaying then anticlinal filaments, outer cells with 1 (-2) short epithallial cells.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Conceptacles axial and deeply embedded in the apex of intergenicula, swelling the intergenicula only slightly, usually with two surmounting branches. Gametangial thalli dioecious. Carpogonial filaments arising on floor of female conceptacles, carposporangia in 2–4-celled filaments arising from the surface of the fusion cells. Male conceptacles with beaks, with or without branchlets, spermatangia terminating short filaments on the base and sides of the chamber.

Tetrasporangia (or bisporangia) borne on separate thalli, conceptacles usually with surmounting branches, sunken within the upper end of intergenicula, with several to numerous tetra (or bi-) sporangia arising from the chamber floor.

Lectotype species: *A. corymbosa* (Lamarck)Decaisne 1842a: 365 (Manza 1937, p. 48).

Arthrocardia is most closely related to *Corallina*, both genera having many tiers of medullary cells of similar length per intergeniculum. *Arthrocardia* has larger numbers of tiers than *Corallina*, with conceptacles sunken in the apices of intergenicula, carposporangial filaments over the surface of the fusion cells, and usually with branching from the tetra (or bi-) sporangial conceptacles.

KEY TO SPECIES OF *ARTHROCARDIA*

1. Thallus robust, (2-) 5–12 cm high, axial intergenicula 1.4–3.5 mm broad and L/W about 1, branching from most axial intergenicula ..... 1. *A. wardii*
1. Thallus slender, 2–4 (-6) cm high, axial intergenicula 0.7–1.4 mm broad, L/W 2–4, branching from about half the axial intergenicula ..... 2. *A. flabellata* ssp. *australica*

1. **Arthrocardia wardii** (Harvey)Areschoug 1852: 551. Guiler 1952: 87. Harvey 1863, synop.: xxix. Millar & Kraft 1993: 12. Sonder 1881: 20. Tisdall 1898: 507. Wilson 1892: 177. Womersley & Johansen 1988: 40, figs 1, 2A, B, 3A–C.
   Amphiroa wardii Harvey 1849a: 99, pl. 38 (upper right); 1859b: 310. Yendo 1905: 8.
   Cheilosporum wardii (Harvey) De Toni 1905: 1828. Lewis 1984: 13. Lucas & Perrin 1947: 397. May 1965: 356.
   Amphiroa mallardiae Harvey 1849a: 99. Yendo 1905: 8.
   Arthrocardia mallardiae (Harvey)Areschoug 1852: 552. Harvey 1863, synop.: xxix. Tisdall 1898: 507.
   Cheilosporum mallardiae (Harvey)De Toni 1905: 1828. Lucas 1929a: 27. Lucas & Perrin 1947: 397. May 1965: 356. Sonder 1881: 20.

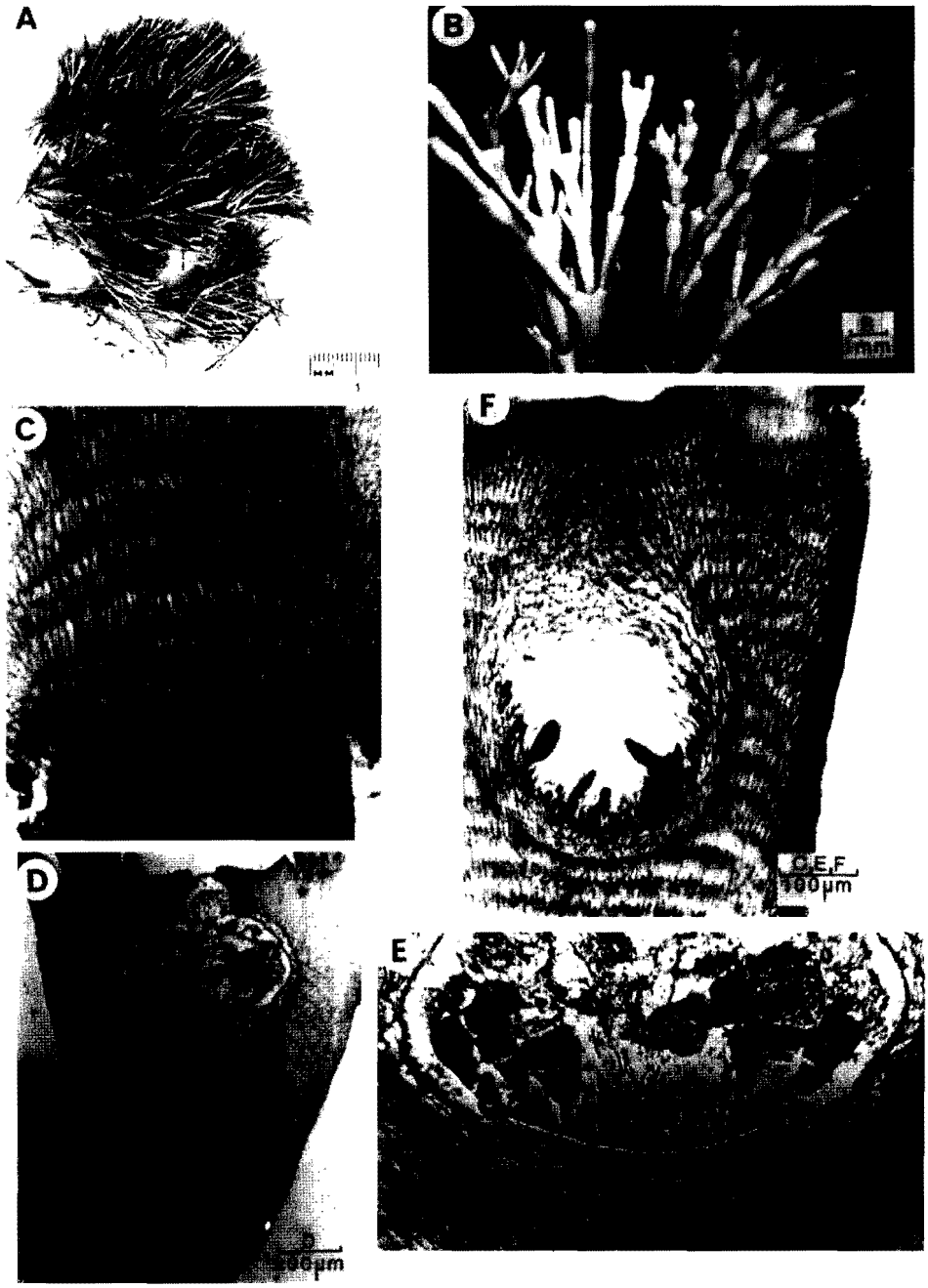


Fig. 134. *Arthrocardia flabellata* ssp. *australica* (**A,** AD, 61609; **B,** AD, A52791; **C,** AD, A52790; **D, E,** Johansen 81-9-43, CUW8548; **F,** AD, A61241). **A.** Habit. **B.** Branches with conceptacles. **C.** Longitudinal section of a geniculum and part intergeniculum. **D.** Longitudinal section of a segment with a carposporangial conceptacle. **E.** Carposporangial conceptacle with thin, broad, fusion cell and peripheral filaments with carposporangia. **F.** Longitudinal section of a bisporangial conceptacle. [**D, E,** Photos H.W.J.]

FIG. 133

Thallus (Fig. 133A, B) light to medium red, robust, (2-) 5–12 cm high, with 2–10 complanately branched fronds, axes densely pinnate with lateral branches from most intergenicula; fertile branchlets often displaced from plane of branching. Intergenicula terete below and 0.5–1 (-1.5) mm in diameter, compressed above, not or slightly lobed, (1.5-) 1.7–3 (-4) mm long and 1.4–3.5 mm broad, L/W 1–1.5. Holdfast crustose, 2–15 mm across; epilithic. *Structure.* Intergenicula (Fig. 133C) with 20–40 (-45) tiers of medullary cells, each tier 50–75 (-95) µm long, cortical filaments of 6–12 cells, 6–10 µm in diameter and L/D 1–2, with 1 (-2) small epithallial cells. Genicula 80–250 µm long. Rhodoplasts laminate to discoid.

Reproduction. Gametangial thalli dioecious. Carposporangial conceptacles (Fig. 133D) with or without surmounting branchlets, chamber 300–500 µm in diameter, fusion cell 250–300 µm in diameter and 8–10 µm thick, bearing 2–4-celled carposporangial filaments, carposporangia subspherical to ovoid, 40–60 µm in diameter. Male conceptacles (Fig. 133E) beaked, usually without branchlets, chambers 250–350 (-390) µm in diameter, 260–330 µm high, canal 300–700 µm long.

Bisporangial (or tetrasporangial) conceptacles (Fig. 133F) common, terminal, surmounted by two branches, chambers 250–520 µm in diameter, 325–500 µm high; bisporangia 160–240 (-260) µm long, 40–65 µm in diameter; tetrasporangia 200–280 µm long, 60–90 µm in diameter.

Type from Port Phillip, Vic. (*Mallard*); holotype in TCD.

Distribution: From Pondalowie Bay, S. Aust., to Norah Head, N.S.W. and around Tasmania.

New Zealand?

Selected specimens: Pondalowie Bay, S. Aust., 0 m deep on platform (AIMS–NCI, Q66C 2298-0, 5.ii.1989; AD, A59758). Cable Hut Bay, Yorke Pen., S. Aust., 5 m deep (*Edyvane*, 27.x.1993; AD, A64434). Cape Willoughby, Kangaroo I., S. Aust., upper sublittoral (*Woelkerling*, 25.ii.1979; LTB, 11563; AD, A57530). Port Fairy, Vic., upper sublittoral (*Woelkerling*, 6.i.1977; LTB, 11339; AD, A57534). Lawrence Rocks, Vic., 12–15 m deep (*Watson*, 30.xi.1981; AD, A52798, bisporangia, male). Lady Julia Percy I., Vic., 5–8 m deep (*Shepherd*, 3.i.1968; AD, A32317, male) and 3–6 m deep (*Shepherd*, 4.i.1968; AD, A32436, with *mallardiae* habit; AD, A32437, cystocarpic and male). Port Phillip, Vic., type of *Amphiroa mallardiae* (*Mallard*; TCD, isotype at BM). Rye (Ocean Beach), Vic., upper sublittoral (*Woelkerling*, 14.ii.1977; LTB, 11342; AD, A57536). Green Cape, N.S.W., 1–6 m deep (*Shepherd*, 13.ii.1973; AD, A43297 and A43298, bisporangial). Port Jackson, N.S.W. (*Harvey*, Alg. Aust. Exsicc. 453; NSW, A3281). Long Reef, N.S.W., below rock platform (*May* 2307, Feb. 1936; NSW). Green Point, Broken Bay, N.S.W., in wave-washed gutters and pools, upper sublittoral (*Martin*, 19.i.1969; NSW, A3284). Tuggerah Lakes, N.S.W. (*Lucas*, April 1911; NSW, A3287). Norah Head, N.S.W., very low eulittoral (*Pope*, 13.xii.1947; AD, A10772). Fluted Cape, Bruny I., Tas., 16 m deep (*Shepherd*, 10.ii.1972; AD, A41485). Lady Bay, Southport, Tas., 2–3 m deep (*Brown & Kenchington*, 14.x.1986; AD, A57658, tetrasporangial).

A. wardii is predominantly a low-light plant, with most collections from 3–22 m deep or from shaded upper sublittoral regions; however, several collections from just below low tide level are known.

Arthrocardia flabellata (Kützing)Manza ssp. **australica** Womersley & Johansen 1988: 43, figs 2C, D, 3D–L, 4.

FIG. 134

Thallus (Fig. 134A, B) pale grey-red, slender, 2–4 (-6) cm high, with fronds in small groups with axes sparsely pinnate (Fig. 134B) from about half the axial intergenicula, largely complanately branched. Intergenicula terete below and 300–500 µm in diameter, above compressed with linear margins and slight to conspicuous obtuse to pointed lobes, 1.5–3.5 mm long and 0.7–1.4 mm broad, L/W 2–4. Holdfast crustose, thick, 2–10 mm across; epilithic. *Structure.* Intergenicula (Fig. 134C) with 20–40 (-50) tiers of medullary cells, each tier 50–75 µm long, cell-fusions numerous, cortex of assurgent filaments 5–10 cells long, 5–9 µm in diameter and L/D 3–6, with single, short, epithallial cells. Genicula 120–250 µm long. Rhodoplasts discoid to laminate.

Reproduction. Gametangial thalli dioecious. Carpogonial conceptacles originating at apices of short lateral branchlets. Carposporangial conceptacles (Fig. 134D) with branchlets on one or both sides, chamber 300–520 µm in diameter, fusion cell 220–310 µm across and 8–10 µm thick, carposporangia in filaments of 3–4 cells (Fig. 134E), 55–80 µm in diameter. Male conceptacles beaked, with branchlets or processes on each side, chambers 375–650 µm in diameter, 400–550 µm high, canal 800–900 µm long.

Tetrasporangial conceptacles (Fig. 134F) only slightly swollen, surmounted by two branches, chambers 500–750 µm in diameter, 600–700 µm high; tetrasporangia 140–280 µm long, 40–80 µm in diameter.

Type from Nora Creina, S. Aust., upper sublittoral in large shaded pool (*Johansen* 81-9-49, 16.xi.1981, carposporangial, male); holotype in AD, A52790.

Distribution: From Streaky Bay, S. Aust., to Walkerville, Vic., and around Tasmania, in shallow water but usually in shaded situations.

Selected specimens: Smooth Pool, near Streaky Bay, S. Aust. (*Johansen* 81-10-21d, 28.x.1981, tetrasporangial). West Bay, Kangaroo I., S. Aust., near low tide (*Woelkerling*, 21.ii.1979; LTB, 11612; AD, A57529). Point Gillian, West I., S. Aust., 0.5–1 m deep (*Shepherd*, 27.v.1967; AD, A31943). Robe, S. Aust., sublittoral (*Jones & Johansen* 81-9-24, 4.ix.1981, carposporangial; AD, A52792). Nora Creina, S. Aust., in large shaded pool (*Johansen* 81-9-25, 5.ix.1981, carposporangial; AD, A52791 and 81-9-43, 15.ix.1981; CUW, 8548). 400 m off Cape Buffon, S. Aust., 5 m deep (*Collings*, 25.i.1991; AD, A61241). Cape Northumberland, S. Aust., in heavily shaded rear-reef pool (*Womersley*, 24.ii.1992; AD, A61609—"Marine Algae of southern Australia" No. 363). Point Lonsdale, Vic., upper sublittoral (*Johansen* 81-8-16, 31.viii.1981, tetrasporangial). Walkerville, Vic., low eulittoral (*Pope & Bennett*, 19.v.1949; AD, A12218). Currie R. mouth, Tas., upper sublittoral (*Womersley*, 28.i.1949; AD, A10326). Stapleton Point, Prosser Bay, Tas., 0–3 m deep (*Shepherd*, 10.ii.1970; AD, A35686). Lady Bay, Southport, Tas., 7 m deep (*Brown & Kenchington*, 14.x.1986; AD, A57693, carposporangial and male).

Arthrocardia flabellata is a South African species, from which ssp. *australica* differs in being slenderer and with conceptacles produced in single intergenicula which rarely branch to produce other fertile intergenicula (Womersley & Johansen 1988, p. 45).

The southern Australian taxon is not common, usually found in shaded low-level pools to a few metres deep.

TRIBE JANIEAE Johansen & Silva 1978: 414

Thallus dichotomously, pinnately or irregularly branched, holdfast crustose, in some taxa with stolons. Intergenicula with 1–6 (-25) tiers of medullary cells each 80–170 µm long. Fusion cell thick and compact (40–130 µm broad), with carposporangial filaments only from the margins; male conceptacles with narrow chambers (90–250 µm), high ceilings and short canals (30–120 µm).

Tetrasporangia large, fewer than 15 per conceptacle, without paraphyses, often with branchlets on conceptacles.

KEY TO GENERA OF JANIEAE

1. Thallus dichotomous with terete or compressed intergenicula bearing axial conceptacles ..... JANIA
1. Thallus pinnate or dichotomous, with compressed intergenicula bearing conceptacles axially in lateral branchlets or in acute lobes 2
    2. Thallus pinnate; axial intergenicula compressed and usually bearing two or more subterete branchlets, sometimes adventitiously, without lobes; conceptacles in branchlets, usually single with apical pores, with 1–3 branchlets arising from spore producing conceptacles ..... HALIPTILON
    2. Thallus subdichotomous; most intergenicula compressed, unbranched and bilobed, lobes acute or rounded; conceptacles embedded within lobes with adaxial or apical pores ..... CHEILOSPORUM

Genus JANIA Lamouroux 1812: 186

Thallus dichotomously branched (with limited development of pinnae in a few non-Australian species), adventitious branchlets rare; intergenicula cylindrical to compressed, unbranched or bearing two branches on broadened upper parts; holdfast small, crustose, or stoloniferous. *Structure* of a medulla of 1–20 (-25) tiers of cells per intergeniculum, cortex thin, of filaments of 1–3 cells arising from the outer medullary filaments, epithallial cells elongate, unistratose, with anterior trichocyte pores.

Reproduction. Conceptacles axial, usually swollen, pores central. Gametangial thalli usually dioecious, monoecious in some species. Female conceptacles bearing (1-) 2 (-4) branchlets, which sometimes consist of several intergenicula, fusion cells biconvex, 8–35 µm thick and 40–130 µm across, gonimoblast filaments marginal. Male conceptacles elongate, lacking branchlets, with spermatangial initials over the upper inner walls.

Tetrasporangial (and bisporangial) conceptacles bearing (1-) 2 (-4) branchlets, conceptacles sometimes in series, each containing up to 10 tetrasporangia, bisporangia or 3-celled sporangia.

Lectotype species: *J. rubens* (Linnaeus)Lamouroux 1816: 272 (Manza 1937: 47).

The southern Australian species of *Jania* were monographed by Johansen & Womersley (1994).

Jania is characterised by its dichotomous branching with axial conceptacles.

KEY TO SPECIES OF *JANIA*

1. Branches less than 200 µm in diameter, terete or almost so, intergenicula with 1–3 tiers of medullary cells 2
1. Lower branches usually more than 200 µm broad, terete or compressed, intergenicula with 4–20 (-25) tiers (indistinct in *J. pusilla*) of medullary cells 4

2. Intergenicula L/D 3–5; conceptacles containing bisporangia or gametangia ..... 1. *J. parva*
2. Intergenicula L/D 1–3; conceptacles containing tetrasporangia, three-celled sporangia, or gametangia 3

3. Thallus 2–4 (-6) cm high, epiphytic on Fucales and seagrasses (rarely epilithic); intergenicula terete, (70-) 100–200 (-250) µm long, 120–200 (-250) µm in diameter below, tapering slightly above, L/D 1–3 with 1 (-2) tiers of medullary cells; propagules unknown; conceptacles amphoroid (i.e. with branchlets from the upper shoulders); tetrasporangia with four spores ..... 2. *J. micrarthrodia*
3. Thallus (1-) 2–6 (-10) mm high, epiphytic on seagrasses or *Myriodesma*; intergenicula terete to slightly compressed, (100-) 110–150 (-165) µm long, (40-) 60–100 (-120) µm in diameter, L/D 1.2–2 (-2.5); propagules common; conceptacles non-amphoroid (i.e. with branchlets from the lower sides); each tetrasporangium replaced by a large, two-nucleate central cell and small uninucleate basal and apical cells ..... 3. *J. minuta*

4. Thallus branched in various planes, branches terete or subterete throughout, epilithic; 4–20 (-25) tiers of medullary cells per intergeniculum ..... 4. *J. verrucosa*
4. Thallus complanately branched, with compressed intergenicula in lower parts, epilithic or epiphytic; usually 4–9 tiers (indistinct in *J. pusilla*) of medullary cells per intergeniculum 5

5. Thallus 2–5 (-10) mm high, 3–10 (-12) intergenicula long, upper intergenicula compressed, 200–600 (-800) µm broad, medullary tiers obscure; conceptacles embedded and inconspicuous; usually epiphytic on *Cystophora* ..... 5. *J. pusilla*
5. Thallus 2–6 cm high, more than 20 intergenicula long, lower intergenicula only compressed and cheilosporoid, (200-) 400–1000 (-1250) µm broad, upper intergenicula terete and janioid, (80-) 100–250 (-300) µm in diameter with swollen conceptacles; 4–9 medullary tiers per intergeniculum; epiphytic on *Sargassum* or other algae (apparently not on *Cystophora*) or epilithic ..... 6. *J. pulchella*

1. **Jania parva** Johansen & Womersley 1994: 609, figs 1–5, 21–26.

FIG. 135

Thallus (Fig. 135A) light grey-red, 2–5 mm high, slender, branching divaricate, with 1–7 erect fronds from each holdfast, stolons lacking; fronds usually 10–30 intergenicula long, branching in varying planes every 2–10 (-15) intergenicula; intergenicula terete, 55–80 μm in diameter below, 30–50 μm in diameter above, 165–275 (-300) μm long and L/D 3–5 (-7).

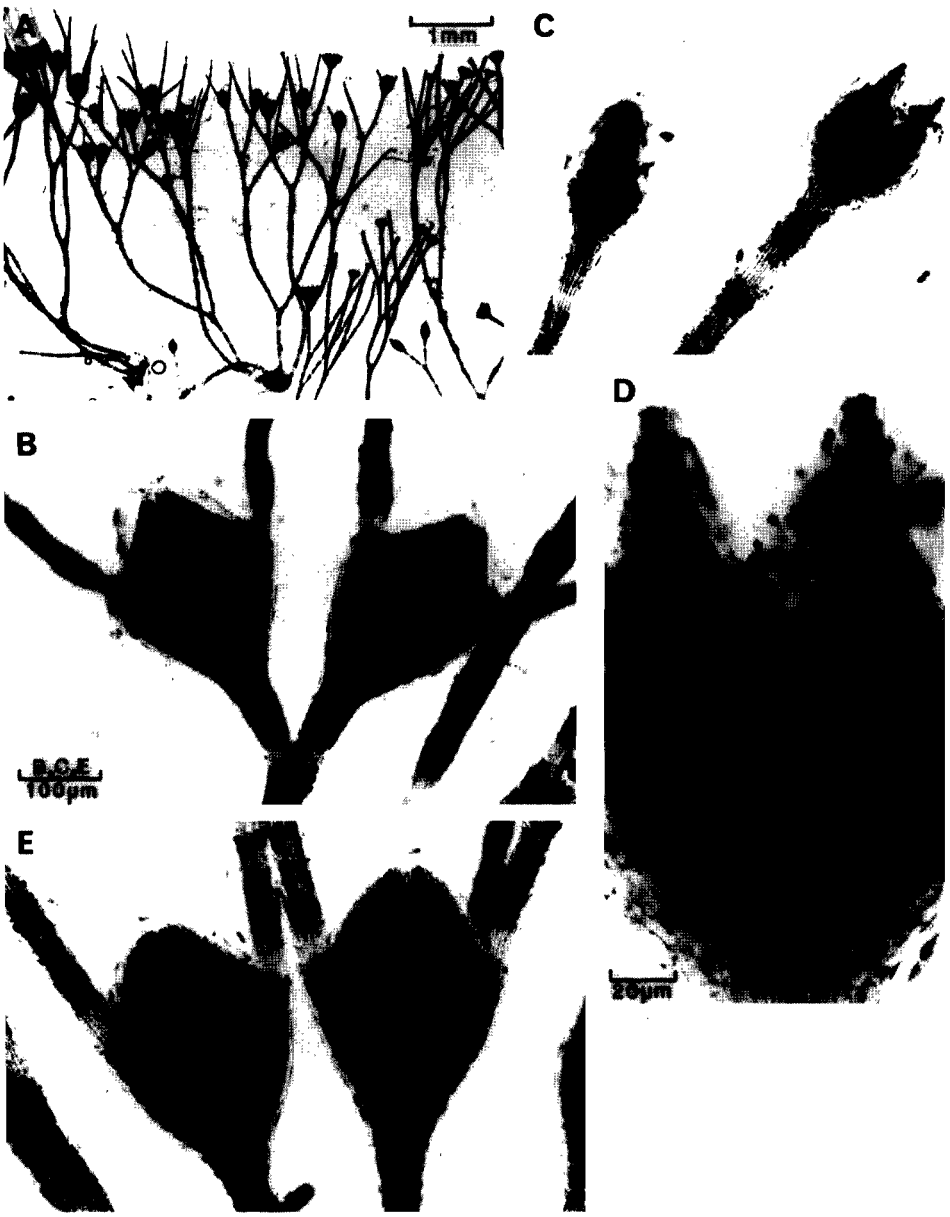


Fig. 135. *Jania parva* (AD, A59922). **A.** Habit. **B.** Carposporangial conceptacles. **C.** Two male conceptacles. **D.** A male conceptacle. **E.** Two bisporangial conceptacles.

Holdfasts thin crusts, (200-) 300–500 μm across; epiphytic on *Posidonia* and *Halophila*. *Structure* of intergenicula with (1-) 2–3 tiers of medullary cells each 60–90 μm long, and a cortex one cell thick; genicula 60–90 μm long.

Reproduction. Gametangial thalli monoecious, with distinct female and male branches from one holdfast. Female conceptacles (Fig. 135A, B) in branched fronds; conceptacles amphoroid, externally 240–330 μm long and 160–240 μm in diameter, internally 100–160 μm in diameter, with 2–5 mature ovoid-angular carposporangia per conceptacle, each 40–65 μm in diameter. Male conceptacles (Fig. 135C, D) terminal in simple or 1–2 branched fronds, externally 200–280 μm long and 100–160 μm in diameter, internal diameter 70–90 μm.

Bisporangial conceptacles (Fig. 135E) amphoroid, externally 250–350 μm long and 200–250 μm in diameter, internal diameter 140–190 μm; tetranucleate (two nuclei in each spore) bisporangia 2–5 per conceptacle, 120–180 μm long and (40-) 60–90 μm in diameter; tetrasporangia unknown.

Holotype from Stansbury, S. Aust., 2–3 m deep on *Posidonia australis* (*Womersley*, 14.x.1989); in AD, A59922.

Distribution: Point Turton, S. Aust., to American R. inlet, Kangaroo I., S. Aust. (probably more widely distributed in calm water localities).

Selected specimens: Point Turton, S. Aust., on *Posidonia sinuosa*, drift (*Womersley*, 15.x.1989; AD, A59928). Stansbury, S. Aust., on *P. australis* drift (*Womersley*, 14.x.1989; AD, A59919). Pelican Lagoon, American R. inlet, Kangaroo I., S. Aust., 1–2 m deep on *P. australis* (*Womersley*, 7.i.1990; AD, A60105 —"Marine Algae of southern Australia" No. 342). Bay of Shoals, Kangaroo I., S. Aust., on *P. australis*, 0–3 m deep (*Womersley*, 5.i.1990; AD, A60107, A60099 and A60118), and on *Halophila australis*, 3 m deep (*Womersley*, 5.i.1990; AD, A60117).

Jania parva is similar in frond size to *J. minuta*, but branching tends to be divaricate rather than fastigiate, intergenicula are longer, intergenicular length to diameter ratios are greater (3–5 vs. 1–2), and sporangial conceptacles are amphoroid. Based on divaricate branching and intergenicular length to diameter ratios, *J. parva* is more closely related to the common tropical *J. adhaerens* Lamouroux than to *J. minuta*.

2. **Jania micrarthrodia** Lamouroux 1816: 271, pl. 9 fig. 5a, B; 1821: 23, pl. 69 figs 7, 8. Adams 1972: 75; 1994: 157, pl. 54 upper right. Adams *et al.* 1974: 219. Areschoug 1852: 555. Chapman & Parkinson 1974: 175, pl. 58A. De Toni 1905: 1855. De Toni & Forti 1923: 63. Guiler 1952: 86. Harvey 1849a: 107; 1855a: 547; 1859b: 310; 1863, synop.: xxix. Huisman & Walker 1990: 412. Johansen & Womersley 1994: 611, figs 6–9, 32–36. Kützing 1849: 710. Levring 1946: 221. Lucas 1929a: 27; 1929b: 53. Lucas & Perrin 1947: 397. Sonder 1881: 21. Tisdall 1898: 508. Wilson 1892: 176. Womersley 1953: 37. Yendo 1905: 38.
Jania antennina Kützing 1843: 389; 1849: 710. Harvey 1849: 107. Sonder 1848: 186. Yendo 1905: 38.
Corallina antennina (Kützing)Kützing 1858: 40, pl. 84a, b, d (not c).
Jania micrarthrodia var. β *antennina* (Kützing)Areschoug 1852: 555.
Jania micrarthrodia f. *antennina* (Kützing)Yendo 1905: 38.
Jania fastigiata Harvey 1849a: 107; 1863, synop.: xxix, pl. 251 (Australian specimens). King *et al.* 1971: 121. Lucas & Perrin 1947: 397, fig 201. Sonder 1881: 21. Tisdall 1898: 508. Wilson 1892: 176. Womersley 1950: 167; 1966: 146.
Jania tenuissima Sonder 1848: 186; 1853: 687; 1855: 521; 1871: 54. Harvey 1849a: 106, pl. 40 centre left. Kützing 1849: 710.
Jania micrarthrodia var. α *tenuissima* (Sonder)Areschoug 1852: 555. Sonder 1881: 21.
Corallina micrarthrodia (Lamouroux)Reinbold 1899: 51.
Corallina tenuissima (Sonder)Kützing 1858: 40, pl. 84 fig. III.
Corallina constricta Kützing 1858: 40, pl. 84e–h. De Toni 1905: 1852. Yendo 1905: 40.
Jania rubens (Linnaeus)Lamouroux *sensu* Lucas 1929b: 53. Lucas & Perrin 1947: 398. Ducker *et al.* 1977: 86.



Fig. 136. *Jania micrarthrodia* (**A, B, D–G,** AD, A60044; **C,** AD, A, 59923; **H,** AD, A30400). **A.** Plants epiphytic on *Cystophora subfarcinata*. **B.** Tetrasporangial thallus. **C.** Longitudinal section of branch showing short intergenicula. **D.** Branches with carposporangial conceptacles. **E.** Fusion cell with young carposporangial filaments. **F.** Male conceptacles. **G.** Longitudinal section of male conceptacle. **H.** Tetrasporangial conceptacles.

FIG. 136

Thallus (Fig. 136A, B) pink to medium red or red-brown, fading to grey-red, densely tufted, 2–4 (-6) cm high. Fronds dichotomous every (2-) 5–18 (-22) intergenicula, complanate or branched in various planes. Intergenicula terete, 120–200 (-250) μm in diameter below, tapering to 80–120 μm in diameter near the apices, (70-) 100–200 (-250) μm long, L/D 1–3. Propagules absent. Holdfast at first discoid, 0.5–4 mm in diameter, bearing several erect branches which may produce recurved tendrils 50–160 μm in diameter; in calm waters, secondary holdfasts form when branch tips contact host or other branches; epiphytic (on larger brown algae, especially *Cystophora*, and the seagrass *Amphibolis*) or occasionally epilithic and comprising turfs in the lower intertidal zone. *Structure*. Medullary cells in 1 (-2) tiers (Fig. 136C) per intergeniculum; hairs common in a ring around upper edge of intergeniculum. Genicula 60–120 (-180) μm long (often longer than intergenicular medullary cells).

Reproduction. Gametangial thalli dioecious. Female conceptacles (Fig. 136D) amphoroid, externally 250–400 μm long and 250–400 μm in diameter, internal diameter 150–240 μm, with a thick fusion cell (Fig. 136E); carposporangia subspherical, 40–65 (-80) μm in diameter. Male conceptacles (Fig. 136F, G) fusiform, externally 400–650 (-800) μm long and 200–320 (-400) μm in diameter, internally 140–250 (-320) μm in diameter, pore canals 80–170 μm long.

Tetrasporangial conceptacles (Fig. 136H) amphoroid, externally 350–500 (-550) μm long and (200-) 250–450 μm in diameter, internal diameter 200–370 μm, mature tetrasporangia 120–240 μm long and 45–65 (-90) μm in diameter.

Type 'sur les *Fucus* de l'Australasie'; holotype in Herb. Lamouroux, CN.

Distribution: Geraldton, W. Aust., to Walkerville, Vic., and around Tasmania, N.S.W. (Millar & Kraft 1993, p. 14).

New Zealand.

Selected specimens: Point Moore, Geraldton, W. Aust., drift (*Womersley*, 17.ix.1979; AD, A51175). Point Valliant, Two People Bay, W. Aust., 1–4 m deep on *Amphibolis* (*Clarke & Engler*, 30.viii.1979; AD, A50968). Point Sinclair, S. Aust., lower eulittoral on granite (*Womersley*, 8.ii.1954; AD, A19557). Coffin Bay, S. Aust., 5–6 m deep on *Posidonia sinuosa* (*Womersley*, 4.xii.1975; AD, A46954 —"Marine Algae of southern Australia" No. 334). Pondalowie Bay, S. Aust., (*Johansen* 81-9-59b, 19.ix.1981; CUW 7260). Gleeson Landing, Yorke Pen., S. Aust., on *Cystophora subfarcinata*, drift (*Womersley*, 15.x.1989; AD, A59923). Dany Beach, Corny Point, S. Aust., drift on *Posidonia sinuosa* (*Womersley*, 15.x.1989; AD, A59894). Shell Rock, West I., S. Aust., 3–6 m deep (*Shepherd*, 27.xii.1965; AD, A30400). Rosetta Bay, Victor Harbor, S. Aust., drift on *C. subfarcinata* (*Womersley*, 17.ix.1989; AD, A59706). Pelican Lagoon, American R. inlet, Kangaroo I., S. Aust., 0.5–1 m deep on *Posidonia australis* (*Womersley*, 7.i.1990; AD, A60103). Pennington Bay, Kangaroo I., S. Aust., on *C. subfarcinata* (*Womersley*, 6.i.1990; AD, A60044 —"Marine Algae of southern Australia" No. 340). Nora Creina, S. Aust., on *Cladostephus*, upper sublittoral (*Johansen* 81-9-30, 5.ix.1981; AD, A52578). Bridgewater Bay, Vic., on *Cystophora subfarcinata*, lower eulittoral (*Beauglehole*, 5.vi.1949; AD, A12023). San Remo, Vic., uppermost sublittoral on *Heterozostera* (*Womersley*, 17.ii.1990; AD, A60086 —"Marine Algae of southern Australia" No. 334C). Walkerville, Vic., low eulittoral on *Cladostephus* (*Pope & Bennett*, 19.v.1949; AD, A12204). Currie River mouth, Tas., on *Cystophora torulosa*, low eulittoral pools (*Womersley*, 28.i.1949; AD, A10305). Bicheno, Tas., epilithic, lower eulittoral (*Womersley*, 4.xi.1982; AD, A56459).

Jania micrarthrodia and *J. minuta* are the only species of Corallinoideae where most intergenicula contain single tiers (occasionally two) of medullary cells. *Jania micrarthrodia* is common on larger brown algae, especially on species of *Cystophora* on rough-water coasts. Epilithic plants are apparently less common than epiphytic plants, and the former are slightly more variable in intergenicular length. Although branching in *Jania micrarthrodia* is often fastigiate, it sometimes becomes divaricate, the angle appearing to depend on wave intensity, with wider angles in calm water and narrower in rough water.

Jania micrarthrodia epiphytic on *Cystophora* on rough-water coasts has short and relatively broad intergenicula, as described and illustrated by Lamouroux (1816, p. 271, pl. 9 fig. 5B) for the type. Under calmer conditions, what appears to be a form of this species

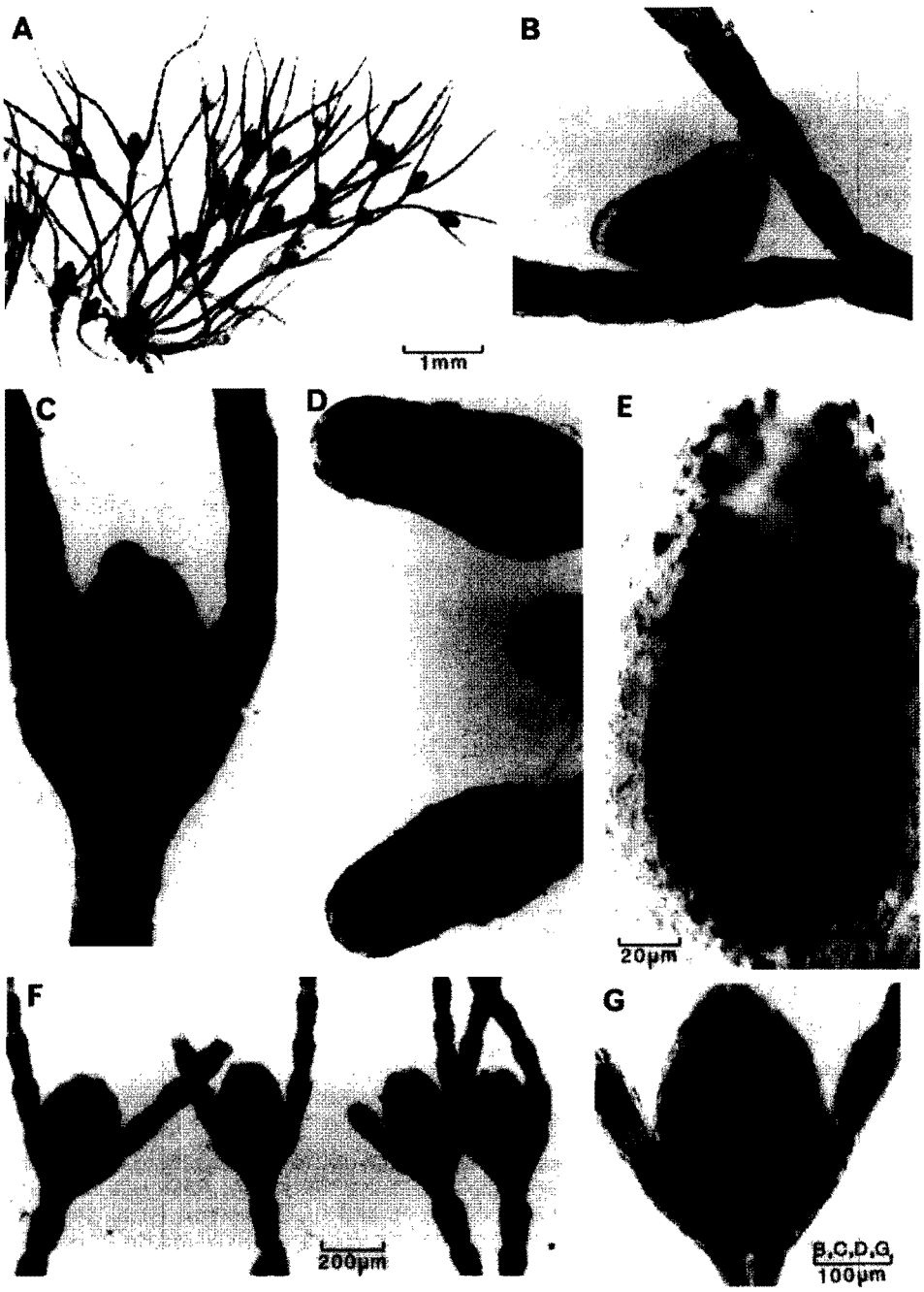


Fig. 137. *Jania minuta* (**A, F, G,** AD, A59883; **B,** AD, A4560; **C, D,** AD, A, 13808; **E,** AD, A38427). **A.** Habit. **B.** Branches with a propagule. **C.** Carposporangial conceptacle. **D.** Male conceptacles. **E.** Male conceptacle with spermatangia lining the walls. **F.** Tetrasporangial conceptacles. **G.** Tetrasporangial conceptacles, upper small cell of tetrasporangia just visible.

(corresponding to *Jania tenuissima* Sonder; lectotype from 'Occid. Nov. Holl.', in MEL, 47436) is epiphytic on seagrasses and other algae, and has longer and more slender intergenicula. These two forms appear to be the extremes dependent on water movement, and connected by intermediate forms in moderate water movement.

The type of *J. antennina* Kützing (from 'Neuholland', *Preiss*, L. 941, 119...4) is a typical specimen of *J. micrarthrodia*, with intergenicular L/D ratios of about 2. The type specimens of two other species from Australia, *J. tennuisima* Sonder and *Corallina constricta* Kützing, also belong to this species, although the intergenicula are slightly longer than in most specimens of *J. micrarthrodia*, with L/D ratios of 2–3.

3. **Jania minuta** Johansen & Womersley 1994: 613, figs 10–14, 27–31.

FIG. 137

Thallus (Fig. 137A) light grey-red, (1-) 2–6 (-10) mm high, (10-) 20–40 intergenicula long, slender; fronds branching every (3-) 5–10 (-20) intergenicula, open to fastigiate, mostly in one plane. Intergenicula terete to slightly compressed, (40-) 60–100 µm in diameter, (100-) 110–150 (-165) µm long, L/D 1.2–2 (-2.5). Holdfasts thin, crustose, 200–600 µm across, each bearing several erect branches; epiphytic on seagrasses or *Myriodesma*. *Structure*. Medullary cells in 1 (-2) tiers (Fig. 137B) per intergeniculum, each tier (30-) 40–60 µm long; cortex one cell thick, organised in two tiers per intergeniculum, the distal of which cuts off apically small cells each of which produces a hair or hair initial. Genicula (35-) 60–80 µm long.

Reproduction. Asexual by propagules (fig. 137B) borne laterally on intergenicula, propagules multicellular, compressed, more or less triangular and becoming bilobed, 120–200 µm long and 140–250 µm across the lobes when well developed, each attached by a pad 5–8 cells across, the lobes potentially developing branch buds which presumably may develop further.

Gametangial thalli monoecious. Female conceptacles (Fig. 137C) non-amphoroid, lying between the diverging arms of furcate intergenicula 200–280 µm long, branchlets containing other conceptacles sometimes growing from the developing arms; externally 280–360 (-400) µm long and 180–240 µm in diameter, chamber diameter 150–200 µm when carposporangial, containing 3–6 subspherical to ovoid carposporangia each 40–100 µm in diameter. Male conceptacles (Fig. 137D, E) terminal on short, simple, branches from the same basal crusts as branches bearing female conceptacles, externally 225–300 (-430) µm long and 100–180 µm in diameter, chambers 70–110 µm in diameter and 425–590 µm high.

Sporangial conceptacles (Fig. 137F, G) between the diverging lobes of furcate intergenicula, the two (occasionally three) arms usually continuing as branchlets; externally 275–370 µm long and 230–270 µm in diameter (excluding arms), chambers 150–230 µm in diameter; each sporangium three-celled, consisting of a large two-nucleate cell and small basal and apical cells containing single nuclei, sporangia (140-) 170–220 µm long and 50–100 µm in diameter.

Type from Barker Rocks, Yorke Pen., S. Aust., on *Posidonia sinuosa*, drift (*Womersley*, 17.x.1989); holotype in AD, A59883.

Distribution: Albany, W. Aust., to Phillip I., Vic., on *Posidonia, Heterozostera* and *Myriodesma*.

Selected specimens: Albany, W. Aust., on *Myriodesma*, drift (*Burbidge*, 24.xi.1935; AD, A4560, with propagules). Point Sinclair, S. Aust., on *Heterozostera*, uppermost sublittoral (*Womersley*, 25.i.1951; AD, A13808). Petrel Bay, St Francis I., S. Aust., on *Posidonia sinuosa*, 3 m deep (*Shepherd*, 7.i.1971; AD, A38427). Waterloo Bay, S. Aust., on *P. sinuosa*, 2 m deep (*Shepherd*, 20.x.1970; AD, A37526). Tiparra reef, S. Aust., on *P. sinuosa*, 5–6 m deep (*Shepherd*, 28.i.1971; AD, A37837). Seal Bay, Kangaroo I., S. Aust., on *Myriodesma integrifolium*, drift (*Womersley*, 24.i.1957; AD, A20757). West I., S. Aust., on *Posidonia*, 5 m deep (*Shepherd*, 18.i.1978; MELU, 22779, 22727). Kitty Miller Bay, Phillip I., Vic., on *Amphibolis antarctica*, drift (*Ducker*, 25.v.1977; MELU, 22610).

Jania minuta is monoecious, has non-amphoroid carposporangial and (tetra)sporangial conceptacles, tetrasporangia replaced by three-celled sporangia, small conceptacle dimensions, and one (or two) tiers of intergenicular medullary cells alternating with genicula. The distinctive propagules in *J. minuta* are similar to those recorded by Dawson

(1953, p. 116, pl. 9 fig. 1) for *J. capillacea* Harvey from Baja California, Mexico. In *J. minuta*, the plants bear either conceptacles or propagules; plants bearing both are unknown.

All asexual conceptacles examined contained the unusual sporangia with four nuclei within three cells, a large, central cell containing two nuclei and smaller uninucleate basal and apical cells.

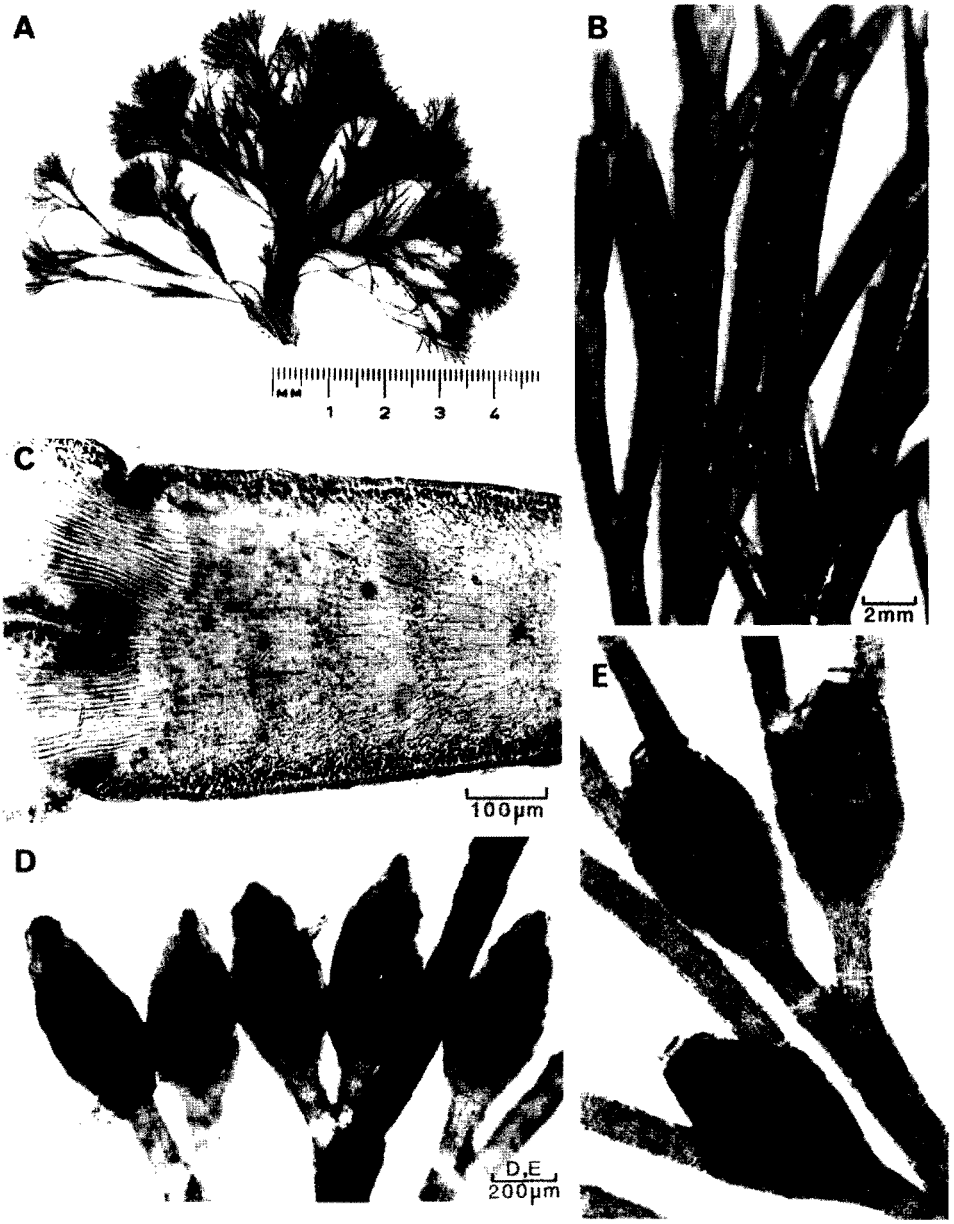


Fig. 138. *Jania verrucosa* (**A, B,** AD, A50415; **C,** AD, A59889; **D, E,** AD, A59704). **A.** Habit. **B.** Branches with long intergenicula. **C.** Longitudinal section of branch with genicula and multi-tiered intergenicula. **D.** Male conceptacles. **E.** Tetrasporangial conceptacles. [**A, B,** as in Johansen & Womersley 1994.]

4. **Jania verrucosa** Lamouroux 1816: 270, pl. 9 fig. 4. Areschoug 1852: 559. De Toni 1905: 1856. Huisman & Walker 1990: 412. Johansen & Womersley 1994: 616, figs 15, 16, 37–39. Kützing 1849: 710.
Corallina verrucosa (Lamouroux)Kützing 1858: 38, pl. 80, fig. III.
Jania pedunculata Lamouroux 1816: 270, pl. 9 fig. 3. Areschoug 1852: 559. Chapman & Parkinson 1974: 177, fig. 54. De Toni 1905: 1856. Harvey 1863, synop.: xxix. Kützing 1849: 711. Sonder 1881: 21.
Corallina pedunculata (Lamouroux)Kützing 1858: 37, pl. 78, fig. II.
Jania crassa Lamouroux 1821: 23, pl. 69 figs 9, 10. Johansen 1976: 418. Millar 1990: 322, fig. 11C, D. Millar & Kraft 1993: 13. Yendo 1905: 39.
Jania micrarthrodia var. γ *crassa* (Lamouroux)Areschoug 1852: 555.
Jania natalensis Harvey 1849a: 107. Chapman & Parkinson 1974: 176, pl. 58B. Dawson 1953: 118, pl. 27 figs 1, 2. De Toni 1905: 1856. Guiler 1952: 86. Sonder 1881: 21. Womersley 1950: 167; 1953: 37. Yendo 1905: 39.
Corallina natalensis (Harvey)Kützing 1858: 38, pl. 79c–f.

FIG. 138

Thallus (Fig. 138A) light to medium red-brown, fading to grey-white, (2-) 3–5 (-10) cm high, usually densely tufted and fastigiate, loose and spreading in calm habitats. Fronds dichotomous in various planes at intervals of (2-) 5–15 (-20) intergenicula with occasional lateral branches below; angles at most dichotomies <30 degrees. Intergenicula terete, in lower parts of fronds (150-) 200–350 (-400) μm in diameter, in upper parts (120-) 150–220 (-240) μm in diameter, length variable (Fig. 138B), 0.4–3.0 (-4.0) mm long, L/D 2–8 (-16). Holdfasts at first discoid and spreading, 0.5–6 mm in diameter, stolons plentiful, arising from lower parts of fronds, tending to recurve, 100–200 μm in diameter; epilithic, rarely epiphytic. *Structure* (Fig. 138C) of 4–20 (-25) tiers of medullary cells each 90–160 μm long per intergeniculum; cortex 2 (-3) cells thick; hairs common. Genicula 80–200 μm long.

Reproduction. Gametangial thalli dioecious. Female conceptacles amphoroid, external diameter 300–470 μm, internal diameter 240–325 μm, carposporangia subspherical, 65–100 μm in diameter. Male conceptacles (Fig. 138D) externally 450–600 μm long and 180–250 μm in diameter, chambers 120–180 μm in diameter, canals 60–100 μm long.

Tetrasporangial conceptacles (Fig. 138E) amphoroid, external diameter 240–600 (-700) μm, chamber diameter 160–400 μm; tetrasporangia 170–220 (-360) μm long and 40–80 μm in diameter.

Type from 'Amerique Meridionale'; holotype in Herb. Lamouroux, CN.

Distribution: Rottnest I., W. Aust., around southern Australia and Tasmania to Coffs Harbour, N.S.W. (probably further north).

New Zealand; South Africa; California, U.S.A.; Baja California, Mexico; Peru.

Selected specimens: King Head, Rottnest I., W. Aust., in shallow reef pools (*Womersley*, 6.ix.1979; AD, A50844). Cowaramup Bay, W. Aust., 2–3 m deep (*Clarke & Engler*, 1.ix.1979; AD, A50648). Waterloo Bay, S. Aust., 4 m deep (*Shepherd*, 29.x.1981; CUW 7267). Smooth Pool, W of Streaky Bay, S. Aust., upper sublittoral (*Johansen* 81-10-14, 25.x.1981; AD, A52754). Pondalowie Bay, S. Aust., lower eulittoral depressions (*Womersley*, 16.x.1989; AD, A59914 —"Marine Algae of southern Australia" No. 337a). Barker Rocks, Yorke Pen., S. Aust., lower eulittoral on platform edge (*Womersley*, 17.x.1989; AD, A59889 and A59887 —"Marine Algae of southern Australia" No. 337). Port Stanvac, S. Aust., lower eulittoral (*Clarke*, 16.xii.1977; AD, A50415). Port Noarlunga, S. Aust., pool edges on off-shore reef (*Johansen* 81-10-13a, 13.x.1981; AD, A52702). Shag Rock, American R. inlet, Kangaroo I., S. Aust., uppermost sublittoral (*Womersley*, 20.xii.1990; AD, A61184 —"Marine Algae of southern Australia" No. 337b). Petrel Cove, Victor Harbor, S. Aust., lower eulittoral pools (*Womersley*, 17.ix.1989; AD, A59704). Nora Creina, S. Aust., (*Johansen* 81-9-40a, 5.ix.1981; AD, A52580 and CUW 1714). Point Lonsdale, Vic., shallow reef pools (*Womersley*, 30.xi.1989; AD, A60016). Walkerville, Vic., eulittoral pools (*Sinkora* A1813, 4.xii.1973; AD, A53514). Guyton Point, Robbins I., Tas., low eulittoral (*Wollaston & Mitchell*, 23.ii.1964; AD, A27626). Half Moon Bay, Bicheno, Tas., upper sublittoral pools (*Wollaston*, 13.viii.1965; AD, A29588). Newport, N.S.W., upper sublittoral on reef (*Womersley*, 30.v.1950; AD, A13069).

Jania verrucosa has more robust fronds than other southern Australian species of *Jania*, with intergenicula typically more than 200 μm in diameter, of variable length but usually

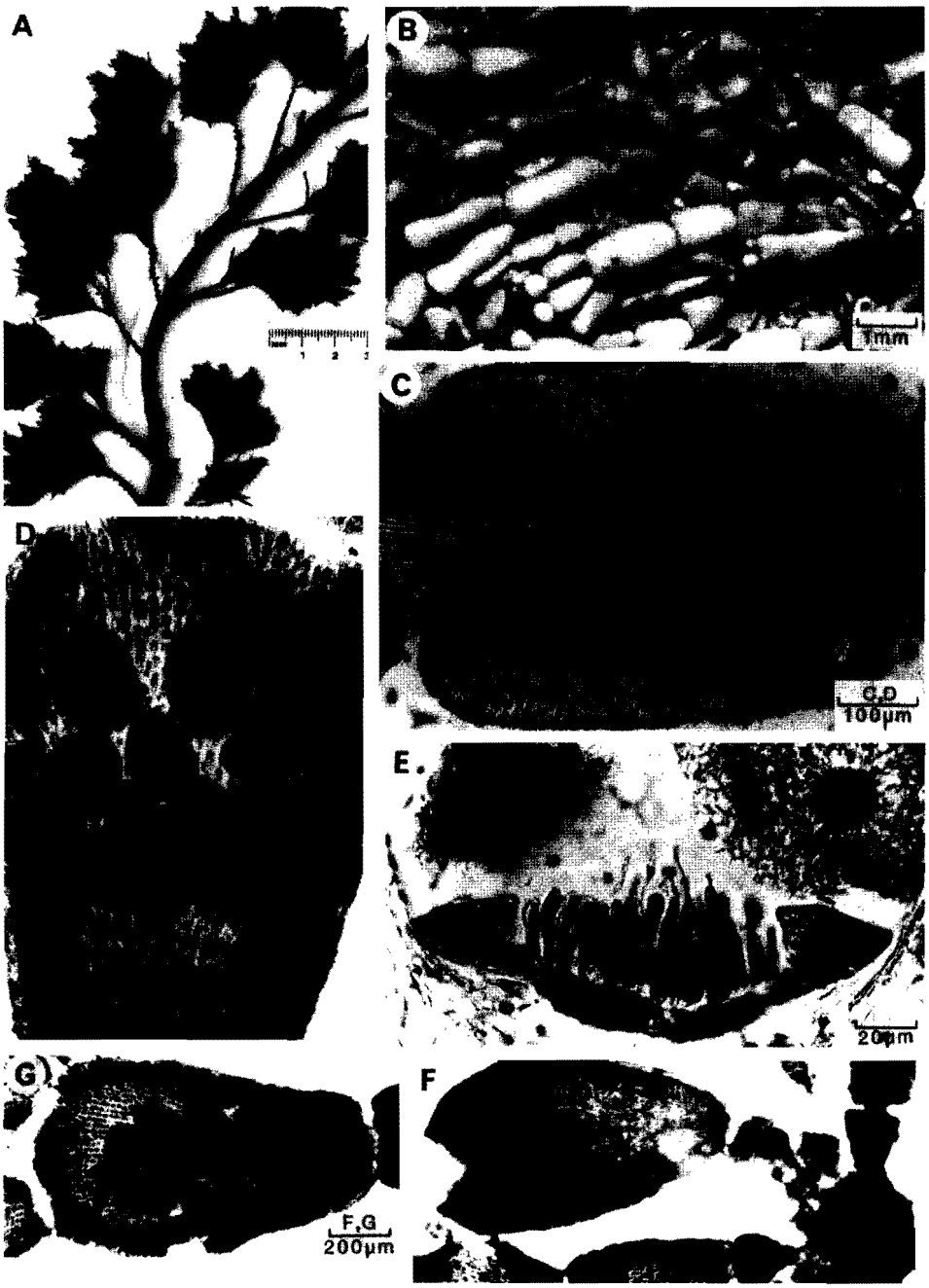


Fig. 139. *Jania pusilla* (AD, A50972). **A.** Plants on *Cystophora harveyi*. **B.** Thalli with branches from discoid holdfasts. **C.** Longitudinal section of an intergeniculum with two genicula. **D.** A carposporangial conceptacle. **E.** Longitudinal section of a carposporophyte with basal fusion cell and peripheral carposporangial filaments. **F.** A male conceptacle. **G.** A tetrasporangial conceptacle. [**A, B,** as in Johansen & Womersley 1994.]

with some more than 1 mm long, and with 4–20 (-25) tiers of medullary cells. Unlike other species, it is almost entirely epilithic, occurring in shallow eulittoral pools or on rocks near low tide level. Occasional specimens with mostly short intergenicula with four or five tiers of medullary cells per intergeniculum resemble *J. rubens* (Linnaeus)Lamouroux from Europe, but the latter is monoecious.

Jania verrucosa (usually reported as *J. crassa*) is widespread in tropical and subtropical areas. In studies in New Zealand, Chapman & Parkinson (1974, p. 176) incorrectly placed *J. crassa* as a synonym of *Jania micrarthrodia*. The Australian specimens are similar to those labelled *J. crassa* in AD from Kaikoura and the Bay of Islands (Lindauer, Alg. Nova-Zel. Exsicc. No. 16) in New Zealand. *Jania verrucosa* is the only species of *Jania* in the present account with a type locality outside southern Australia.

Although both *Jania verrucosa* and *J. crassa* were described by Lamouroux, the former preceded the latter (1816 vs 1821), although the latter name has been used more often. They are, however, almost certainly conspecific, at least in southern Australia.

Jania pedunculata was also described by Lamouroux (1816) from 'Australasie', but the type is not present in the Lamouroux herbarium in Caen. According to R. Meslin (pers. comm. to HWJ, 1968), the type in Caen was probably lost during a reorganisation of the herbarium in 1956 and a search in 1967 (HWJ) for the types of Lamouroux failed to locate a type of *J. pedunculata*. However, a fragment reputedly in P was obtained by Bornet; we have not seen it. Kützing's illustration (1858, pl. 78f–m) of *J. pedunculata* shows a branch with the dimensions of *J. verrucosa* that has 8–11 tiers of medullary cells per intergeniculum.

5. **Jania pusilla** (Sonder)Yendo 1905: 39. Ducker *et al.* 1976: 1, figs 1, 3–7, 9–14. Johansen & Womersley 1994: 618, figs 17, 18, 40.
Corallina pusilla Sonder 1881: 21. Tisdall 1898: 508.
Corallina lenormandiana Grunow *ex* De Toni 1905: 1851. Lucas & Perrin 1947: 400. Mazza 1918: No. 654. Womersley 1950: 167.
Corallina? nana Lenormand *ex* Harvey 1863, synop.: xxix. Tisdall 1898: 508. Wilson 1892: 176. (non *Corallina nana* Zanardini 1844: 1024.)

FIG. 139

Thallus (Fig. 139A, B) medium red to red-brown, fading to grey-red, 2–5 (-10) mm high, epiphytic on *Cystophora* spp. and *Platythalia angustifolia*. Fronds 3–10 (-12) intergenicula long, complanately branched every one or two intergenicula. Intergenicula subterete below, compressed and ovate to cuneate above, increasing in size upwards, 400–1200 µm long, 200–600 (-800) µm broad and 180–340 µm thick, 300–500 µm thick where conceptacles are present. Holdfasts discoid to pulvinate crusts, 200–1000 µm across, bearing up to 12 fronds each. *Structure*. Medullary cell tiers indistinct (Fig. 139C). Genicula (80-) 100–160 (-200) µm long.

Reproduction. Gametangial thalli dioecious; conceptacles deeply embedded and inconspicuous, terminal, or bearing simple branches. Female conceptacles internal diameter 100–200 µm when procarpic and 300–450 µm when carposporangial (Fig. 139D), with a thick fusion cell (Fig. 139D, E); carposporangia subspherical to ovoid, 100–160 µm in diameter. Male conceptacles (Fig. 139F) internally 130–360 µm in diameter and 350–560 µm high, canal about 100 µm long.

Tetrasporangial conceptacles (Fig. 139G) usually bearing two branches; internal diameter 300–450 µm; tetrasporangia 200–420 µm long and 100–160 µm in diameter.

Type from Port Fairy, Vic., on *Cystophora* (*Harvey*, Alg. Aust. Exsicc. 452); holotype (or lectotype) in TCD. Ducker *et al.* (1976, p. 6), selected a MEL (501722) specimen of Harvey's 452 as lectotype, but it would be a more usual practice to regard the holotype (or lectotype if necessary) to be in the Harvey herbarium in TCD.

Distribution: Yallingup, W. Aust., to Cape Patterson, Vic., and the NW coast (at least) of Tasmania.

Selected specimens: Yallingup, W. Aust., on *Platythalia angustifolia*, drift (*Smith & Scagel*, Sept. 1962; UWA, A364; AD, A26353). Point Valiant, Two People Bay, W. Aust., on *Cystophora harveyi*,

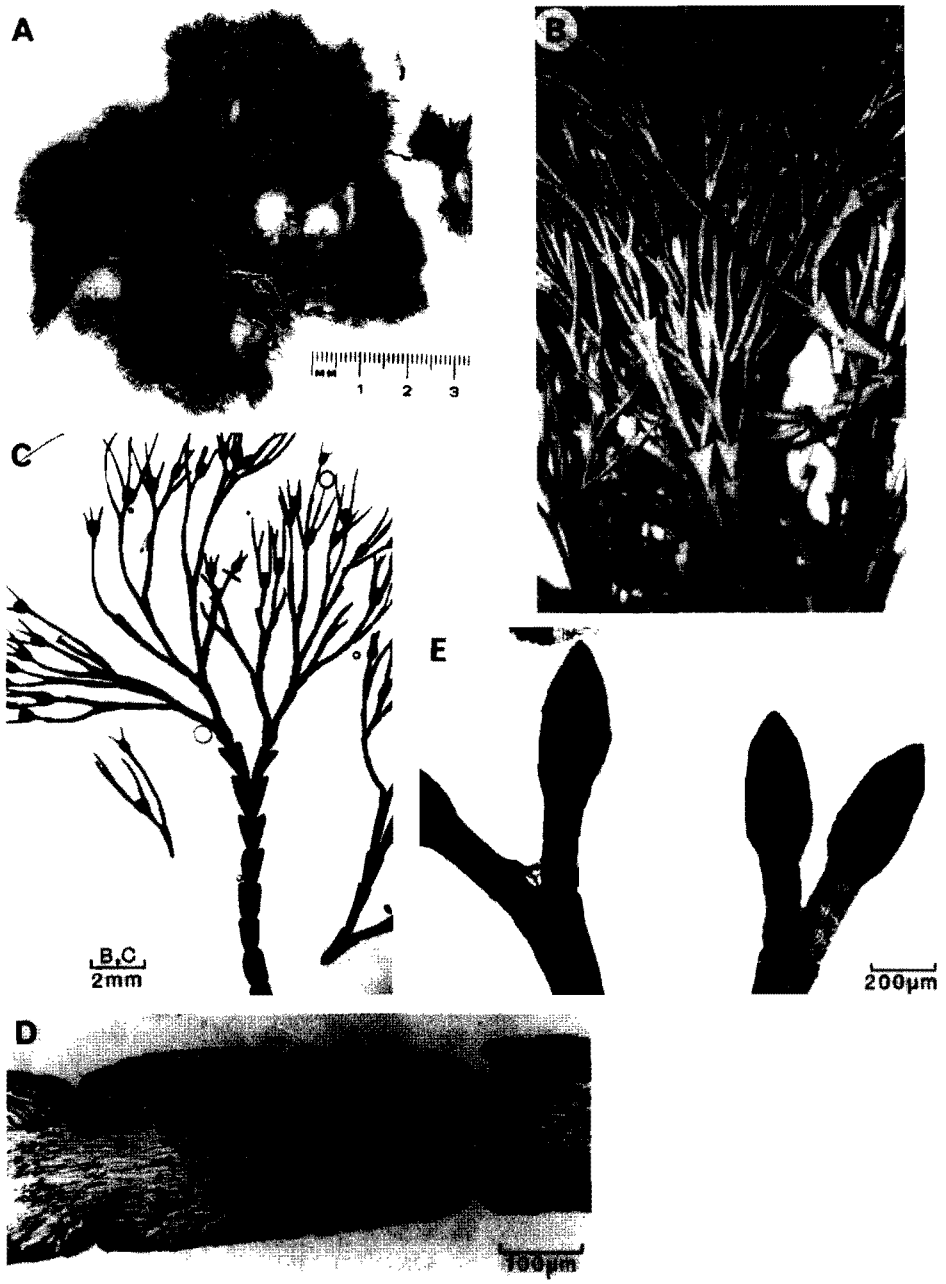


Fig. 140. *Jania pulchella* (**A–C,** AD, A27229; **D,** AD, A542; **E,** AD, A28574). **A.** Habit. **B.** Lower cheilosporoid segments and upper janioid branches. **C.** Ditto, tetrasporangial plant. **D.** Longitudinal segment of branch with 3 tiers in the intergeniculum. **E.** Male conceptacles.

sublittoral fringe (*Womersley*, 30.viii.1979; AD, A50972 —"Marine Algae of southern Australia" No. 333). Head of Great Australian Bight, S. Aust., on *C. subfarcinata*, drift (*Womersley*, 4.ii.1954; AD, A19194). Cape Carnot, S. Aust., on *C. subfarcinata*, in sublittoral pools (*Womersley*, 8.i.1951; AD, A13832). Louth Bay, S. Aust., on *C. subfarcinata*, upper sublittoral (*Womersley*, 4.i.1951; AD, A13659). S side of Ellen Point, Vivonne Bay, Kangaroo I., S. Aust., on *C. subfarcinata*, in large sublittoral pool (*Womersley*, 29.i.1957; AD, A20792). Pennington Bay, Kangaroo I., S. Aust., on *C. congesta*, drift (*Womersley*, 31.xii.1949; AD, A12852). Port Elliot, S. Aust., on *C. congesta*, drift (*Womersley*, 17.x.1948; AD, A9406). Apollo Bay, Vic., on *C. siliquosa* in upper sublittoral pools (*Johansen* 81-9-1, 1.ix.1981; AD, A52606). Cape Patterson, Vic., on *C. siliquosa*, drift (*Ducker*, 18.v.1972; MELU, 21418). Granville Harbour, Tas., on *Cystophora*, 1–4 m deep (*Blackman* 79-11, 27.i.1979; AD, A58553).

Jania pusilla is distinctive in size and habit, and common on species of *Cystophora* (especially *C. subfarcinata*) in shallow water on rough-water coasts in southern Australia; it was described in detail by Ducker *et al.* (1976). It is characterised by small fronds with unusually broad intergenicula. *Jania radiata* Yendo (see Segawa 1946) from Japan, resembles *J. pusilla* except that it has more delicate fronds.

6. **Jania pulchella** (Harvey)Johansen & Womersley 1994: 619, figs 19, 20, 41, 42.
Cheilosporum pulchellum Harvey 1855a: 547; 1863, synop.: xxix. De Toni 1905: 1834. Huisman & Walker 1990: 411. Lucas & Perrin 1947: 397. May 1965: 356. Sonder 1881: 20. Srimanobhas *et al.* 1990: 110.
Jania affinis Harvey 1855a: 547; 1863, synop.: xxix. De Toni 1905: 1857. De Toni & Forti 1923: 63? Huisman & Walker 1990: 412. Sonder 1881: 21. Yendo 1905: 39.

FIG. 140

Thallus (Fig. 140A, B) medium to dark red to red-brown, 2–6 cm high, branches compressed below, terete above. Fronds erect, more or less complanately branched, intergenicula dimorphic (Fig. 140B, C), flat and broad below (like *Cheilosporum*) and terete above (like *Jania*). Lower intergenicula compressed and bilobed, lobes pointed to broadly rounded (occasionally very slight), intergenicula (300-) 400–1000 (-1500) µm long and (200-) 500–1000 (-1250) µm broad. Upper intergenicula terete or subterete (300-) 500–1200 (-1500) µm long and (80-) 100–250 (-300) µm in diameter. Genicula (60-) 80–110 (-200) µm long. Holdfasts stoloniferous, stolons terete to slightly compressed, 150–300 µm in diameter; usually epiphytic on larger algae, possibly epilithic. *Structure.* Lower intergenicula of (3-) 4–9 tiers (Fig. 140D) of medullary cells each (80-) 100–140 (-160) µm long; upper intergenicula of (3-) 5–9 (-14) tiers of medullary cells each 80–160 (-200) µm long.

Reproduction. Gametangial thalli dioecious. Female conceptacles amphoroid with short necks, externally 350–450 µm long and 350–400 µm in diameter; carposporangia subspherical, 60–80 µm in diameter. Male conceptacles (Fig. 140E) terminal, elongate-ovoid to fusiform; externally (400-) 550–650 µm long and 200–280 µm in diameter, internally 140–240 µm in diameter, canal 70–100 µm long.

Tetrasporangial conceptacles bearing 2–3 (-4) terete branches, only occurring in terete branches which arise from apices of flat intergenicula or adventitiously from their surfaces; external diameter 450–500 µm, internal diameter 100–350 µm; tetrasporangia 150–300 µm long and 35–80 µm in diameter.

Type from Rottnest I., W. Aust., (*Harvey*, Trav. Set 250); holotype in TCD, isotypes (*Harvey*, Alg. Aust. Exsicc. 446) in other herbaria.

Distribution: Houtman Abrolhos, W. Aust., to Lawrence Rocks, Portland (probably to Gabo I.), Vic., in deep water on rough-water coasts, epiphytic on various algae.

Selected specimens: Coronation I., Houtman Abrolhos, W. Aust., on *Sargassum fallax* (Aquinas Coll. Exp. B14, 24.viii.1970; AD, A43856). Limestone Bay, Middle I., Recherche Arch., W. Aust., on *Sargassum*, drift (*Willis*, 25.xi.1950; AD, A15892). Waldegrave I., S. Aust., 22 m deep (*Shepherd*, 23.x.1970; AD, A37403). Waterloo Bay, S. Aust., 5–7 m deep inside bar (*Shepherd*, 30.x.1981; AD, A52572, A52749). Pearson I., S. Aust., on steep slopes 22 m deep (*Shepherd*, 8.i.1969; AD, A52599) and 22 m deep (*Shepherd*, 12.i.1969; AD, A34028). Thistle I., S. Aust., 16 m deep (*Baldock*, 2.i.1964; AD, A27229). Port Elliot, S. Aust., drift (AD, A542). Lawrence Rock, Portland, Vic., 12–15 m deep

(*Watson*, 30.xi.1981; AD, A52796). Lonsdale Bight, Port Phillip Heads, Vic., 3 m deep (*Macpherson*, 21.v.1961; AD, A28574)? Gabo I., Vic., 8 m deep (*Shepherd*, 19.ii.1973; AD, A52778).

Jania pulchella is distinctive in having lower intergenicula like those in *Cheilosporum* (although variable in degree of development) and upper intergenicula as in *Jania*. It appears to be a deep water species, usually epiphytic.

Genus **HALIPTILON** (Decaisne)Lindley 1846: 25

Thallus tufted, with few to numerous erect, pinnate, geniculate fronds, often with adventitious branchlets, intergenicula usually compressed and cuneate in main branches, terete in branchlets; holdfast crustose, often becoming stoloniferous, epilithic or epiphytic. *Structure*. Intergenicula with 3–6 tiers of medullary cells with lateral cell-fusions but without lateral pit-connections. Genicula of single tiers of elongate, darker staining cells. Cortex present on intergenicula, filaments assurgent to anticlinal, outer cells bearing short epithallial cells.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Conceptacles axial and terminal, branchlets usually present on carposporangial and tetrasporangial conceptacles. Gametangial thalli dioecious. Carpogonial filaments 2-celled, arising on floor of female conceptacles, carposporangia in short filaments near the margins of a relatively thick fusion cell. Male conceptacles without branchlets, elongate-ovoid to fusiform and not beaked, spermatangia produced basally and on the sides of the chamber.

Tetrasporangia in swollen conceptacles, ovoid-urceolate, with relatively few (<15) tetrasporangia.

Lectotype species: *Haliptilon cuvieri* (Lamouroux)Johansen & Silva (1978, p. 417) = *H. roseum* (Lamarck)Garbary & Johansen.

Haliptilon roseum (Lamarck)Garbary & Johansen 1982: 218. Adams 1994: 158, pl. 54 lower. Huisman & Walker 1990: 411. Johansen & Womersley 1986: 552, figs 1–6. Millar 1990: 320, fig. 11A, B. Millar & Kraft 1993: 13.

Corallina rosea Lamarck 1815: 235. Areschoug 1852: 573. De Toni 1905: 1849. Kützing 1849: 708; 1858: 34, pl. 72, fig. II. Lucas 1935: 228. Manza 1940: 279. Sonder 1855: 521; 1881: 21. Yendo 1905: 35.

Corallina rosea var. *crispa* Lamarck 1815: 235.

Jania rosea (Lamarck)Decaisne 1842b: 123. Harvey 1849a: 105, pl. 40 upper right.

Cornicularia rosea (Lamarck)Chapman & Parkinson 1974: 184, pls 60B, 62B.

Corallina plumosa Lamarck 1815: 235.

Corallina cuvieri Lamouroux 1816: 287, pl. 9 fig. 8. Adams 1972: 75. Adams *et al.* 1974: 219. Areschoug 1852: 572. Borowitzka & Vesk 1978: 295. Cribb 1954: 35. De Toni 1905: 1848. De Toni & Forti 1923: 62. Etchverry 1986: 210? Guiler 1952: 86. Harvey 1863, synop.: xxviii. Kützing 1849: 708; 1858: 33, pl. 70, fig. I. Levring 1946: 221. Lucas 1929a: 27; 1929b: 53. Lucas & Perrin 1947: 399, fig. 202a, b. Manza 1940: 279. Reinbold 1899: 51. Saenger 1974: 80. Sonder 1853: 687; 1855: 521; 1871: 53(?); 1881: 21. Tisdall 1898: 508. Wilson 1892: 176. Womersley 1950: 166; 1953: 37; 1966: 146. Yendo 1905: 35.

Jania cuvieri (Lamouroux)Decaisne 1842b: 123. Harvey 1849a: 105; 1855a: 547; 1859b: 310. Tisdall 1898: 508.

Cornicularia cuvieri (Lamouroux)Chapman & Parkinson 1974: 184, fig. 56, pl. 59B.

Haliptilon cuvieri (Lamouroux)Johansen & Silva 1978: 417.

Corallina crispata Lamouroux 1816: 289, pl. 10 fig. 3. Kützing 1849: 708; 1858: 34, pl. 71, fig. 1. Sonder 1855: 522. Tisdall 1898: 508.

Jania crispata (Lamouroux)Decaisne 1842b: 123.

Haliptilon crispata (Lamouroux)Garbary & Johansen 1982: 218.

Corallina cuvieri var. *crispata* (Lamouroux)Areschoug 1852: 572. Harvey 1863, synop.: xxviii. Lucas & Perrin 1947: 399, fig. 202c, d. Sonder 1881: 21. Yendo 1905: 35.

Corallina gracilis Lamouroux 1816: 288, pl. 10 fig. 1a, B. Cribb 1954: 36, 37. Kützing 1849: 707. Manza 1940: 279.
Jania gracilis (Lamouroux)Montagne 1845: 147. Harvey 1849a: 105. Hooker & Harvey 1845: 539.
Haliptilon gracilis (Lamouroux)Johansen 1971: 243(?).
Cornicularia gracilis (Lamouroux)Chapman & Parkinson 1974: 183.
Corallina pilifera Lamouroux 1816: 290. Areschoug 1852: 571. De Toni 1905: 1848. Guiler 1952: 86. Harvey 1863, synop.: xxviii. Kützing 1849: 708; 1858: 35, pl. 74 fig. II. Lucas 1915: 57. Lucas & Perrin 1947: 400. Manza 1940: 280. Sonder 1853: 687; 1855: 521; 1881: 21. Tisdall 1898: 508. Wilson 1892: 176. Womersley 1950: 167; 1953: 37. Yendo 1905: 35.
Cornicularia pilifera (Lamouroux)Chapman & Parkinson 1974: 185.
Haliptilon piliferum (Lamouroux)Garbary & Johansen 1982: 218.
Corallina turneri Lamouroux 1816: 289, pl. 10 fig. 2. Kützing 1849: 706.
Corallina cuvieri var. *turneri* (Lamouroux)Kützing 1858: 34.
Haliptilon turneri (Lamouroux)Garbary & Johansen 1982: 218.
?*Jania compressa* Lamouroux 1824: 624, pl. 90 figs 8–10.
Corallina calliptera Kützing 1849: 705; 1858: 34, pl. 72 fig. I. Areschoug 1852: 575. De Toni 1905: 1853. Harvey 1863, synop.: xxviii. Sonder 1881: 21.
Corallina cuvieri var. *calliptera* (Kützing)Grunow 1868: 78. Yendo 1905: 35.
Corallina plumifera Kützing 1849: 705; 1858: 34, pl. 71 fig. II. Areschoug 1852: 576. De Toni 1905: 1854. Harvey 1863, synop.: xxviii.
Haliptilon plumiferum (Kützing)Garbary & Johansen 1982: 218.
Corallina clavigera Kützing 1858: 36, pl. 75, fig. 1. De Toni 1905: 1854. Sonder 1881: 21. Yendo 1905: 35.
Corallina denudata (Sonder)Kützing 1858: 34, pl. 73. De Toni 1905: 1854. Guiler 1952: 86. Manza 1940: 280.
Corallina cuvieri var. *denudata* Sonder 1855: 521; 1881: 21. Yendo 1905: 35.
Corallina trichocarpa Kützing 1858: 35, pl. 74 fig. 1. De Toni 1905: 1854. De Toni & Forti 1923: 62. Levring 1946: 221. Manza 1940: 280. Yendo 1905: 35.
Haliptilon trichocarpum (Kützing)Garbary & Johansen 1982: 218.

Taxa that have been incorrectly recorded from southern Australia, probably based on *Haliptilon roseum*.

Corallina granifera Ellis & Solander, *sensu* De Toni & Forti 1923: 62. Ducker *et al.* 1977: 86. Kützing 1849: 708. Sonder 1881: 21.
Jania granifera (Ellis & Solander)Decaisne *sensu* Harvey 1849a: 106. Sonder 1848: 187.
Corallina subulata Ellis & Solander *sensu* Kützing 1849: 705.
Jania subulata (Ellis & Solander)Sonder 1848: 186. Harvey 1849a: 106, pl. 40. Tisdall 1898: 508.
Jania subulata var. *crispata* (Lamouroux)Harvey 1849a: 106.
Corallina cuvieri var. γ *subulata* (Ellis & Solander)Areschoug 1852: 572. Kützing 1858: 33, pl. 70 fig. II. Sonder 1881: 21. Yendo 1905: 35.
Haliptilon subulatum (Ellis & Solander)Johansen 1970: 79, figs 10, 12. Ducker *et al.* 1977: 86. King *et al.* 1971: 121.

PLATE 4 fig. 4; FIG. 141

Thallus (Fig. 141A–C) light to medium grey-red, often bleached, (2-) 5–10 (-12) cm high, usually in densely branched tufts of numerous erect fronds. Fronds pinnately branched, axes sparsely dichotomous with occasional main lateral branches, bearing short (largely determinate) branchlets distichously and often adventitiously (Fig. 141C), often denuded below. Axial intergenicula in mid and upper parts slightly to strongly compressed, subterete to cuneate, with branchlets from the opposite shoulders and often adventitious branchlets not in the main plane of branching. Determinate branchlets (Fig. 141D) usually markedly slenderer than indeterminate axes, simple to di- or trichotomous 2–4 times, ultimately tapering to subacute apices. Axial intergenicula 300–700 (-825) μm long, 300–900 μm

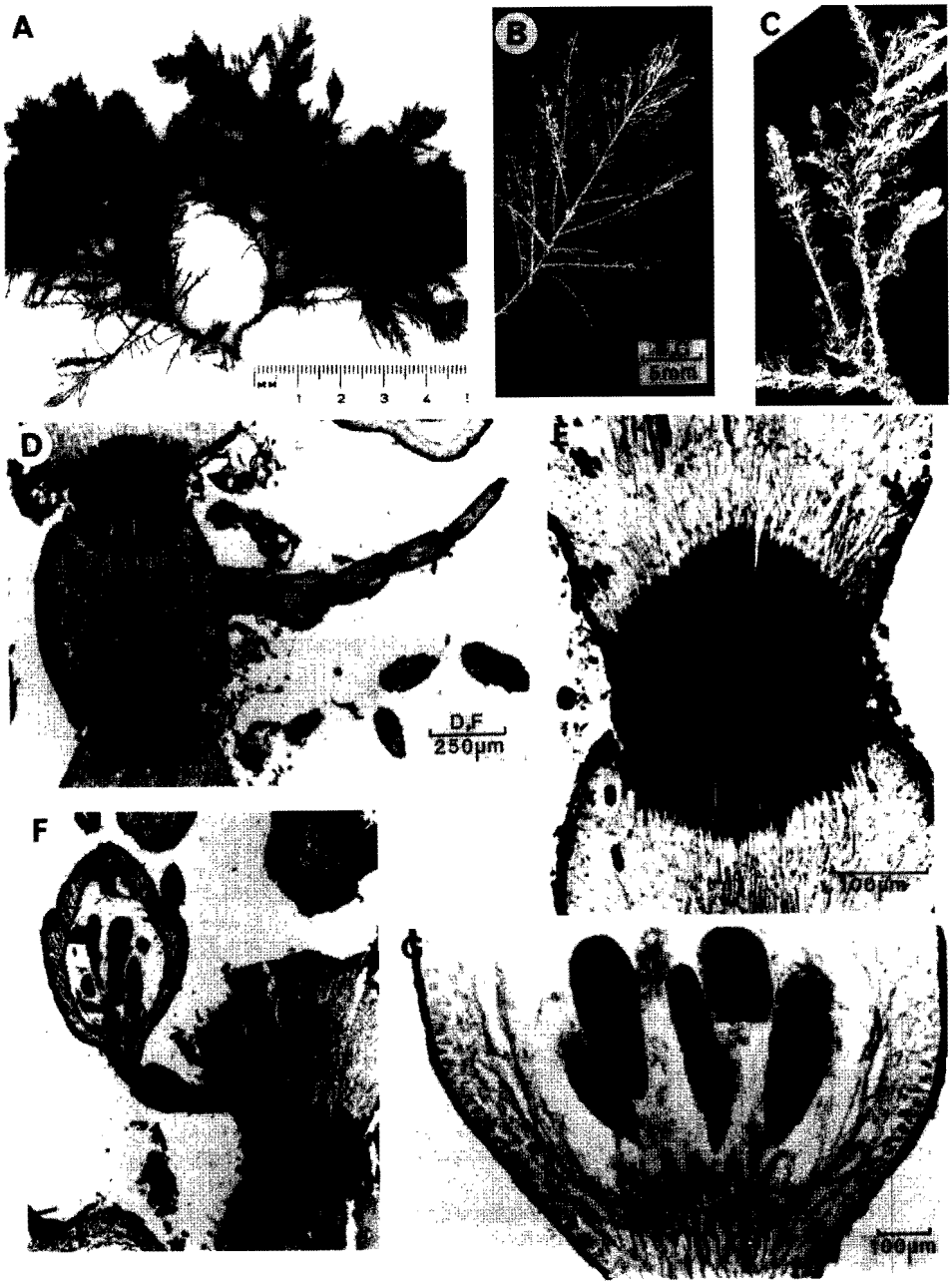


Fig. 141. *Haliptilon roseum* (**A, B,** AD, A64428; **C,** AD, A33654; **D–F,** Johansen 81-9-57a, CUW8546; AD, A52675; **G,** Johansen 9027). **A.** Habit. **B.** Habit, branch. **C.** Habit of plant with numerous adventitious branchlets. **D.** Longitudinal section of branch with genicula and intergenicula, and an adventitious branchlet. **E.** Longitudinal section of geniculum and part intergenicula. **F.** Longitudinal section of branch and branchlet with tetrasporangial conceptacle. **G.** Longitudinal section of a tetrasporangial conceptacle. [**D–G,** Photos H.W.J.]

broad, L/B 1–2 (-3). Branchlet intergenicula terete to subterete, 200–600 µm long and 150–250 µm in diameter near base, 60–80 µm in diameter near apices. Holdfasts crustose when young, later developing entangling and attaching stolons with terete intergenicula 300–600 µm long and 200–400 µm in diameter; epilithic as low mats or epiphytic on larger algae or *Amphibolis*. *Structure*. Intergenicula (Fig. 141D) with 3–5 (-6) tiers of medullary cells, each (50-) 70–100 (-145) µm long, with lateral cell-fusions but without lateral pit-connections. Cortex 2–3 cells thick. Genicula (Fig. 141E) 240–370 µm long in axes, less in determinate branchlets. Rhodoplasts discoid.

Reproduction. Gametangial thalli dioecious. Conceptacles swollen, axial and terminal. Carposporangial conceptacles usually with two simple surmounting branchlets each consisting of 1–3 intergenicula; external diameter 250–300 µm, chamber diameter 150–200 µm, fusion cells 50–70 µm in diameter and 20–30 µm thick, with carposporangial filaments marginal, carposporangia subspherical, (70-) 80–100 (-160) µm in diameter. Male conceptacles terminal on determinate branchlets, without surmounting branchlets, elongate-ovoid to lanceolate, 200–250 µm in external diameter, chamber 90–130 µm in diameter and 240–340 µm high, canal 50–90 µm long, with spermatangia produced on floor and walls of chamber.

Tetrasporangial conceptacles (Fig. 141F) at apices of determinate branchlets, swollen, surmounted by 1–3 small branchlets each with 1–3 intergenicula, (300-) 400–500 µm in external diameter, chamber 280–330 µm in diameter, each conceptacle containing 6–10 mature tetrasporangia (Fig. 141G) 160–330 µm long, zonately divided.

Type from 'les mers Australes' (*Péron & Lesueur*), probably from south-western Australia, or SW Tas.; holotype in PC.

Distribution: Kalbarri, W. Aust., around southern Australia and Tasmania to Port Denison, Queensland.

New Zealand; Juan Fernandez I.? (Etcheverry 1986: 210).

Selected specimens: Jacques Point, Kalbarri, W. Aust., uppermost sublittoral (*Womersley*, 15.ix.1979; AD, A51285). Pearson Is, S. Aust., 6–8 m deep (*Shepherd*, 7.i.1969; AD, A33654). Wanna, S. Aust., upper sublittoral pools (*Womersley*, 19.ii.1959; AD, A22444). Barker Rocks, Yorke Pen., S. Aust., on *Scaberia* (*Johansen* 81-9-63, 20.ix.1981; AD, A56370). Pondalowie Bay, S. Aust., upper sublittoral on *Amphibolis antarctica* (*Johansen* 81-9-56b & -57a, 19.ix.1981; AD, A52674 & A52675 respectively). Port Adelaide, S. Aust. (*Mueller* 1849; MEL, 592652), illustrated by Kützing 1858, pl. 74C, D as *C. pilifera*. Port Noarlunga, S. Aust., on reef (*Womersley*, 21.x.1944; AD, A1677). Fishery Beach, Cape Jervis, S. Aust., 4–6 m deep (*Gowlett-Holmes*, 24.ii.1996; AD, A64605). Abalone Cove, West I., S. Aust., 4–5 m deep (*Kildea*, 12.ix.1995; AD, A64428). South Coast, Kangaroo I., S. Aust., on *Amphibolis* (*Cork*, winter 1939; AD, A2477). Nora Creina, S. Aust., drift (*Johansen* 81-9-40 & -53c, 5.ix.1981; AD, A56368, and 15.ix.1981; *Johansen*, 9027). MacDonnell Bay, S. Aust. (*Wehl*; MEL, 592647). Bridgewater Bay, Vic., low eulittoral (*Johansen* 81-9-13 & -15, 3.ix.1981; AD, A52604, and A56367, respectively). Queenscliff, Vic., drift (*Johansen* 81-8-1a on *Codium galeatum*, 30.viii.1981; AD, A52589; 81-8-1c (on *Amphibolis antarctica*), 31.viii.1981; AD, A52603 and 81-8-1d; AD, A52696). Queenscliff, Vic., low eulittoral on *Amphibolis antarctica* (*Johansen* 81-8-14, 31.viii.1981; AD, A52585). Popes Eye, Port Phillip Bay, Vic., sublittoral (*Kain & Johansen* 81-8-8 and -8a, 31.viii.1981; AD, A52851 and A56366, respectively). St Leonards, Port Phillip, Vic., outside breakwater 1.5–3 m deep (*Womersley*, 9.viii.1959; AD, A23100). Gabo I., Vic., 8 m deep (*Shepherd*, 19.ii.1973; AD, A43522). Ulverstone, Tas., upper sublittoral (*Wollaston*, 7.viii.1965; AD, A29586). Triabunna, Tas., sublittoral (*Cribb* 41.13, 18.iii.1950; AD, A16211). Fluted Cape, Bruny I., Tas., 4–5 m deep (*Shepherd*, 10.ii.1972; AD, A41760). Byron Bay, N.S.W., 6 m deep (*Silvester*, 21.vii.1973; AD, A43881). Caloundra, Qld, drift (*McKeon*, 30.i.1949; AD, A16644).

H. roseum is a common species, ranging from the lower eulittoral zone where plants are turf-like, to the sublittoral where it occurs both on rocks and epiphytically on larger algae and the seagrass *Amphibolis*.

Details of the type specimens of the numerous synonyms of *H. roseum* are given by Johansen & Womersley (1986, p. 563), who also discuss the variation in habit within the species.

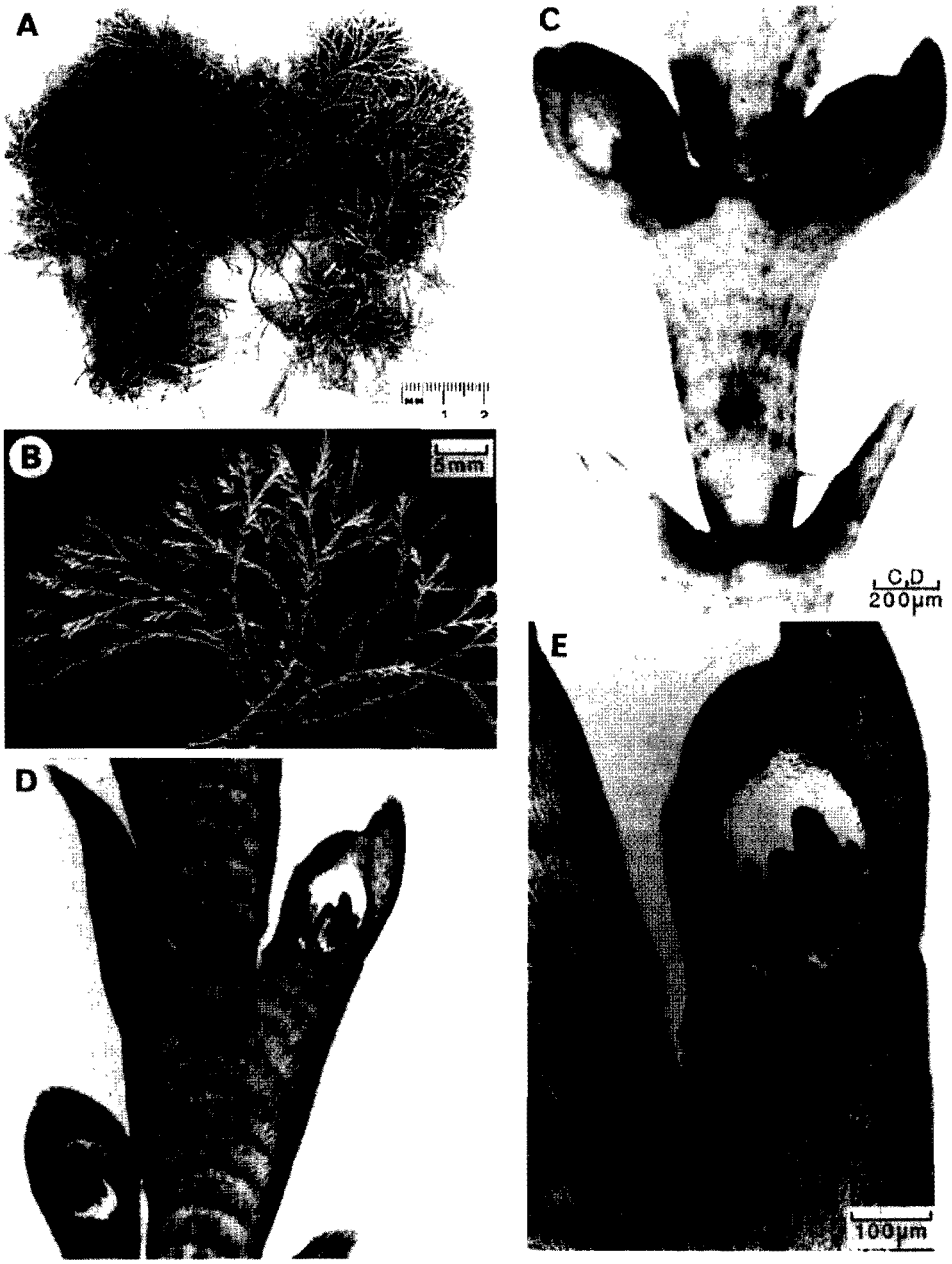


Fig. 142. *Cheilosporum sagittatum* (**A–C**, AD, A52707; **D, E**, AD, A60412). **A.** Habit. **B.** Branches showing acute lobes on intergenicula. **C.** Branch with tetrasporangial conceptacles. **D.** Longitudinal section of branch with tetrasporangial conceptacles. **E.** Longitudinal section of tetrasporangial conceptacle.

Genus CHEILOSPORUM (Decaisne)Zanardini 1844: 1025

Thallus tufted, with several to numerous erect, subdichotomous fronds, complanately branched, with compressed intergenicula each bearing two compressed lobes; holdfasts crustose, developing basal stolons with new erect fronds, epilithic or epiphytic. *Structure.* Intergenicula with 5–10 (-12) tiers of medullary cells with lateral cell-fusions but without lateral pit-connections, extending to 20 tiers in the lobes. Genicula of single tiers of elongate cells, with darkly staining walls. Cortex present on intergenicula, of splaying filaments of elongate cells, outer cells with short epithallial cells.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Conceptacles single (-3), embedded within the fertile lobes, pore adaxial or apical. Gametangial thalli dioecious. Carpogonial filaments 2-celled, arising on the floor of female conceptacles, carposporangia terminal in 2–4 celled filaments on the margins of the relatively thick fusion cells. Male conceptacles elongate, chamber narrow, with spermatangia arising on the floor and sides.

Tetrasporangial conceptacles on separate thalli, with tetrasporangia arising from the chamber floor.

Lectotype species: *C. sagittatum* (Lamouroux)Areschoug 1852: 545. (Schmitz 1889: 455.)

Cheilosporum is a distinctive genus, with each intergeniculum bearing two upwardly-projecting lobes, with the conceptacles formed within the lobes and opening on their adaxial edges. It contains some 5 species (Srimanobhas *et al.* 1990), most confined to tropical-subtropical waters but one (*C. sagittatum*) present in temperate seas.

Cheilosporum sagittatum (Lamouroux)Areschoug 1852: 545. Adams 1994: 159, pl. 55 upper right. De Toni 1905: 1832. Harvey 1863: pl. 250. Johansen 1977: 178. Lucas & Perrin 1947: 396, fig. 200. Manza 1940: 292. May 1965: 356. Millar 1990: 319, fig. 10D–F. Sonder 1881: 20. Srimanobhas *et al.* 1990: 110. Tisdall 1898: 507.

Corallina sagittata Lamouroux 1824: 625, pl. 95 figs 11, 12.

Amphiroa sagittata (Lamouroux)Decaisne 1842b: 125. Harvey 1849a: 102. Kützing 1849: 704; 1858, 28, pl. 56c, d. Sonder 1848: 188.

Amphiroa elegans Hooker & Harvey *in* Harvey 1849a: 101, pl. 38 (lower left); 1859b: 310. Kützing 1858: 28, pl. 57a, b. Tisdall 1898: 507.

Cheilosporum elegans (Hooker & Harvey)Areschoug 1852: 546. Chapman & Parkinson 1974: 173, pls 55A, 57B. Guiler 1952: 87. Womersley 1966: 146.

FIG. 142

Thallus(Fig. 142A, B) medium red-brown, fading to grey-red, 4–10 cm high, in dense tufts of numerous erect fronds, axes and main branches dichotomously and largely complanately branched, each intergeniculum with two opposite, strongly developed, compressed, acute lobes (Fig. 142B) with upper margins (400-) 600–1300 µm long, lower margin passing to the base or to 2/3 up the intergeniculum, intergenicula 500–1250 µm long and 250–400 µm broad below the lobes. Holdfasts crustose, soon developing terete to slightly compressed, unlobed stolons 250–400 µm in diameter in an entangled mass 0.5–12 mm across; epilithic. *Structure.* Branch apices with a thin mucilaginous cover and without epithallial cells. Intergenicula with 5–10 (-12) arched tiers of medullary cells (Fig. 142D), extending to 18 tiers including the lobes, each tier 50–120 µm long, with lateral cell-fusions but without lateral pit-connections. Cortical filaments 5–8 cells long, cells elongate-ovoid, 6–10 µm in diameter, with short epithallial cells. Genicula 130–240 µm long. Rhodoplasts discoid.

Reproduction. Gametangial thalli probably dioecious. Conceptacles (Fig. 142C) slightly swollen, adaxial or terminal in the lobes with the pores opening on the upper edge or terminally. Carposporangial conceptacles unknown. Male conceptacles elongate, chamber narrow, spermatangia arising on the floor and walls.

Tetrasporangial conceptacles (Fig. 142C–E) swollen on the adaxial sides of the lobes, with the pore adaxial and usually subapical (Fig. 142C, D), lobe apices usually pointed

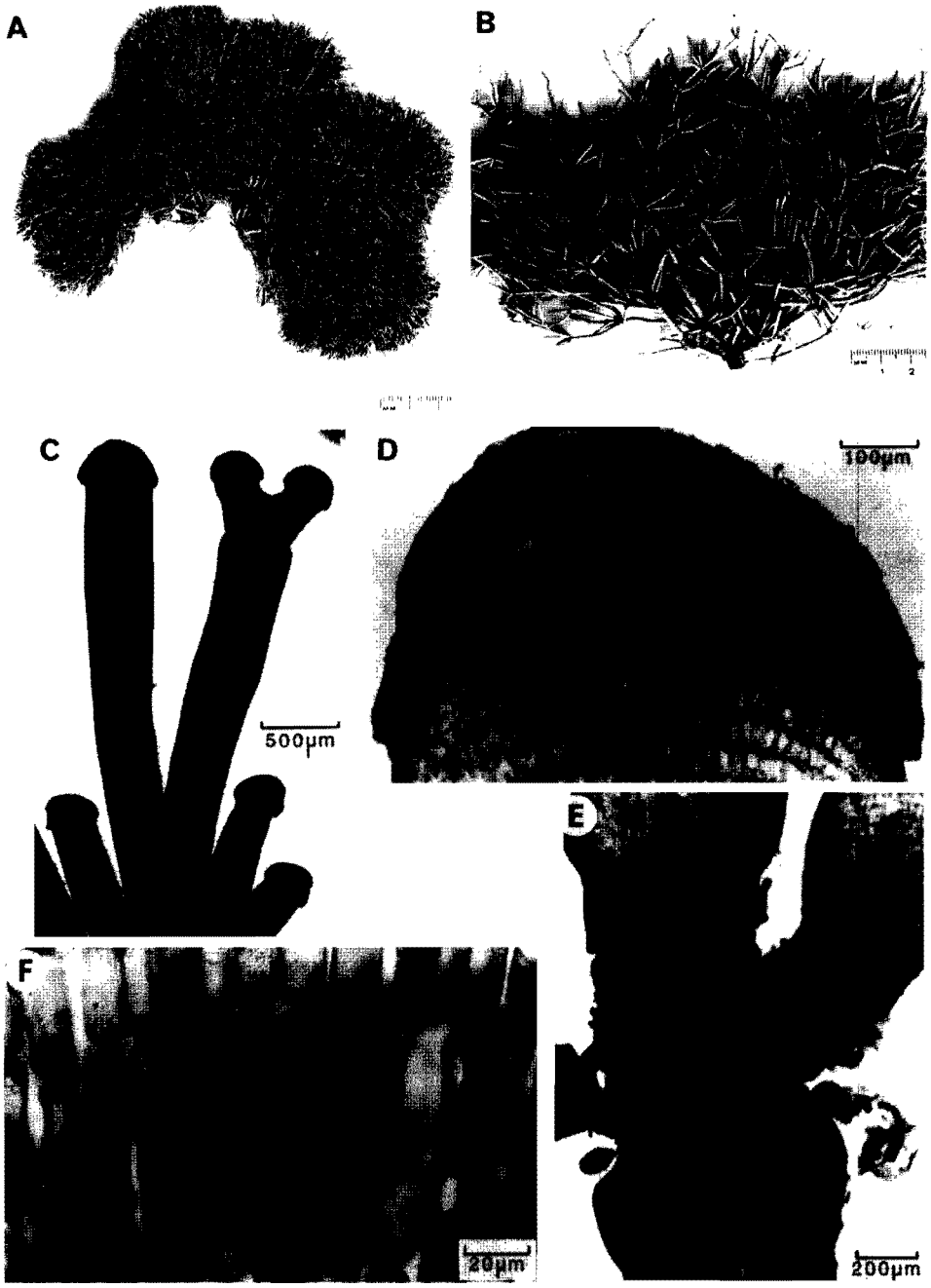


Fig. 143. *Metagoniolithon radiatum* (**A,** AD, A10933; **B, F,** AD, A47006; **C, D,** AD, A35182; **E,** AD, A55360). **A.** Habit. **B.** Habit, coarse plant. **C.** Branches with apical mucilaginous caps. **D.** Longitudinal section of branch with mucilaginous cap. **E.** Longitudinal section of geniculum and intergenicula. **F.** Longitudinal section of medulla with lateral cell fusions.

(rarely rounded), chamber ovoid, 200–300 μm in diameter, tetrasporangia arising basally in the chamber, elongate-ovoid to clavate, 40–75 μm in diameter, zonately divided.

Type from Ile de France (Mauritius); holotype in Herb. Lamouroux, CN.

Distribution: Mauritius; South Africa; Philippines; Brazil.

In Australia, from "Swan R." W. Aust., (Harvey 1863, pl. 250) to Coffs Harbour, N.S.W. (Millar 1990, p. 319). Northern Aust. (see Lewis 1984, p. 13).

Selected specimens: Pondalowie Bay, S. Aust., drift (*Womersley*, 14.iv.1963; AD, A26546). Althorpe Is, S. Aust., 10–12 m deep, N side (*Baldock*, 4.i.1964; AD, A27227). Troubridge Point, S. Aust., 2–5 m deep (*Shepherd*, 7.ii.1969; AD, A33834). Port Stanvac, S. Aust., mid eulittoral pool (*Clarke*, 16.xii.1977; AD, A50416). Port Noarlunga, S. Aust., reef pools (*Womersley*, 21.x.1944; AD, A1679). Aldinga, S. Aust., outer pools (*Johansen* 81-10-1, 13.x.1981; AD, A52707 — "Marine Algae of southern Australia" No. 336). Penguin Rock, West I., S. Aust., 5–6 m deep (*Shepherd*, 28.xii.1965; AD, A35503). Lady Julia Percy I., Vic., 8–10 m deep (*Shepherd*, 5.i.1968; AD, A32368). Lighthouse Point, Queenscliff, Vic., 12–14 m deep (*Goldsworthy*, 9.ii.1990; AD, A60154). Cape Woolamai, Vic., 13 m deep (AIMS–NCI, Q66C 3519-Q, 17.ii.1990; AD, A60298). Bicheno, Tas., 17 m deep (*McCauley*, 26.ii.1990; AD, A60412). Marion Bay, Tas., 10 m deep (*Shepherd*, 13.ii.1970; AD, A35663). Long Reef, N.S.W. (*I. & V. Warnock*, 3.i.1935; AD, A49938 – Tilden "South Pacific Plants, Ser. 2, 331).

Cheilosporum sagittatum is common on southern Australian coasts, especially in the lower Gulf region of South Australia. Lewis (1984, p. 13) gave references to records from northern Australia, Joly (1965, p. 137) gave records from Brazil, and Silva, Menez & Moe (1987, p. 34) recorded it from the Philippines.

C. elegans, from New Zealand, seems to be indistinguishable from *C. sagittatum*, certainly for the southern Australian specimens.

SUBFAMILY METAGONIOLITHOIDEAE Johansen 1969: 47

by H.B.S. Womersley & H.W. Johansen

Thallus with an encrusting non-geniculate holdfast and erect, terete, geniculate fronds, di- or trichotomous or with several clustered lateral branches from the genicula. *Structure* of branches multiaxial, apices with conspicuous mucilaginous caps but without epithallial cells; intergenicula with multi-tiered medulla, with lateral cell-fusions but without lateral pit-connections; genicula of many-celled untiered filaments, producing lateral branches. Cortex on both intergenicula and genicula (less well developed), of short splaying filaments with short epithallial cells.

Life history triphasic, with isomorphic gametophytes and tetrasporophytes.

Reproduction. Conceptacles uniporate, borne laterally on the intergenicula. Gametangial thalli dioecious. Carpogonial filaments 2-celled, carposporangia terminating short gonimoblast filaments arising from the margins of a thin basal fusion cell. Spermatangia on short filaments on the male chamber floor.

Tetrasporangia arising from the floor of the conceptacle chamber, usually peripherally.

Type genus: *Metagoniolithon* Weber-van Bosse 1904: 101.

The Metagoniolithoideae contains the single genus *Metagoniolithon*, probably confined to southern and south-western Australian coasts. The conspicuous apical mucilaginous caps, branching from the genicula, non-tiered genicula, multitiered intergenicula, cell-fusions, and conceptacles borne on the surfaces of terete branches, distinguish the subfamily and genus.

Genus METAGONIOLITHON Weber-van Bosse 1904: 86, 101

With the characteristics of the subfamily.

Lectotype species: *M. charoides* (Lamouroux)Weber-van Bosse (Manza 1937: 45) [= *M. radiatum* (Lamarck)Ducker].

The three species of *Metagoniolithon* were monographed by Ducker (1979), who discussed the numerous synonyms of the species and their type specimens. Ducker (1979, p. 68) discussed and rejected records of the species from outside Australia.

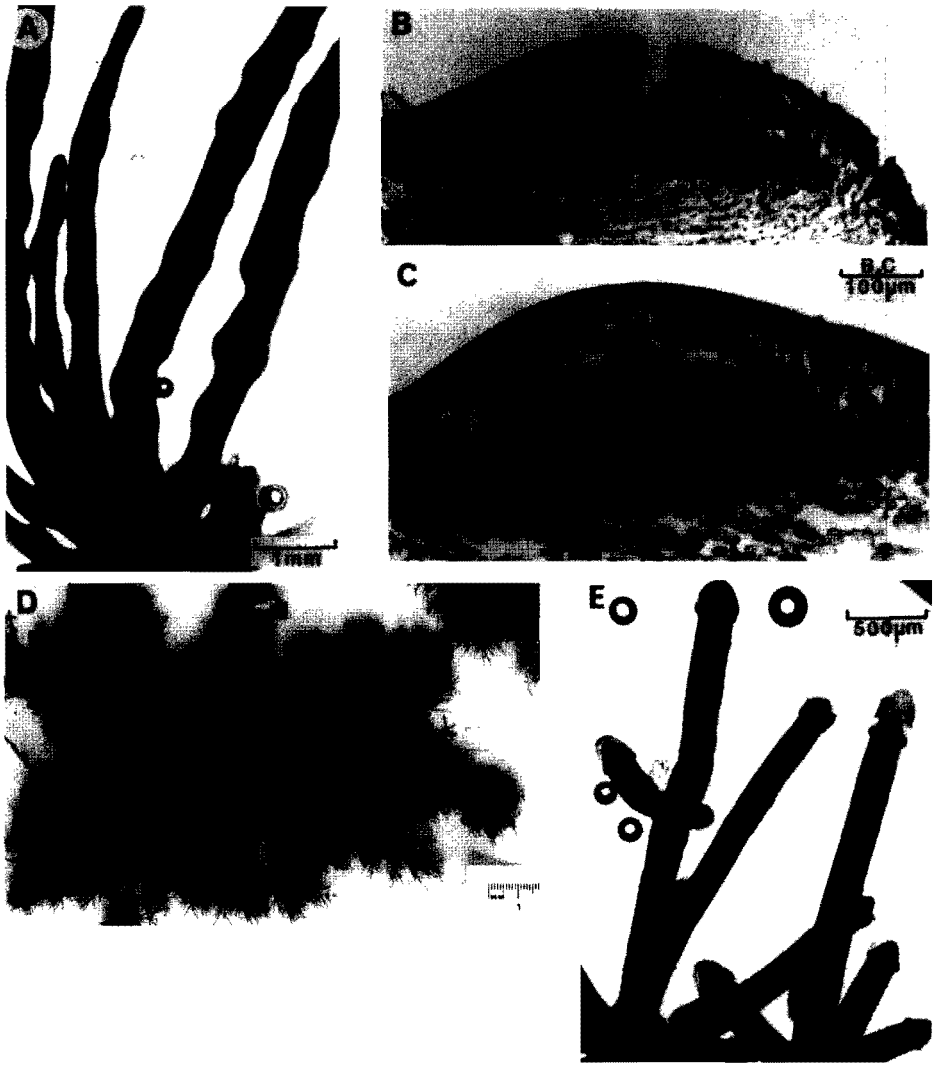


Fig. 144. A–C. *Metagoniolithon radiatum* (**A, B,** AD, A10933; **C,** AD, A52595). **A.** Branches with male conceptacles. **B.** Longitudinal section of a male conceptacle. **C.** Longitudinal section of a tetrasporangial conceptacle. **D, E.** *Metagoniolithon stelliferum* (**D,** AD, A52193; **E,** AD, A64300). **D.** Habit. **E.** Branches with mucilaginous caps.

KEY TO SPECIES OF *METAGONIOLITHON*

1. Thallus epilithic, robust, branches 1–2 (-3) mm in diameter below, 400–800 μm in diameter below apices ..... 1. *M. radiatum*
1. Thallus epiphytic, usually on *Amphibolis*, branches less than 1 mm in diameter below, mostly 200–300 μm in diameter above 2
    2. Genicula with several to many clustered, spreading, branches, intergenicula of varying length and width ..... 2. *M. stelliferum*
    2. Genicula with 2–3 (-4) fastigiate branches, intergenicula of uniform length, often synchronous and even in appearance ..... 3. *M. chara*

1. **Metagoniolithon radiatum** (Lamarck)Ducker 1979: 85, figs 4–8. Huisman & Walker 1990: 413. Johansen 1981: 75, fig. 16B.
Corallina radiata Lamarck 1815: 240. Areschoug 1852: 541.
Amphiroa radiata (Lamarck)Blainville 1834: 552.
Amphiroa charoides Lamouroux 1816: 301. Areschoug 1852: 539. Decaisne 1842b: 124. De Toni 1905: 1810. Harvey 1849a: 96, pl. 39 lower right; 1855a: 547; 1859b: 309; 1863, synop.: xxx. Kützing 1849: 702. Lucas 1929a: 27. Lucas & Perrin 1947: 394. Sonder 1848: 187; 1853: 687; 1881: 20. Tisdall 1898: 507. Wilson 1892: 177.
Metagoniolithon charoides (Lamouroux)Weber-van Bosse 1904: 102, pl. 15 fig. 11. Cabioch 1972: 233, fig. 34. De Toni 1905: 1861. De Toni & Forti 1923: 61. Ganesan 1971: 248. Guiler 1952: 86. King *et al.* 1971: 121. Lucas 1929b: 53. Lucas & Perrin 1947: 394. Manza 1940: 310, pl. 19. May 1965: 356. Womersley 1950: 167; 1953: 38. Yendo 1905: 12.
Amphiroa stellata Kützing 1849: 702; 1858: 25, pl. 52 fig. II.

PLATE 4 fig. 3; FIGS 143, 144A–C

Thallus (Fig. 143A, B) medium red-brown, 5–15 cm high, densely tufted with few to many erect axes from a crustose holdfast, much branched from the genicula, with few to numerous clustered branches of varying ages and lengths, intergenicula 1–2 (-3) cm long below and 1–2 (-3) mm in diameter, decreasing to 3–10 (-15) mm long, and 400–800 μm in diameter above; branch apices covered by a mucilaginous cap (Fig. 143C, D) 35–250 μm thick. Holdfast 2–5 mm across with several to many erect axes; epilithic. *Structure.* Intergenicula of numerous tiers (Fig. 143D) 30–50 μm long, cells 10–15 μm in diameter with numerous lateral cell-fusions (Fig. 143F). Genicular filaments untiered (Fig. 143E). Apical cells separated, without epithallial cells. Cortex present in both intergenicula and genicula, of short splaying filaments 7–11 μm in diameter, with short epithallial cells and often bands of hairs. Rhodoplasts discoid to laminate.

Reproduction. Conceptacles uniporate, borne on the surface of the intergenicula. Gametangial thalli dioecious. Female conceptacles 700–800 μm in external diameter; carposporophyte with a broad, thin, fusion cell bearing marginal short filaments with large, terminal, ovoid, carposporangia 100–120 μm in diameter. Male conceptacles (Fig. 144A, B) 600–800 μm in diameter, with spermatangia cut off from initials on the chamber floor.

Tetrasporangial conceptacles (Fig. 144C) usually numerous, 660–800 μm in external diameter, with 9–14 tetrasporangia peripheral in chambers, each tetrasporangium 110–200 μm long and 80–130 μm in diameter, zonately divided.

Type from Nouvelle-Hollande, *Péron & Lesueur*; holotype in PC.

Distribution: Port Denison, W. Aust., to Walkerville, Vic., and around Tasmania.

Selected specimens: Port Denison, W. Aust., outer reef pools (*Gordon*, 8.xi.1968; AD, A33150). Two People Bay, W. Aust., 15 m deep (*Huisman*, 3.iv.1993; AD, A63238). Near Smooth Pool, W of Streaky Bay, S. Aust., upper sublittoral (*Johansen* 81-10-16C, 26.x.1981; AD, A52759). St Francis I., Isles of St Francis, S. Aust., 10–13 m deep (*Shepherd*, 6.i.1971; AD, A37979). "The Hotspot", W of Flinders I., S. Aust., 32 m deep (*Branden*, 21.vi.1988; AD, A59312). SE of Wanna, S. Aust., upper sublittoral (*Johansen* 81-11-1a, 2.xi.1981; AD, A52773). Aldinga, S. Aust., upper sublittoral pools (*Shepley*, 7.iii.1954; AD, A20210). Fishery Beach, Cape Jervis, S. Aust., 4–6 m deep (*Gowlett-Holmes*,

24.ii.1966; AD, A64606). Middle River, Kangaroo I., S. Aust., drift (*Womersley*, 8.i.1946; AD, A3381). Pennington Bay, Kangaroo I., S. Aust., sublittoral fringe (*Womersley*, 5.i.1947; AD, A4377). Cape Willoughby, Kangaroo I., S. Aust., 1 m deep (*Womersley*, 12.i.1947; AD, A4226). Robe, S. Aust., drift (*Womersley*, 29.viii.1949; AD, A10933). Nora Creina, S. Aust., upper sublittoral (*Johansen* 81-9-33, 5.ix.1981; AD, A52583). Carpenter Rocks, S. Aust., upper sublittoral (*Womersley*, 5.ii.1970; AD, A35182 —"Marine Algae of southern Australia" No. 80). 1.3 km off Middle Point, Cape Northumberland, S. Aust., 15 m deep (*Shepherd*, 13.ii.1976; AD, A47006). Lawrence Rocks, Portland, Vic., 22 m deep (*Watson*, 20.xii.1982; AD, A55360). Point Lonsdale, Vic., upper sublittoral (*Christensen & Johansen* 81-8-17, 31.viii.1981; AD, A52595). Walkerville, Vic., drift (*Sinkora* A1852, 6.xii.1973; AD, A53541). Granville Harbour, Tas., 1–4 m deep (*Blackman*, 27.i.1979; AD, A58552). Guyton Point, Robbins I., Tas., upper sublittoral (*Wollaston & Mitchell*, 23.ii.1964; AD, A27620). Currie R. mouth, Tas., upper sublittoral (*Womersley*, 28.i.1949; AD, A10306). Lady Bay, Southport, Tas., 2–3 m deep (*Brown & Kenchington*, 14.x.1986; AD, A57656).

M. radiatum is common along rough-water coasts of southern Australia, but less so on coasts of moderate water movement. It occurs from low tide level to 32 m deep, with deeper water plants and those from SE southern Australia often more robust.

2. **Metagoniolithon stelliferum** (Lamarck)Weber-van Bosse 1904: 103, pl. 15 figs 9, 13. Ducker 1979: 83, figs 1–3. Huisman & Walker 1990: 413. Johansen 1981: 74, fig. 16D.
Corallina stellifera Lamarck 1815: 239.
Amphiroa stellifera (Lamarck)Blainville 1834: 552.
Amphiroa stellif(g)era (Lamarck)Decaisne 1842b: 124. J. Agardh 1885: 14. Areschoug 1852: 540. De Toni 1905: 1809. Endlicher 1843: 49. Harvey 1849a: 96; 1855a: 547; 1859b: 310; 1862: pl. 230. Kützing 1849: 701. Lucas 1929b: 53. Lucas & Perrin 1947: 394, fig. 199. Sonder 1853: 687; 1881: 20. Tisdall 1898: 507. Wilson 1892: 177.
Amphiroa stelligera var. *interrupta* Kützing 1858: 26, pl. 52h.
Amphiroa stelligera var. *densa* Kützing 1858: 26, pl. 53a, e–g.
Amphiroa stelligera var. *laxa* Kützing 1858: 26, pl. 53b.
Amphiroa stelligera var. *nuda* Kützing 1858: 26, pl. 53c, d.
Metagoniolithon stelligerum (Lamarck)Weber-van Bosse 1904: 103, pl. 15 figs 9, 13. De Toni 1905: 1861. De Toni & Forti 1923: 61. Ganesan 1971: 248, figs 1–12. Guiler 1952: 87. Johansen 1969, pl. 15. King *et al.* 1971: 121. Lucas 1915: 57. Lucas & Perrin 1947: 394, fig. 199. Manza 1940: 311, pl. 20. May 1965: 356. Womersley 1950: 167; 1953: 38; 1966: 146.
?*Corallina interrupta* Lamarck 1815: 239.
Amphiroa interrupta (Lamarck)Lamouroux 1816: 301, pl. 11 fig. 5. Areschoug 1852: 540. Decaisne 1842b: 124. Endlicher 1843: 49. Harvey 1849a: 96. Kützing 1849: 701.
Amphiroa jubata Lamouroux 1816: 301, pl. 11 fig. 6. Areschoug 1852: 540. Decaisne 1842b: 124. Endlicher 1843: 49. Harvey 1849a: 96. Kützing 1849: 701.
Amphiroa verrucosa Lamouroux 1816: 300, pl. 11 fig. 4. Blainville 1834: 552. Decaisne 1842b: 124. Endlicher 1843: 49. Harvey 1849a: 96. Kützing 1849: 701; 1858: 20, pl. 42 fig. III (?).
Amphiroa elegans Sonder 1845: 55; 1848: 187; 1881: 20. Kützing 1849: 702.

FIG. 144D, E

Thallus (Fig. 144D) medium red-brown but often bleached, 5–20 (-30) cm high, with one to a few axes from a crustose holdfast, much branched from the genicula with clustered branches of varying lengths, ultimate branchlets of 1–2 (-3) intergenicula, intergenicula 3–15 (-20) mm long below and 0.5–1 mm in diameter, decreasing to (1-) 2–4 mm long and 200–300 (-400) µm in diameter above; apices of branches with a mucilaginous cap (Fig. 144E) 25–30 µm thick. Holdfasts 1–3 mm across; epiphytic on *Amphibolis* directly or more often on other epiphytic crustose coralline algae, or on larger algae. *Structure*. Intergenicula of numerous medullary tiers 25–45 µm long, cells 6–14 µm in diameter with numerous lateral cell-fusions. Genicula relatively long, of untiered filaments. Apical cells separated, without epithallial cells. Cortex present on both intergenicula and genicula, below extending

over the genicula as calcified collars, of short splaying filaments 7–10 μm in diameter, with short epithallial cells and often scattered hairs. Rhodoplasts discoid to elongate.

Reproduction. Conceptacles uniporate, borne on the surface of the intergenicula. Gametangial thalli dioecious. Female conceptacles 300–350 μm in external diameter, bearing 2-celled carpogonial filaments on the chamber floor; carposporophyte with a broad, thin, fusion cell with short marginal gonimoblast filaments developing ovoid, terminal carposporangia 20–30 μm in diameter. Male conceptacles 300–400 μm in external diameter, with spermatangia cut off from initials only on the chamber floor, ovoid, 1.5–3 μm in diameter.

Tetrasporangial conceptacles prominent, conical, 300–420 μm in diameter, with 2–6 tetrasporangia at the periphery of the chamber, each 75–120 μm long and 30–65 μm in diameter, zonately divided.

Type from Nouvelle-Hollande (*Péron & Lesueur*); holotype in PC.

Distribution: Yanchep, W. Aust., to Refuge Cove, E of Wilsons Prom., Vic., and N Tasmania. (see Ducker 1979, p. 84).

Selected specimens (on *Amphibolis* unless stated): Green I., Rottnest I., W. Aust., 1–1.5 m deep (*Clarke & Engler*, 6.ix.1979; AD, A51066). Point Valliant, Two People Bay, W. Aust., 1–4 m deep (*Clarke & Engler*, 30.viii.1979; AD, A50967). Smooth I., Isles of St Francis, S. Aust., 22 m deep (*Shepherd*, 29.iii.1980; AD, A51937). Waterloo Bay (Elliston), S. Aust., 5–8 m deep (*Shepherd & Turner*, 31.x.1981; AD, A52775). Memory Cove, S. Aust., on *Scaberia*, upper sublittoral (*Womersley*, 25.ii.1959; AD, A22287). Pondalowie Bay, S. Aust., upper sublittoral (*Gordon-Mills*, 23.v.1981; AD, A52193). Aldinga, S. Aust., drift (*Womersley*, 13.i.1973; AD, A42986 —"Marine Algae of southern Australia" No. 201). Between Knob Point & Cape Cassini, Kangaroo I., S. Aust., 8 m deep (AIMS–NCI, Q66C 2176-H, 29.i.1989; AD, A59754). Carpenter Rocks, S. Aust., on *Heterozostera* in shallow pools (*Womersley*, 5.iii.1995; AD, A64300 —"Marine Algae of southern Australia" No. 201a). Queenscliff, Vic., drift (*Johansen* 81-8-2, 30.viii.1981; AD, A52576). Kitty Miller Bay, Phillip I., Vic., 1–2 m deep (*Sorokin*, 12.ii.1990; AD, A60141). Walkerville, Vic., drift (*Sinkora* A1795, 3.xii.1973; AD, A53496). Rocky Cape, NW Tas., lower eulittoral pools (*Womersley*, 17.x.1982; AD, A55553). Currie R. mouth, Tas., upper sublittoral (*Womersley*, 28.i.1949; AD, A10307).

M. stelliferum is common near low tide on coasts of moderate water movement, usually indirectly epiphytic on *Amphibolis* and occasionally on various larger algae or *Heterozostera*.

3. **Metagoniolithon chara** (Lamarck)Ducker 1979: 88, figs 9–14, 15A. Huisman & Walker 1990: 412. Millar & Kraft 1993: 14.
Corallina chara Lamarck 1815: 240. Areschoug 1852: 541. De Toni 1905: 1809.
Amphiroa chara (Lamarck)Decaisne 1842a: 359, pl. 17 fig. 9.
?*Corallina gallioides* Lamarck 1815: 239. Areschoug 1852: 539.
?*Amphiroa gallioides* (Lamarck)Blainville 1834: 552.
Amphiroa charoides sensu Kützing 1858: 25, pl. 52 fig. I.
Amphiroa intermedia Harvey 1855a: 547; 1863, synop.: xxx. De Toni 1905: 1820. Sonder 1881: 20.
Amphiroa granifera Harvey 1855a: 547; 1863, synop. xxx. De Toni 1905: 1819. Lucas & Perrin 1947: 394. Sonder 1881: 20. Tisdall 1898: 507.
Metagoniolithon graniferum (Harvey)Weber-van Bosse 1904: 103, pl. 15 figs 10, 12. De Toni 1905: 1861. Manza 1940: 311. May 1965: 356. Segawa 1949: 52.
Amphiroa similis Sonder 1881: 20.
Metagoniolithon gracile (Harvey)Yendo *sensu* Womersley 1950: 167.

FIG. 145

Thallus (Fig. 145A, B) medium red-brown to grey-red, 2–5 cm high, loosely to densely tufted, much branched with mainly synchronous production of even-length intergenicula and resultant even-topped outline, branching di- or trichotomous, occasionally more (-5). Intergenicula terete to slightly compressed, 2–3 (-4) mm long and 400–600 μm in diameter, decreasing to 1–2 mm long and 200–300 μm in diameter above, in larger plants to 7 mm long below and 700–1000 μm in diameter; genicula (Fig. 145C) untiered; apices with a mucilaginous cap 25–75 μm thick. Holdfasts 0.5–2 mm across, each with one to several

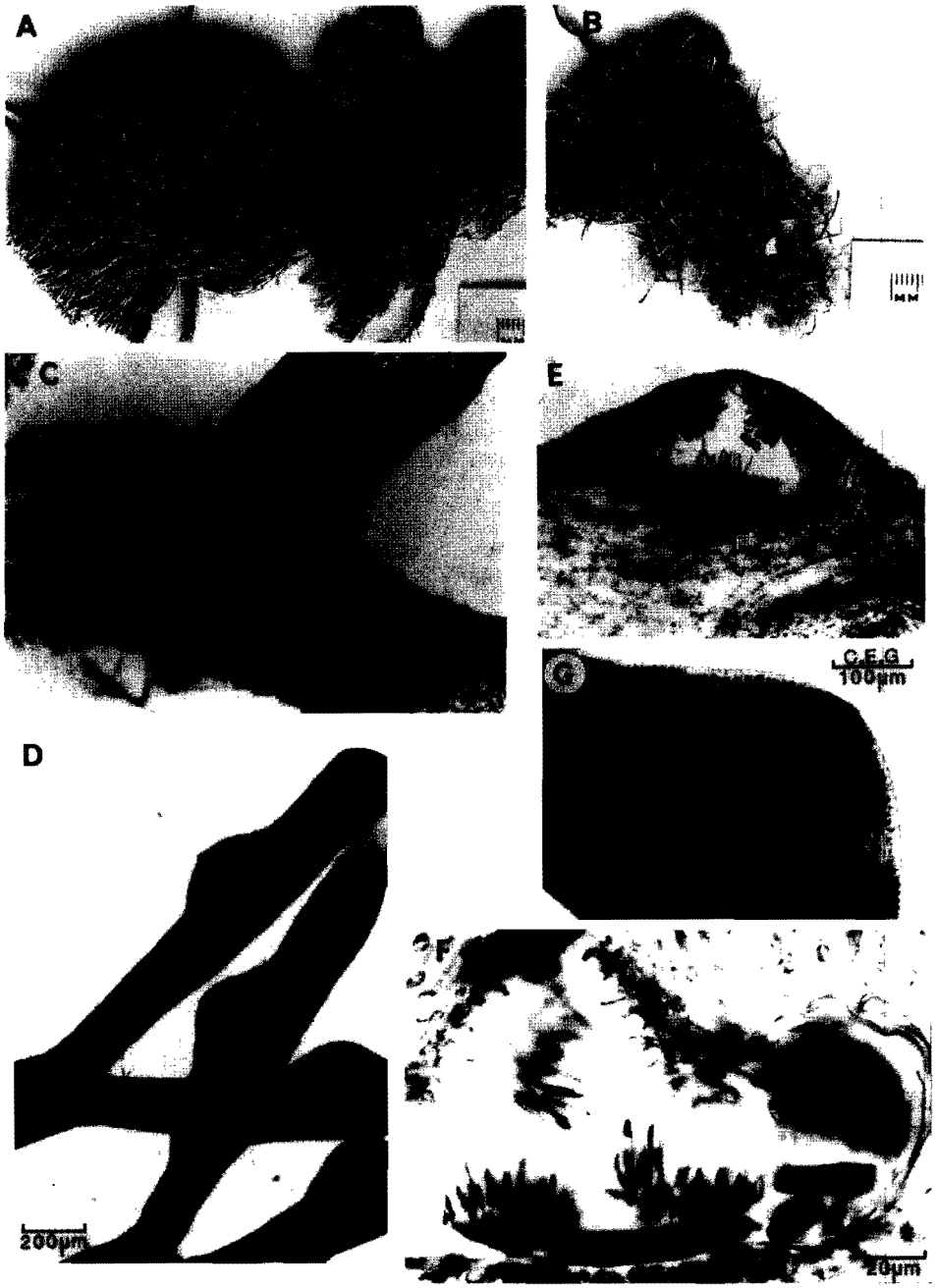


Fig. 145. *Metagoniolithon chara* (**A,** AD, A51095; **B,** AD, A6956; **C, G,** AD, A35994; **D–F,** AD, A34218). **A.** Habit, well developed plants. **B.** Habit. **C.** Longitudinal section of geniculum and intergenicula. **D.** Branches with carposporangial conceptacles. **E.** Female conceptacle (without carposporangia). **F.** Carposporangial conceptacle with fusion cell and carposporangial filament. **G.** Tetrasporangial conceptacle.

fronds; epiphytic on stems of *Amphibolis* or some larger algae. *Structure*. Intergenicula of numerous arched medullary tiers 45–70 µm long, cells 9–15 µm in diameter with frequent lateral cell-fusions. Genicula 180–400 µm long. Apical cells slightly separate, without epithallial cells. Cortex present in both intergenicula and genicula, of short splaying to anticlinal filaments (5-) 7–11 µm in diameter, with short epithallial cells and scattered hairs. Rhodoplasts discoid.

Reproduction. Conceptacles uniporate, borne on the surface of the intergenicula. Gametangial thalli dioecious. Carposporangial conceptacles (Fig. 145D) 400–600 (-800) µm in external diameter, each with a thin fusion cell (Fig. 145E, F) bearing marginally up to 15 carposporangia terminating short filaments (Fig. 145F), more or less ovoid and 50–90 µm in diameter. Male conceptacles low, 600–800 µm in external diameter, with spermatangia on initials over the chamber floor, ovoid, 1–2 µm in diameter.

Tetrasporangial conceptacles (Fig. 145G) hemispherical, 600–750 µm in external diameter, each with a ring of 8–11 ovoid tetrasporangia, each 120–200 µm long and 45–110 µm in diameter, zonately divided.

Type from Nouvelle-Hollande (*Péron & Lesueur*), probably from Rottnest I. (or Shark Bay), W. Aust.; holotype in PC.

Distribution: Port Denison, W. Aust., to Walkerville, Vic., and on King I., Bass Strait, mainly on *Amphibolis*. N.S.W. (Millar & Kraft 1993, p. 14).

Selected specimens: (see also Ducker 1979, p. 94). All on *Amphibolis*. Flat Rocks, S of Geraldton, W. Aust., drift (*Mitchell*, 17.ix.1966; AD, A31084). Jacques Point, Kalbarri, W. Aust., uppermost sublittoral (*Womersley*, 15.ix.1979; AD, A51284 —"Marine Algae of southern Australia" No. 200). Lady Edeline Beach, Rottnest I., W. Aust., (*Ducker*, 9.viii.1973; MELU, 21850; AD, A49364). Strickland Bay, Rottnest I., W. Aust., drift (*Womersley*, 5.ix.1979; AD, A51095). Sarge Bay, Cape Leeuwin, W. Aust., drift (*Parsons*, 16.xi.1968; AD, A34218). Eucla, W. Aust., drift (*Womersley*, 2.ii.1954; AD, A19354). W of Tiparra reef, S. Aust., 12 m deep (*Shepherd*, 27.vii.1970; AD, A35994). Glenelg, S. Aust., 13 m deep (*Glover*, 18.iv.1961; AD, A24842). Kingscote, Kangaroo I., S. Aust., drift (*Womersley*, 12.i.1948; AD, A6956). Flinders, Western Port, Vic., drift (*Sinkora* A842, 16.viii.1970; AD, A62588). San Remo, Vic., drift (*Ducker*, 1.v.1977; MELU, 22581; AD, A49363).

Ducker (1979, p. 96) described var. *dichotomum* from Rottnest I., W. Aust., based on the dichotomous (rather than trichotomous) branching. An isotype specimen in AD, A49364 of MELU, 21850 has mostly dichotomous branching but several trichotomies and even a few genicula with 4 branches. Var. *dichotomum* is considered to be not worth recognising.

Lewis (1984, p. 17), following earlier authors, recorded *M. chara* from Queensland localities, but these records probably apply to other species.

Ducker (1979, p. 89) included *Amphiroa verrucosa* Lamouroux as a synonym of *M. chara*. However, her photograph of the type (Fig. 9C) shows a fragment more like *M. stelliferum* and *A. verrucosa* is here referred with doubt to that species rather than *M. chara*. Other authors (e.g. Areschoug 1852, p. 539) have referred *A. verrucosa* to *M. charoides* (= *M. radiatum*).

ORDER **BONNEMAISONIALES*** Feldmann & Feldmann 1942: 163

Thallus (gametophytes and some tetrasporophytes) erect, much branched radially or complanately, branches terete or compressed. *Structure* uniaxial, axial filament usually conspicuous throughout, subapical cells producing periaxial filaments radially and spirally arranged, or opposite, or in alternate pairs at right angles; gland (vesicular) cells present or absent; secondary pit-connections absent; pit-plugs without cap layers.

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* Modifications to the key to the orders (Part IIIA, p. 20) are necessary. The couplet for 9. Bonnemaisoniales should read: "Thallus uniaxial, few to several cells thick or broad, with the axial cells cutting off 2 or 4 periaxial cells, with three pericentral cells in the ramuli; gland cells usually present; pit-plugs with no cap layers; carposporophyte with a well-developed cellular pericarp (Bonnemaisoniaceae) or diffuse in the cortex (Naccariaceae)."

Tetrasporophytes in some taxa isomorphic, in most taxa heteromorphic and small, filamentous, tufted or prostrate.

Life history triphasic, with isomorphic or heteromorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli monoecious or dioecious. Carpogonial branches 3- or 4-celled, borne on inner cortical cells, cells of carpogonial branches with or without accessory cells. Fertilized carpogonium developing directly or after fusion with the hypogynous cell, fusion cell branched or lobed, producing branched gonimoblast filaments with terminal carposporangia, either within a cellular pericarp as a distinct cystocarp or diffuse within the cortical filaments and without a pericarp. Spermatangia cut off from cortical cells or on ovoid pedicellate structures.

Tetrasporangia (where known) lateral on filaments of tufted or prostrate tetrasporophytes, or in nemathecia on isomorphic thalli, cruciately divided.

The order Bonnemaisoniales was separated by Feldmann & Feldmann (1942, p. 163) from the Nemaliales on account of their then known heteromorphic alternation of generations. However, the Helminthocladiaceae (Nemaliales) are now known to be heteromorphic, and some Bonnemaisoniales are isomorphic. The Bonnemaisoniales are now recognised at ordinal level on the basis of their uniaxial structure, with subapical cells producing periaxial filaments, direct development of the gonimoblast from the fertilized carpogonium or hypogynous cell, and terminal carposporangia. The ultrastructure of the pit-plugs which lack cap layers (Pueschel 1989, p. 627) and the plastids (Chihara & Yoshizaki 1972, p. 248) are also important.

KEY TO FAMILIES OF BONNEMAISONIALES

1. Carposporophyte enclosed by a cellular pericarp forming a defined cystocarp ..... BONNEMAISONIACEAE
1. Carposporophyte diffuse, with the gonimoblast filaments ramifying between the cortical filaments and without a pericarp ..... NACCARIACEAE

FAMILY BONNEMAISONIACEAE Schmitz *in* Engler 1892: 20

Thallus (gametophyte, and tetrasporophyte in some taxa) erect, much branched radially or complanately and distichously, branches opposite or alternate, terete or compressed; attachment by a discoid or fibrous holdfast or by retrorse spinous branchlets if epiphytic. Tetrasporophyte isomorphic, or small and of tufted, branched, filaments, or prostrate, minute, of branched filaments. *Structure* uniaxial, axial filament conspicuous throughout, with the subapical cells each cutting off either two opposite periaxial cells which may diverge on a ¼ spiral, or two pairs at right angles with the first formed of each pair forming a longer lateral periaxial filament which gives rise to the ramuli, and the shorter transverse filaments contributing to the cortex; lateral filaments remaining separate or coherent laterally in compressed thalli. Ramuli with three pericentral cells, some half the length of the axial cells, and in some taxa many cells of the ramuli and branch cortex cut off small globose gland (vesicular) cells, usually on their inner sides.

Life history triphasic, with isomorphic or heteromorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli monoecious or dioecious. Carpogonial branches 3-celled, with (in *Asparagopsis*) or without lateral nutritive cells, borne on a supporting cell in the inner cortex or on an indeterminate branchlet. Fertilized carpogonium developing directly or after fusing with the hypogynous cell, forming a fusion cell with branched gonimoblast filaments producing swollen terminal carposporangia. Pericarp distinct, of small cells, either globular and stalked or sunken within the cortex of a branch. Spermatangia forming a surface layer on the ramuli or on distinct, ovoid, pedicellate structures.

Tetrasporangia in surface nemathecia, elongate-ovoid, cruciately divided (in *Delisea* spp. and *Leptophyllis*), or borne laterally on the filaments of prostrate or tufted tetrasporophytes (e.g. Falkenbergia stage of *Asparagopsis*).

A family of 5 genera, all present on southern Australian coasts; plus *Pleuroblepharidella* Wynne (1980) provisionally referred to the family.

KEY TO GENERA OF BONNEMAISONIACEAE

1. Branch axes terete or slightly compressed, radially or distichously branched; lateral periaxial filaments separate from each other 2
1. Branch axes compressed to flat, 0.5–4 mm broad, marginally branched; lateral periaxial filaments adherent to form the flat branch 4

2. Axes slightly compressed, lateral periaxial filaments forming marginal, distichous (at least at first) often spinous ramuli; cystocarps sessile on the axes between the ramuli; nutritive filaments present; where known, gametophytes and tetrasporophytes isomorphic ..... DELISEA
2. Axes terete, lateral periaxial filaments discrete, slender, not spinous; cystocarps pedicellate; nutritive filaments absent; gametophytes and tetrasporophytes heteromorphic (except *Leptophyllis*) 3

3. Branching radial, with opposite periaxial filaments spirally arranged on a ¼ divergence; cystocarps on a 9–11-celled stalk; tetrasporophyte tufted, of discrete, erect branches ..... ASPARAGOPSIS
3. Branching bilateral and distichous; cystocarps on a 5–8-celled stalk; tetrasporophyte a prostrate crust ..... BONNEMAISONIA

4. Thallus delicate, branches 4–5 cells thick, axial filament without a sheath of small cells; axial cells with two lateral periaxial cells only; gametophytes and tetrasporophytes isomorphic ..... LEPTOPHYLLIS
4. Thallus relatively robust, branches 10–15 cells thick in mid thallus, axial filament with a sheath of small cells; axial cells each with two pairs of lateral and transverse periaxial cells; only sexual thalli known ..... PTILONIA

Genus **ASPARAGOPSIS** Montagne 1841: xv

Thallus (gametophyte) erect, much branched with long, terete axes bearing dense, plumose laterals on all sides, the laterals densely covered with indeterminate branchlets and unbranched determinate ramuli; attachment by retrorsely spinous branches when epiphytic or by stolons when epilithic. *Structure* uniaxial, with a small but distinct apical cell and the subapical cells producing two opposite periaxial cells with a divergence of about ¼ on the axial cells, the larger of the two often forming a lateral indeterminate branch and the smaller often forming an unbranched determinate ramulus; the periaxial cells, whether forming a filament or not, cut off primary cortical cells laterally to form a continuous cortex which becomes several cells thick in older axes, with a space between the axial filament and the inner cortex in which sparse, branched, rhizoidal filaments develop upwards and downwards from periaxial cells on the swollen anterior ends of the axial cells. Determinate ramuli developing 5 cells around each axial cell, one the full length of the axial cell and two pairs of half-length cells (3 in sectional view of ramulus), with many of these cells cutting off on their inner side, by a strongly concave wall, a small gland cell.

Tetrasporophyte ("Falkenbergia" stage) tufted, 0.5–2 cm high, much branched, epilithic or epiphytic. *Structure* filamentous, with an axial cell and 3 pericentral cells of similar length, some cells also cutting off on their inner side a small gland cell.

Life history triphasic, heteromorphic with a large gametophyte and small, filamentous tetrasporophyte.

Reproduction. Gametangial thalli monoecious or dioecious. Carpogonial branches 3-celled, with lateral nutritive cells from the lower cells, borne on a supporting cell on 1–3

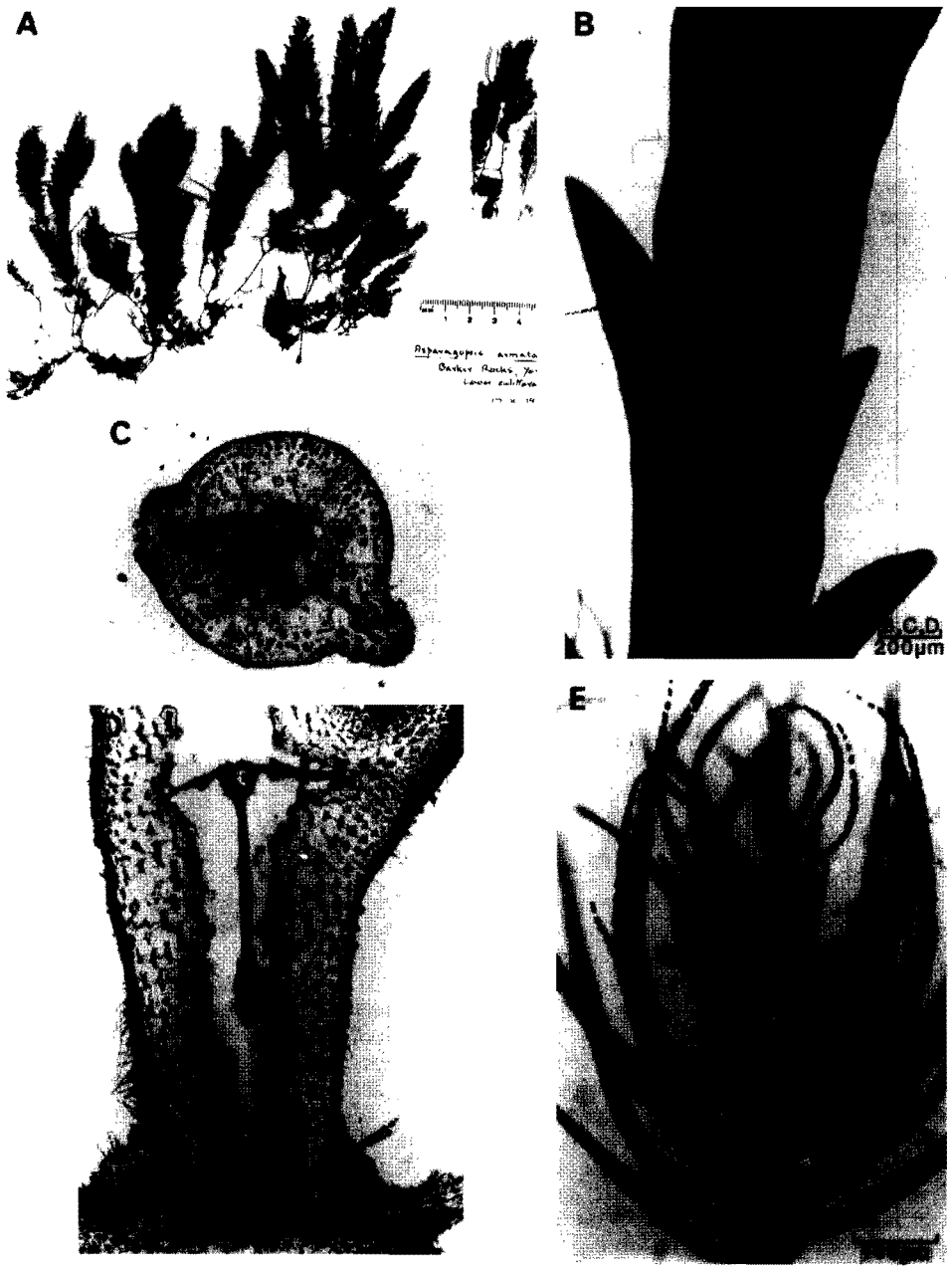


Fig. 146. *Asparagopsis armata* (AD, A59878). **A.** Habit. **B.** Spines on spinous branches. **C.** Transverse section of a main branch showing axial filament in central space. **D.** Longitudinal section of branch with axial filament in the central space. **E.** Branch apex with axial filament, groups of cortical cells from periaxial cells, and lateral ramuli each with five periaxial cells (three in section).

subapical cells of a determinate lateral 9–11 cells long, reportedly with the gonimoblast originating from the hypogynous cell; carposporophyte developing a basal, branched, dendroid, fusion cell with branched gonimoblast filaments producing terminal, clavate, carposporangia. Pericarp developing early (pre-fertilization) and forming prominent, stalked, ostiolate cystocarps. Spermatangia borne on specialised ovoid heads, cut off from outer cells of compact cells surrounding an axial filament.

Tetrasporangia transformed from one of the pericentral cells of the tetrasporophyte, cruciately divided, released through a pore in the outer cell wall.

Type species: *A. delilei* (Montagne)Montagne 1841: xiv. [= *A. taxiformis* (Delile)Trevisan]

The life history and distinctive features of *Asparagopsis* and *Falkenbergia* were elucidated by Feldmann & Feldmann (1942), but it has been doubted whether the two taxa described below really are distinct species (see Dixon & Irvine 1977, p. 155). However, they are readily recognisable underwater at Rottnest I., W. Aust. (G.T. Kraft, pers. comm.).

KEY TO SPECIES OF *ASPARAGOPSIS* (GAMETOPHYTES)

1. Thallus epiphytic, attached by lateral branches with retrorse spines; dioecious or monoecious; spermatangial heads 90–150 µm in diameter, 250–450 µm long ..... 1. *A. armata*
1. Thallus epilithic (or epiphytic), attached by basal stolons, spinous branchlets absent; monoecious; spermatangial heads 180–280 µm in diameter, 350–650 µm long .....2. *A. taxiformis*

1. **Asparagopsis armata** Harvey 1855a: 544; 1859b: 305; 1862: pl. 192. Adams 1972: 70. Adams *et al.* 1974: 213. J. Agardh 1876: 666. Bonin & Hawkes 1987: 579, figs 2–15, 17–30. Chapman 1969: 80, fig. 31, pl. 18. De Toni 1900b: 772; 1924: 367. Dixon 1964: 902. Dixon & Irvine 1977: 153, fig. 57. Feldmann & Feldmann 1942: 82, 102, figs 1–6. Guiler 1952: 84. Huisman & Walker 1990: 398. Levring 1953: 528. Lucas 1929a: 20; 1929b: 50. 1933: 133, pl. x. Lucas & Perrin 1947: 244, fig. 107. May 1965: 376. Millar & Kraft 1993: 33. Reinbold 1897: 55; 1899: 47. Sonder 1881: 30. Svedelius 1933: 7, figs 1–42. Tisdall 1898: 512. Wilson 1892: 169. Womersley 1950: 162.
Asparagopsis delilei sensu Harvey 1849: 88, pl. 35 [NON *A. delilei* Montagne = *A. taxiformis* (Delile)Trevisan 1845: 45].
Polysiphonia rufolanosa Harvey 1855a: 540. J. Agardh 1863: 939. Kützing 1864: 20, pl. 54f, g.
Falkenbergia rufolanosa (Harvey)Schmitz *in* Schmitz & Falkenberg 1897: 479. Adams *et al.* 1974: 213. De Toni 1903: 865. Feldmann & Feldmann 1942: 90, figs 3–6.
Polysiphonia vagabunda Harvey 1859b: 300. J. Agardh 1863: 940. Kützing 1864: 12, pl. 37d, e.
Falkenbergia vagabunda (Harvey)Falkenberg 1901: 690, pl. 21 figs 20–26. De Toni 1903: 865. Feldmann & Feldmann 1942: 90, 91.
Falkenbergia olens Lucas 1919: 175. De Toni 1924: 389. Feldmann & Feldmann 1942: 90, 91.

FIGS 146, 147

Thallus (gametophyte) (Fig. 146A) grey-brown to dark red, 8–25 cm high, with long, plumose, main branches covered with densely and irregularly radially branched laterals mostly 5–10 mm long, with crowded ramuli 1–2 mm long when mature and 50–110 µm in basal diameter, tapering gradually; scattered (sometimes clustered), bare, but retrorsely spinous branches (Fig. 146B) 1–3 cm long, with spirally arranged (divergence ¼) spines 0.25–1 mm long, also occur. Attachment by the spinous branches, which can develop adhesive pads; epiphytic on various algae and seagrasses. *Structure* uniaxial (Fig. 146E), each subapical cell with two opposite periaxial cells diverging on about a ¼ spiral, with the larger forming an indeterminate branch or a determinate ramulus, the smaller opposite one often forming a determinate ramulus. Cortex formed from cells cut off laterally from the



Fig. 147. *Asparagopsis armata* (**A, B,** AD, A59878; **C,** AD, A43326; **D,** AD, A19029). **A.** Main branch with a lateral branch bearing two young cystocarps. **B.** Carposporophyte with basal fusion cell, much branched gonimoblast filaments and terminal carposporangia. **C.** Spermatangial organs on a lateral branch. **D.** *Falkenbergia* stage with tetrasporangia.

periaxial cells, becoming continuous within a few axial cells of the apices and on older branches several cells thick, with a space (Fig. 146C, D) between the axial filament and inner cortical cells within which sparse (in young branches) to denser rhizoidal filaments develop; inner cortical cells ovoid to angular, 35–60 μm in diameter, outer cortical cells angular in surface view, 10–25 μm across; axial filament becoming 40–150 μm in diameter, with swollen ends (Fig. 146D). Ramuli developing 5 periaxial cells around each axial cell (three in sectional view), one full length and two pairs of half length, almost cubical, cells each 25–35 μm across; many cells with small gland cells on their inner sides. Rhodoplasts discoid, numerous, in chains in inner cortical cells.

Tetrasporophytes (Fig. 147D) densely tufted, 0.5–2 cm high, much branched with filaments 40–60 μm in diameter, segments 45–85 μm long (L/D 1–1.5), with 3 pericentral cells around each axial cell, most pericentral cells cutting off inwardly a small gland cell. Attachment by short multicellular haptera; epilithic or epiphytic.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 3-celled, borne on a supporting cell 9–11 axial cells along a lateral branchlet, with the lower cells of the carpogonial branch producing lateral nutritive cells. Carposporophyte (Fig. 147B) with a basal, dendroid, fusion cell and a densely branched tuft of gonimoblast filaments bearing terminal, clavate to elongate-ovoid, carposporangia 15–25 μm in diameter. Cystocarps (Fig. 147A) often paired near the base of lateral branches, globular, stalked by the lateral branchlet, 1–1.5 mm in diameter, pericarp 3–4 cells thick, ostiolate. Spermatangial heads (Fig. 147C) short stalked, elongate-ovoid, 90–150 μm in diameter and 250–450 μm long, with a cortex of large inner cells and small outer cells producing several elongate spermatangia 1–2 μm in diameter.

Tetrasporangia (Fig. 147D) transformed from pericentral cells, forming an irregular series, shortly ovoid and 25–35 μm in diameter, cruciately divided.

Type from Garden I., W. Aust. (*Harvey*); lectotype in Herb. Harvey, TCD (Trav. Set 193).

Distribution: Yanchep, W. Aust., around southern Australia and Tasmania to Port Stephens, N.S.W. (Millar & Kraft 1993, p. 33). Northern Australia ?(Lewis 1984, p. 5).

Western Europe (Mediterranean to Ireland); Chile (Santelices & Abbott 1978, p. 218); New Zealand (Chapman 1969, p. 80).

Selected specimens: Yanchep, W. Aust., drift (*Kraft* 8438 & *Herrington*, 5.ix.1990; MELU). Point Clune, Rottnest I., W. Aust., 10–15 m deep (*C. & M. O'Brien*, 2.xii.1980; MELU, Kraft 7133; AD, A63409). Whitfords Beach, W. Aust., 4 m deep (*Cook*, 20.viii.1979; AD, A50583). Egg I., Isles of St Francis, S. Aust., 32–38 m deep (*Shepherd*, 11.i.1971; AD, A38041). Hopkins I., S. Aust., 33 m deep (*Branden*, 8.i.1989; AD, A60002). Barker Rocks, Yorke Pen., S. Aust., lower eulittoral (*Womersley*, 17.x.1989; AD, A59878 —"Marine Algae of southern Australia" No. 67a). Blanche Harbor, S. Aust., 13 m deep (*Branden*, 10.ix.1987; AD, A59345). Abalone Cove, West I., S. Aust., 2 m deep (*Shepherd*, 17.xii.1972; AD, A42923 —"Marine Algae of southern Australia" No. 67). Vivonne Bay, Kangaroo I., S. Aust., 5–6 m deep (*Mitchell*, 21.viii.1963; AD, A26960). Robe, S. Aust., sublittoral fringe outer reefs (*Womersley*, 27.viii.1949; AD, A11083). Double Corner Beach, Portland, Vic., drift (*Beauglehole* 460, 22.vii.1951; AD, A21731). Point Lonsdale, Vic., drift (*Sinkora* A1018, 14.xi.1970; AD, A54219). Gabo I., Vic., 13 m deep (*Shepherd*, 14.ii.1973; AD, A43326). Bombay Rock, Tamar Est., Tas. (*Perrin*, April 1949; AD, A61891). Great Taylor Bay, Bruny I., Tas., 10 m deep (*Shepherd*, 7.ii.1970; AD, A35294). Newport, N. Sydney, N.S.W. (*Benes*, 12.xi.1950; AD, A17187).

Tetrasporophyte (*Falkenbergia*) phase: Vivonne Bay, Kangaroo I., S. Aust., in shaded high level pool, S side Ellen Point (*Womersley*, 29.viii.1950; AD, A15465). Flat Rock, Bridgewater Bay, Vic., lower eulittoral (*Womersley*, 21.viii.1953; AD, A19029). Guyton Point, Robbins I., Tas., on *Halopteris*, upper sublittoral (*Wollaston & Mitchell*, 23.ii.1964; AD, A27628). Cloudy Bay, Bruny I., Tas., free-floating (*Kraft & Scott*, 20.xii.1993; AD, A63412 — "Marine Algae of southern Australia" No. 372).

Dixon (1964, p. 902) considered the only difference between *A. armata* and *A. taxiformis* is the spinous branches of the former and he questioned their distinctness, as did Dixon & Irvine (1977, p. 153) who recorded only *A. armata* from the British Isles. Differences in habit, whether monoecious or dioecious, and whether epilithic or epiphytic (see key above), are also useful but require further investigation.



Fig. 148. *Asparagopsis taxiformis* (**A, E,** AD, A43572; **B–D,** AD, A19864). **A.** Habit. **B.** Branch apex. **C.** Branch with upper spermatangial organs and two lower cystocarps. **D.** Carposporophyte with basal fusion cell, gonimoblast filaments and clavate carposporangia. **E.** Branch with ramuli and a spermatangial organ.

Guiry & Dawes (1992) have studied temperature and daylength control of tetrasporogenesis in the *Falkenbergia* phase. The Cloudy Bay, Tas., collection was from an extensive free-floating bloom present during several years (C. Sanderson, pers. comm.).

A. armata was first recorded from Europe (Atlantic France) by Sauvageau (1925) and has since spread to other European coasts and the southern and western shores of the British Isles (Dixon & Irvine 1977, p. 153).

Plants from calm water situations have slenderer ramuli than those from rough-water habitats, and the cortex closes between the segments further from the apices.

2. **Asparagopsis taxiformis** (Delile)Trevisan 1845: 45. Børgesen 1919: 352, figs 347–351. Bonin & Hawkes 1987: 586, fig. 16. Chapman 1969: 81, pl. 19. Chihara 1961: 139, figs 11, 13, 14. Dixon 1964: 902; 1965: 67. Huisman & Walker 1990: 398. Levring 1953: 528. Lewis 1984: 5. May 1965: 376. Millar & Kraft 1993: 34.
Fucus taxiformis Delile 1813: 295, pl. 57 fig. 2.
Lictoria taxiformis (Delile)J. Agardh 1841: 23. Hooker & Harvey 1847: 402.
Asparagopsis delilei Montagne 1841: xiv. J. Agardh 1852: 776; 1876: 666. De Toni 1900b: 771. Harvey 1849a: 88, pl. 35. Kützing 1849: 802; 1864: 32, pl. 92. Wilson 1892: 169.
Asparagopsis sanfordiana Harvey 1855a: 544; 1858, pl. 6. J. Agardh 1876: 666. De Toni 1900b: 771; 1924: 367. Lucas & Perrin 1947: 245. Sonder 1881: 30.

PLATE 2 fig. 4; FIG. 148

Thallus (gametophyte) (Fig. 148A) mid to dark brown-red, fading to grey-red, 10–30 cm high, with long, plumose, main branches covered with densely and irregularly radially branched laterals (Fig. 148B) mostly 1–2 cm long with crowded determinate ramuli 0.5–1 (-1.5) mm long when mature and 35–65 (-90) µm in basal diameter, tapering gradually; spinous branches absent. Attachment by basal stolons and rhizoids; usually epilithic. *Structure* uniaxial, with development of indeterminate branches and determinate ramuli as in *A. armata*. Cortex and axial filament also similar but slightly slenderer; axial filament 20–30 µm in diameter with swollen ends 70–90 µm in diameter, inner cortical cells ovoid and 20–30 µm in diameter, outer cortical cells angular and 9–14 µm across. Structure of ramuli as in *A. armata*, mature half-length cells 20–30 µm across. Rhodoplasts discoid, in chains in inner cells.

Reproduction. Gametangial thalli monoecious, with spermatangial heads nearer the branch apices than the cystocarps. Carposporophyte (Fig. 148D) with a basal fusion cell and much branched gonimoblast filaments bearing terminal clavate carposporangia. Cystocarps (Fig. 148C) borne on stalks 9–11 axial cells long, globular, 1–1.5 mm in diameter, pericarp 3–4 cells thick, ostiolate. Spermatangial heads (Fig. 148E) broadly clavate, 180–280 µm in diameter and 350–650 µm long, with spermatangia cut off as a dense surface layer.

Tetrasporophyte apparently indistinguishable from that of *A. armata*.

Type from Egypt (Alexandria); holotype(?) in Herb. Lamouroux, CN.

Distribution: Tropical/subtropical oceans generally.

Northern Australia to Rottnest I., W. Aust., and southern Qld; Lord Howe I. The Gulf Region of S. Aust.

Selected specimens: South Passage, Shark Bay, W. Aust., 5 m deep (*Cambridge*, 16.viii.1979; AD, A51767). King Head, Rottnest I., W. Aust., 4–6 m deep (*Clarke & Engler*, 6.ix.1979; AD, A50796). Kangaroo Reef, N end Boston I., Port Lincoln, S. Aust., 5–6 m deep (*Womersley*, 28.ii.1959; AD, A22558). Tiparra Reef, Spencer Gulf, S. Aust., 5 m deep (*Shepherd*, 25.v.1973; AD, A43572). Seacliff, S. Aust., 12 m deep (*Rowland*, 2.ii.1986; AD, A57028). Port Noarlunga, S. Aust., 19 m deep (*Branden*, 26.iii.1987; AD, A57445). Port Willunga, S. Aust., upper sublittoral pools (*Womersley*, 23.ii.1955; AD, A19864). Elliot Heads, Qld, drift (*McKeon*, 12.ix.1948; AD, A9573).

A. taxiformis is a tropical/subtropical species, occurring on the western and eastern coasts of Australia and also in the Gulf Region of South Australia. Thalli are epilithic and the branches and ramuli slightly slenderer than in *A. armata*, and are also monoecious. Further studies are needed on the validity of these distinctions.

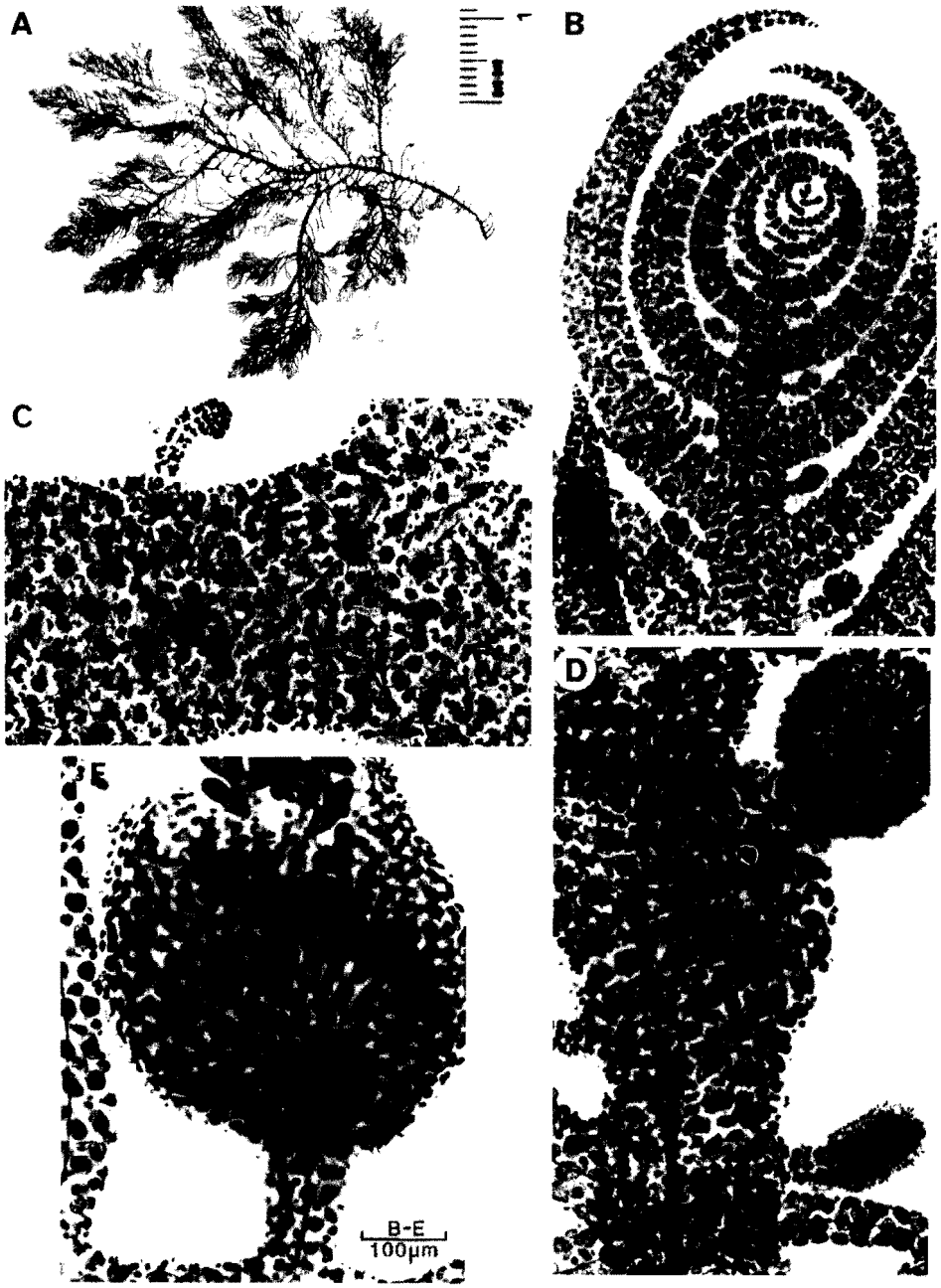


Fig. 149. *Bonnemaisonia australis* (**A**, AD, A8744; **B**, AD, A29661; **C**, AD, A42659; **D**, AD, A59340; **E**, AD, A59351). **A.** Habit. **B.** Apex of branch, with developing cystocarps. **C.** Branch showing surface cell pattern. **D.** Branch with cystocarp (above) and young spermatangial organ (lower right). **E.** Cystocarp.

Genus **BONNEMAISONIA** C. Agardh 1822: 196

Thallus (gametophyte) erect, much-branched with long, terete to slightly compressed branches bearing opposite pairs of distichous (or spiral) branchlets, usually with a longer determinate branchlet opposite a short branchlet which often produces the sexual organs or develops further as a branch; attachment rhizoidal, discoid or by hamate branchlets, epiphytic or epilithic. *Structure* uniaxial, with small but prominent apical cells, the apical filament conspicuous throughout the thallus, with subapical cells producing opposite and distichous periaxial cells which develop the branchlets; cortication of the branches by the first periaxial cells each cutting off about 4 cortical cells (which may subdivide) which become relatively large, with two or more corresponding lengthwise to each axial cell and 6–8 around the branch, then cutting off small, rounded, outer cortical cells which often form rosettes, some developing darkly staining contents (gland or iodine cells); inner cortex separated by a "space" from the axial filament. Branchlets with axial cells cutting off 3 periaxial cells which develop a cortex as in the branches, with or without spines.

Tetrasporophytes filamentous, branched, tufted or prostrate.

Life history triphasic, heteromorphic.

Reproduction. Gametangial thalli monoecious or dioecious. Carpogonial branches 3-celled, borne on the subapical cell of short branchlets, with the hypogynous cell forming a tuft of nutritive filaments; following fertilization the carpogonium produces branched gonimoblast filaments with terminal carposporangia, a fusion cell develops by union of the cells of the carpogonial branch and adjacent cells, and the supporting cell and adjacent periaxial cells produce erect filaments which form the pericarp. Cystocarps pedicellate (on 5–8 axial cells), urceolate, ostiolate. Spermatangial organs shortly pedicellate, ovoid to elongate with a central row of 4–8 axial cells, each cutting off radially several periaxial filaments which form an outer layer of spermatangial initials and spermatangia.

Tetrasporophytes [known in, e.g. *B. asparagoides* (*Hymenoclonium*) and *B. hamifera* (*Trailliella*)] uniseriate, branched, tufted or prostrate, bearing lateral tetrasporangia, tetrahedrally or irregularly divided.

Lectotype species: *B. asparagoides* (Woodward)C. Agardh 1822: 197.

A genus of about seven species, with two on southern Australian coasts. The structure and development of the female and male reproductive organs appears uniform in all species, with some differences in the heteromorphic tetrasporophytes (see Feldmann & Feldmann 1942, and Shevlin & Polanshek 1978) which are unknown for the southern Australian species. The type species has been studied in detail by Kylin (1916) and Svedelius (1933, p. 39, figs 43–48).

Bonnemaisonia is most closely related to *Asparagopsis*, differing in having distichous compared to radial branching, and in the pedicel of the cystocarp being 5–8 axial cells long compared to 9–11 cells (Hudson & Wynne 1969).

KEY TO SPECIES OF *BONNEMAISONIA*

1. Spines absent; primary cortical cells not in tiers, subspherical with 2–4 covering the axial cell; rosettes of small secondary cortical cells present ..... 1. *B. australis*
1. Spines present, of (4-) 5–6 (-9) cells; primary cortical cells forming two tiers per axial cell (spines on the first tier); rosettes slight, secondary cortical cells small and sparse ..... 2. *B. spinescens*

1. **Bonnemaisonia australis** Levring 1953: 515, fig. 43. May 1965: 374.
Bonnemaisonia asparagoides (Woodward)C. Agardh var. *hypnoides* Reinbold 1899: 47. Lucas 1929b: 50. Lucas & Perrin 1947: 243. Tisdall 1898: 512. Wilson 1892: 169. Womersley 1950: 163.

FIG. 149

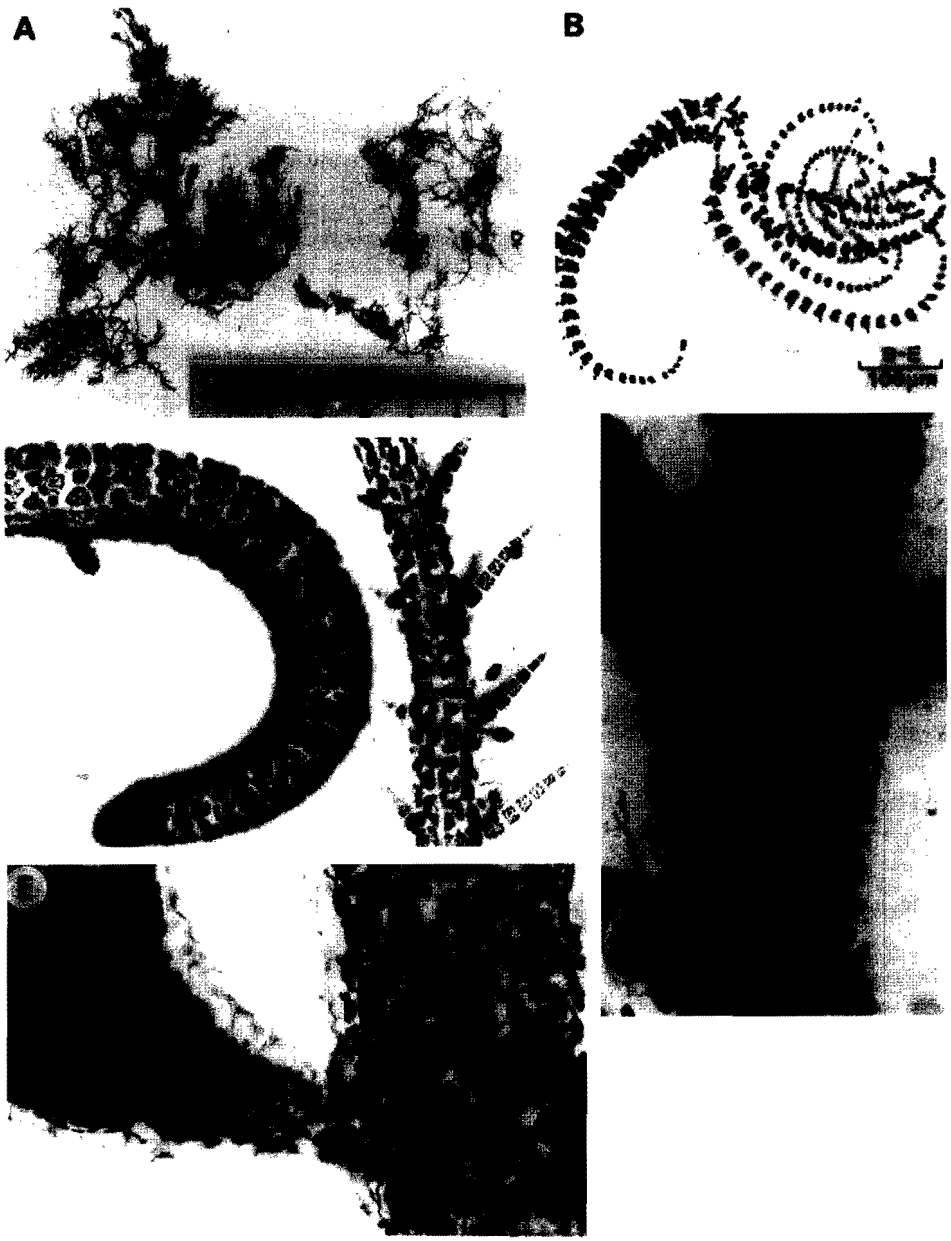


Fig. 150. *Bonnemaisonia spinescens* (**A, D,** AD, A38223; **B, C, E,** AD, A33440). **A.** Habit of holotype. **B.** Apex of branch. **C.** Curved branch end and branch with spines. **D.** Mature branch with cortical cells. **E.** Branch with cystocarp and showing internal structure with rhizoids at node.

Thallus (Fig. 149A) medium red, 4–12 cm high, delicate, much branched and spreading, branching essentially distichous on long main laterals, with main branches terete, 400–600 (-800) µm broad, bearing opposite simple branchlets, alternately long and short; the longer 1.5–2.5 (-3.5) mm long and 100–150 (-200) µm in basal diameter and tapering gently, the lower ones with hamate ends, and the opposite short branchlets often becoming fertile or developing as longer branches. Attachment mainly by lower hamate branchlets; probably epiphytic. *Structure* uniaxial (Fig. 149B), with a small but prominent apical cell, the subapical cells cutting off two opposite periaxial cells which develop alternately into full sized branchlets and opposite short branchlets; periaxial cells dividing, mainly basally, to produce 2–4 primary cortical cells which cover the axial cell which becomes 15–30 µm in diameter and L/D (10-) 20–30; cortex separated from the axial filament by a space, mature primary cortical cells subspherical, 30–45 µm in diameter, with small secondary cortical cells forming rosettes, often bearing slender hairs. Branchlets (Fig. 149B) with 3 periaxial cells, becoming radially elongate and each with 4 primary cortical cells becoming subspherical and 20–28 µm in diameter, with sparse small outer cells. Rhodoplasts ribbon shaped, numerous per cell.

Reproduction. Gametangial thalli monoecious (Fig. 149D), reproductive organs formed on the shorter of the branchlet pairs. Carpogonial branches 3-celled, with a lateral tuft of nutritive filaments, borne on a stalk 5–6 axial cells long. Cystocarps (Fig. 149E) pedicellate, broadly urceolate and ostiolate, 400–500 µm in diameter, gonimoblast much branched, arising from a basal fusion cell, with large, terminal, elongate-ovoid carposporangia 30–50 µm in diameter; pericarp of numerous, branched, erect filaments with an outer cortical layer 1–2 cells thick. Spermatangial organs (Fig. 149D) with a firm mucilaginous sheath, ovoid, 100–130 µm long and 60–90 µm in diameter, with a row of 4–6 axial cells each cutting off several periaxial cells which produce clusters of initials which cut off ovoid spermatangia about 2 µm in diameter.

Tetrasporophyte unknown.

Type from Port Phillip Heads, Vic. (*Wilson*, 1884); holotype in Herb. Agardh, LD, 37379.

Distribution: Whyalla to Brighton, S. Aust., Port Phillip, Vic., and Low Head, Tasmania.

Selected specimens: Whyalla, S. Aust., 12 m deep (*Branden*, 15.v.1984; AD, A55402). Fitzgerald Bay, Point Lowly, S. Aust., 14 m deep (*Branden*, 13.ix.1987; AD, A59340). Blanche Harbor, N Spencer Gulf, S. Aust., 13 m deep (*Branden*, 10.ix.1987; AD, A59351). N Spencer Gulf, S. Aust., 10 m deep (*Shepherd*, 5.ix.1973; AD, A44233). Sturt Bay, S. Aust., drift (*Davey*; AD, A442). 10 km W of Outer Harbor, S. Aust., 23 m deep (*R. Lewis*, 10.ix.1972; AD, A42659). Brighton, S. Aust., drift (*Bienert*, 12.xi.1965; AD, A29661). Pennington Bay, Kangaroo I., S. Aust., drift (*Womersley*, 29.viii.1948; AD, A8744). Low Head, Tas., 2–12 m deep (*Perrin*, Oct. 1937; AD, A8500).

B. australis is usually a deep water alga, most known specimens being from the Gulf region of South Australia.

It differs from *B. asparagoides* of European coasts in being more lightly corticated, with periaxial filaments less branched (2–3 branches before the cortex in the latter), in having slenderer axial filaments (15–30 µm compared to 40–60 µm), in that the small outer, rounded, cortical cells do not appear as gland cells, and in having numerous lower branchlets with hamate ends.

The Sturt Bay (Davey) specimen (AD, A442) is probably an isotype of *B. asparagoides* var. *hypnoides* Reinbold.

2. **Bonnemaisonia spinescens** Womersley, *sp. nov.*

FIGS 150, 151

Thallus (Fig. 150A) medium red, 3–8 cm high, delicate, much branched and spreading, branching essentially distichous on irregular main branches, larger branches terete, 300–600 µm in diameter, usually bearing opposite branchlets alternately long and short (occasionally both of similar length or the short one absent); the longer branchlets 2–6 mm long, 80–120 µm in basal diameter and gently tapering, with two tiers of large cortical cells per axial cell and (4-) 5–6 (-9) -celled spines (Fig. 150C) 70–150 (-180) µm long on the first cortical cell

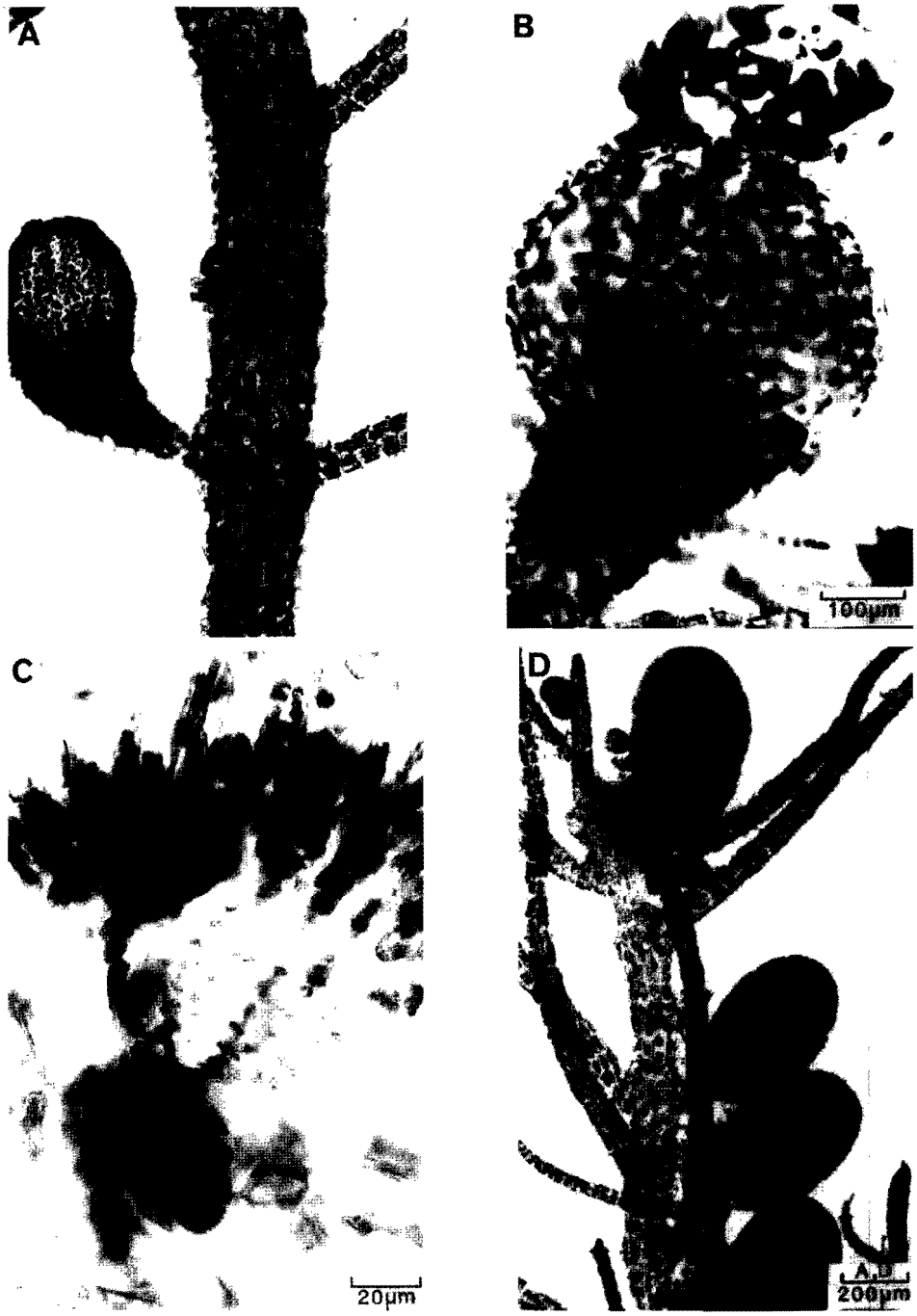


Fig. 151. *Bonnemaisonia spinescens* (**A,** AD, A33440; **B,** AD, A38166; **C, D,** AD, A38223). **A.** Branch with cystocarp. **B.** Cystocarp with carposporophyte and discharged carposporangia. **C.** Carposporophyte with basal fusion cell. **D.** Mature spermatangial organs.

from the periaxial cells and thus on alternating tiers; spines usually unilaterally arranged, occasionally opposite or in spirally situated pairs separated by 4–5 tiers; lower branchlets often with hamate ends (Fig. 150C). Short branchlets often becoming fertile or developing as longer branches. Attachment by a tuft of rhizoids or by hamate branchlets; probably epiphytic. *Structure* uniaxial (150B), with a small but prominent apical cell, the subapical cell cutting off two opposite periaxial cells which develop into branchlets; in branches, periaxial cells each cutting off 4–6 primary cortical cells which cover the axial cell (2–3 lengthwise, 6–8 around the branch), soon becoming subspherical and 35–50 μm across and cutting off small outer cells which form slight rosettes (Fig. 150D); inner cortex separated from the axial filament (Fig. 150E), with slender rhizoidal filaments bearing gland cells. Branchlets with 3 periaxial cells, each cutting off cortical cells to form two tiers per axial cell and 6 (-8) around the branchlet, cells rectangular in surface view and 15–35 μm across, L/D 1.5–2, with 2–3 small rounded cells cut off their upper ends. Rhodoplasts discoid, often in chains, numerous per cell.

Reproduction. Gametangial thalli dioecious, reproductive organs on the short branchlets. Carpogonial branches 3-celled, with a lateral tuft of nutritive filaments, on a stalk 5–7 axial cells long. Cystocarps (Fig. 151A) pedicellate, broadly ovoid, ostiolate, 400–500 μm in diameter, gonimoblast (Fig. 151B, C) much branched, arising from a basal fusion cell, with terminal ovoid carposporangia 20–35 μm in diameter; pericarp of numerous branched, erect, filaments with an outer cortical layer 1–2 cells thick. Spermatangial organs (Fig. 151D) with a firm mucilaginous sheath, shortly pedicellate, ovoid, (300-) 400–700 μm long and 300–500 μm in diameter, with a row of 5–8 axial cells each cutting off radially elongate periaxial cells branched 3–4 times, with an outer layer of 1–2 short cells producing radially elongate initials cutting off elongate-ovoid spermatangia.

Tetrasporophyte unknown.

Thallus 3–8 cm altus, tenuis, distiche vel irregulatim ramosus, ramis majoribus teretibus, 300–600 μm in diametro, ramulis oppositis plerumque longis et brevibus alterne. Rami longiores in duobus stratis cellularum magnarum corticalium per cellulam axialem et (4-) 5–6 (-9) cellularium spinarum 70–150 (-180) μm longarum in cellulis primis corticalibus ab cellulis periaxialibus, itaque in stratis alternantibus. Spinae plerumque unilaterales; ramuli inferiores in extremitate hamati. Structura uniaxialis, cellula parva apicali et cellula subapicali cum duobus cellulis oppositis periaxialibus ramulos producentibus; 4–6 cellulae primariae corticales super cellulas axiales ex cellulis periaxialibus excisae, et rosulae externae laeves; cortex interior de filamento axiali disiunctus. Ramuli cum 3 cellulis periaxialibus et duobus stratis cellularum corticalium per cellulam axialem.

Reproductio. Dioecia, organa reproductionis in ramulis brevibus. Rami carpogoniales 3-cellulares, caespite laterali filamentorum nutritivorum, stipite 5–7 cellulas axiales longo. Cystocarpia pedicellata, ovoidea, 400–500 μm in diametro, ostiolata. Gonimoblasti multiramosi cellula basali coalescenti et carposporangibus terminalibus; pericarpi numerosorum filamentorum erectorum cortice exteriori. Organa spermatangialia breviter pedicellata, ovoidea, vagina firma mucosa, (300-) 400–700 μm longa et 300–500 μm in diametro, cellulis periaxialibus 3–4 plo ramosis et spermatangiis externis ex 5–8 cellulis axialibus excisis. Tetrasporophyta ignota.

Holotype from Investigator Strait, S. Aust., 33 m deep (*Watson*, 24.i.1971); in AD, A38223.

Distribution: Known from Investigator Strait, S. Aust., 41 m deep (*Watson*, 14.i.1971; AD, A38166), 31 m deep (*Watson*, 23.i.1971; AD, A41104), and 33 m deep (*Watson*, 24.i.1971; AD, A41061). Off Troubridge Light (Edithburg), S. Aust., 17 m deep (*Shepherd*, 4.ii.1969; AD, A33440). 6–8 km off Outer Harbor, S. Aust., 16 m deep (*Loan*, 9.viii.1963; AD, A26653). Off Cape Jervis, S. Aust., 10–12 m deep (*Shepherd*, 29.xi.1983; AD, A54607).

Bonnemaisonia spinescens is a deep-water species, typical of the genus in its reproduction and structure, but differing from other species in having spines on the branchlets which have relatively sparse outer cortical cells and rectangular larger (inner) cortical cells.



Fig. 152. *Delisea elegans* (**A, C, D,** AD, A30350; **B, E,** AD, A27476). **A.** Habit. **B.** Apex of a branch. **C.** Longitudinal flat section of a branch with cystocarp. **D.** Carposporophyte. **E.** Branch with spermatangial sori.

Genus **DELISEA** Lamouroux 1819: 41

Thallus erect, much branched essentially complanately with compressed axes and alternate, terete to compressed and spinous, distichous, simple or branched ramuli; holdfast discoid. *Structure* uniaxial with a small apical cell, subapical cells each cutting off two pairs of periaxial cells, each pair developing lateral and transverse periaxial filaments, the first formed lateral filaments developing the alternate ramuli, the second lateral filament extending to the sinus between ramuli, and the transverse filaments contributing to the cortex. Branches with a prominent axial filament becoming surrounded by a sheath of small-celled rhizoidal filaments, and a large-celled inner and small-celled outer cortex; cortical gland cells absent or present.

Life history triphasic with isomorphic gametophytes and tetrasporophytes (known in *D. pulchra* and *D. plumosa*), or with heteromorphic crustose tetrasporophytes.

Reproduction. Gametangial thalli monoecious or dioecious. Carpogonial branches 3-celled, borne on lower cells of the shorter of the lateral periaxial filaments, with a basal fusion cell producing a tuft of branched gonimoblast filaments with terminal carposporangia, and with a group of darker staining nutritive filaments (probably from the hypogynous cell) at the base of the carposporophyte. Cystocarps immersed in the swollen branch cortex between two ramuli, with a relatively thick pericarp, ostiolate. Spermatangial sori covering parts of the ramuli or lesser branches.

Tetrasporangia (where known) in raised nemathecia on upper branches, among elongate-clavate paraphyses, obliquely divided, or probably in small discoid crusts (Bonin & Hawkes 1988a).

Lectotype species: *D. elegans* Lamouroux (see Silva 1957, p. 143)

A genus of 6 species, four from southern Australia, four from New Zealand (3 Australian also) and one from Japan.

Delisea differs from *Ptilonia* (with which it was united by Chihara & Yoshizaki 1978) in having the alternate lateral periaxial filaments developing into discrete ramuli (spinous in some species) whereas in *Ptilonia* the lateral periaxial filaments remain adherent to form the flat branches, with only small spines representing the ends of the filaments.

KEY TO SPECIES OF *DELISEA*

1. Ramuli terete, tapering gently from the base 100–200 µm in diameter 2
1. Ramuli compressed, tapering markedly from the base when young, 150–400 µm broad basally 3

    2. Ramuli unbranched, 1–1.5 mm long, remaining regularly distichous, complanately branched ..... 1. *D. elegans*
    2. Ramuli simple or commonly with 1–3 branches, mostly 1–2 (-3) mm long, distichous only near the apices and becoming flexed below so that the frond is not complanately branched ..... 2. *D. hypneoides*

3. Ramuli compressed throughout, with many between the indeterminate branches, without minute opposite ramuli; basal width 250–400 µm ..... 3. *D. pulchra*
3. Indeterminate laterals usually separated by 4 ramuli, two on each side; often with minute opposite ramuli; ramuli becoming subterete, 1–2 (-3) mm long and 150–300 µm in basal width ..... 4. *D. plumosa*

1. **Delisea elegans** Lamouroux 1819: 42. Adams 1972: 70; 1994: 239, pl. 88 lower right. Adams *et al.* 1974: 213. J. Agardh 1852: 781; 1876: 670. Bonin & Hawkes 1988a: 624, figs 20, 21, 24–27. Chapman 1969: 83, pl. 21. De Toni 1900b: 760. Guiler 1952: 84. Harvey 1849: 89, pl. 34 upper. Kützing 1849: 770; 1868: 24, pl. 69a–c. Levring 1953: 519, figs 47, 48. Lucas 1929a: 20. Lucas & Perrin 1947: 240, fig.

104. May 1965: 374. Sonder 1881: 30. Tisdall 1898: 512. Wilson 1892: 169. Womersley 1966: 145.
Bonnemaisonia elegans C. Agardh 1822: 198; 1824: 246. Harvey 1844: 442.
Calocladia elegans (C. Agardh)J. Agardh 1841: 21.

FIG. 152

Thallus (Fig. 152A) medium red to dark red-brown, fading to yellow-grey, 10–30 cm high, complanately and alternately much branched, branches slender, terete to compressed, 250–500 μm broad above, 0.5–1 mm broad and subterete below where mostly denuded of ramuli. Lesser branches with regularly spaced, alternately distichous, terete ramuli 1–1.5 mm long and 100–200 μm in diameter near their base. Holdfast discoid, becoming knobby, 1–3 mm across with a single stipe; epilithic or occasionally epiphytic. *Structure* uniaxial (Fig. 152B, C), with a small apical cell, the subapical cell(s) cutting off two pairs of lateral and transverse periaxial cells, the lateral of the first pair producing the more strongly developed filament forming the alternate ramuli (Fig. 152C), with the lateral periaxial cell of the second pair remaining ovoid and not forming a distinct filament of elongate cells; the latter and the transverse periaxial cells contribute to the cortex near the compressed apices. Main branches 12–20 cells thick, the axial filament 20–50 μm in diameter, with a sheath of smaller cells; inner cortical cells ovoid, 30–100 μm in diameter, with a few intermixed small cells, outer cortical cells angular, 6–12 μm across, with occasional scattered gland cells. Rhodoplasts discoid, numerous per cell, becoming ribbon like in inner cells.

Reproduction. Gametangial thalli monoecious. Carpogonial branches unknown. Carposporophyte (Fig. 152D) associated with the less well developed lateral periaxial filament, probably arising from the basal cell, thus lying between two ramuli, with a basal fusion cell adjacent to a group of darker-staining (nutritive?) cortical cells, and a short tuft of slender, branched, gonimoblast filaments with terminal elongate-ovoid carposporangia 20–60 μm in diameter. Cystocarps (Fig. 152C) lying on the flat surface between ramuli near branch ends, sessile, 400–600 μm across with a thick pericarp (with inward growing branched filaments) and an ostiole. Spermatangial sori (Fig. 152E) in scattered patches or covering the ramuli, with elongate spermatangia cut off from outer cortical cells, 2–3 μm in diameter.

Tetrasporangia uncertain, possibly formed on small crusts (Bonin & Hawkes 1988a, p. 624).

Type from "Nouvelle-Hollande"; lectotype(?) in Herb. Lamouroux, CN. (Probably from SE Tasmania.)

Distribution: "Occid. N. Holl." (W. Aust.), to Gabo I., Vic., and around Tasmania.
New Zealand (Wellington south).

Selected specimens: "Occid. N. Holl." (Herb. Agardh, LD, 37407, type of *B. elegans* C. Agardh). Egg I., Isles of St Francis, S. Aust., 32–38 m deep (*Shepherd*, 11.i.1971; AD, A62810). Investigator Strait, S. Aust., 31 m deep (*Watson*, 25.i.1971; AD, A38183). Dubious Rock, West I., S. Aust., 13 and 16 m deep (*Shepherd*, 3.i.1966; AD, A30350 and A30231 resp.). Portland, Vic., 10–13 m deep (*Kraft* 6326, 30.xii.1976; MELU). Warrnambool, Vic., drift (*Kraft* 8249, 30.xii.1989; MELU). Queenscliff, Vic., drift (*Norris*, 21.i.1963; AD, A27476). Portsea, Vic., 3–5 m deep at jetty (*Kraft* 8955 & *Saunders*, 24.iii.1992; MELU). Waratah Bay, Vic., drift (*Sinkora* A2343, 3.iii.1977; AD, A48348). Gabo I., Vic., 28 m deep (*Shepherd*, 19.ii.1973; AD, A43532). Ulverstone, Tas. (*Perrin & Lucas*, April 1936; AD, A61901). Low Head, Tas. (*Perrin*, 8.x.1950; AD, A47161). Marion Bay, Tas., 3–5 m deep (*Shepherd*, 13.ii.1970; AD, A35593). Great Taylor Bay, Bruny I., Tas., 6 m deep (*Shepherd*, 7.ii.1970; AD, A35531).

D. elegans is a delicate, complanately branched, species, with most ramuli unbranched.

2. **Delisea hypneoides** Harvey 1859b: 305; 1860b: pl. 134. J. Agardh 1876: 670. De Toni 1900b: 761. Guiler 1952: 85. Levring 1953: 520, figs 49–51. Lucas 1929a: 20; 1929b: 50. Lucas & Perrin 1947: 241, fig. 103. May 1965: 374. Reinbold 1898: 48; 1899: 47. Sonder 1881: 30. Tisdall 1898: 512. Wilson 1892: 169. Womersley 1950: 163.

FIG. 153

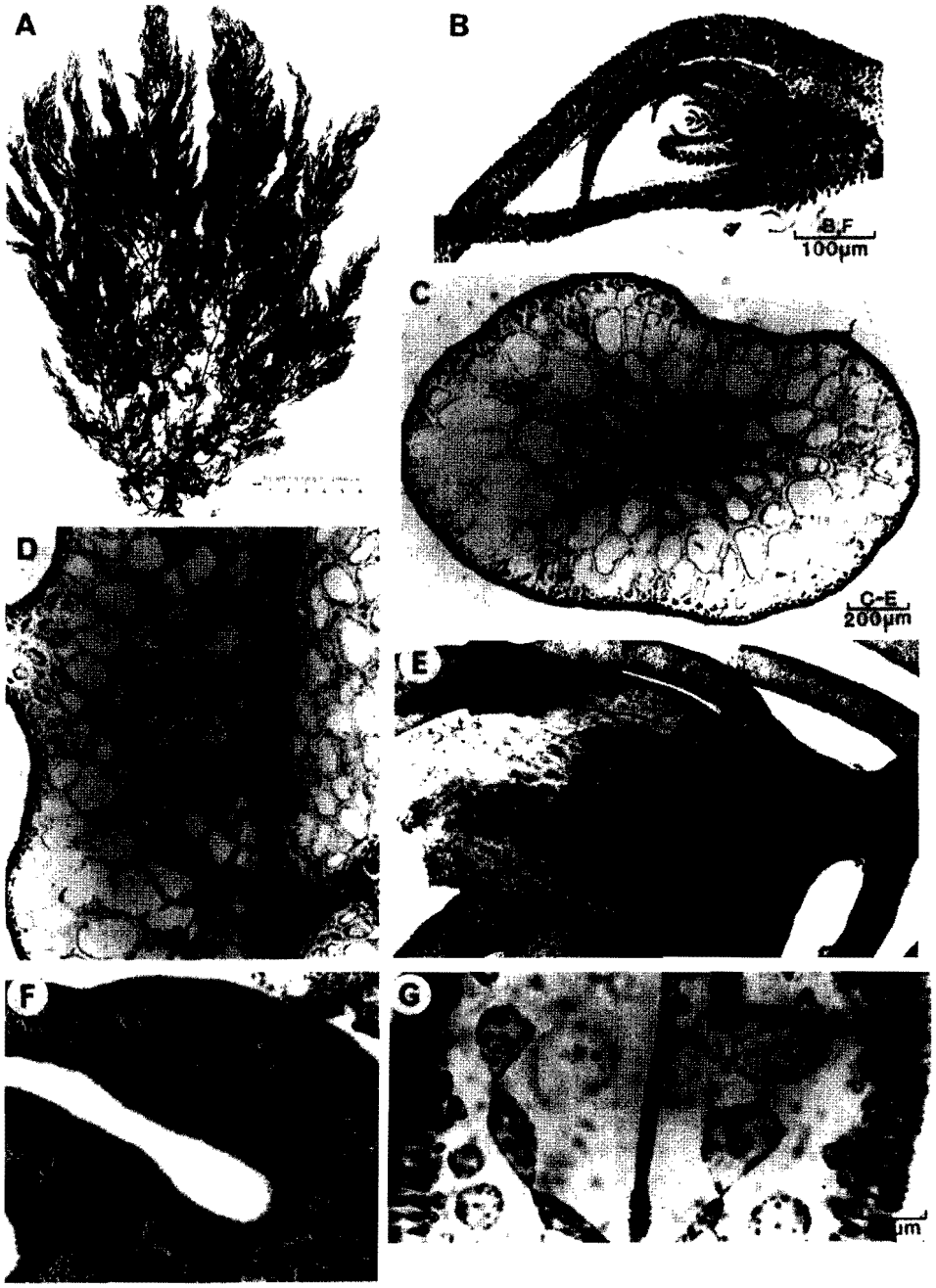


Fig. 153. *Delisea hypneoides* (**A**, AD, A47838; **B–F**, AD, A63248; **G**, AD, A28594). **A.** Habit. **B.** Apex of branch. **C.** Transverse section of branch. **D.** Longitudinal flat section of branch. **E.** Cystocarp with carposporophyte. **F.** Spermatangial sori. **G.** Longitudinal section of branch with spermatangia.

Thallus (Fig. 153A) medium to dark red-brown, 10–40 cm high, much branched irregularly and alternately, with distichous branching only close to apices (Fig. 153B), branches slender, slightly to moderately compressed, 200–600 µm broad above, 0.5–1 mm broad and only slightly compressed below where often denuded of ramuli. Lesser branches with alternate ramuli, at first distichous near the apices but soon flexed so that the distichous arrangement is lost, ramuli terete, simple or with 1–3 branches, (0.5-) 1–2 (-3) mm long and 100–200 µm in diameter near their bases. Attachment to the host by curled branchlets with small discoid pads; epiphytic (on *Amphibolis* and various algae) or possibly epilithic. *Structure* uniaxial (Fig. 153C, D), with a small apical cell, the subapical cells each cutting off two pairs of lateral and transverse periaxial cells, the lateral of the first pair producing the more strongly developed filament forming the originally distichous and alternate ramuli, with the lateral cell of the second pair usually remaining ovoid and not forming a distinct filament, or occasionally developing to form an opposite ramulus; the transverse periaxial cells contribute to the cortex. Main branches (Fig. 153C, D) 12–20 cells thick, the axial filament 30–60 µm in diameter, developing a thin sheath of small cells (Fig. 153C); inner cortical cells ovoid, 40–100 µm in diameter, becoming thick walled and with few intermixed small cells; outer cortical cells angular, 4–8 µm across, usually with few, scattered, gland cells; hairs often profuse; older axes with a secondary cortex of anticlinal filaments. Rhodoplasts discoid, becoming ribbon like in inner cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches 3-celled, borne on the first cell of shorter lateral periaxial filaments (Levring 1953, fig. 51F). Carposporophyte (Fig. 153E) associated with the less well developed lateral periaxial filament, with a basal fusion cell, an adjacent group of darker staining (nutritive) filaments, and a short tuft of branched gonimoblast filaments with terminal elongate-ovoid carposporangia 20–35 µm in diameter. Cystocarps lying between ramuli, sessile and immersed, 500–800 µm across, with a thick pericarp (with internal branched cell filaments) and a protruding beak with a prominent ostiole. Spermatangial sori (Fig. 153F) covering lower parts of ramuli and on lesser branches, with the outer cortical cells cutting off 2–3 elongate, tapering initials (Fig. 153G) producing 2–3 elongate spermatangia 2–3 µm in diameter.

Tetrasporangia unknown.

Type from Georgetown, Tas. (*Fereday*); holotype in Herb. Harvey, TCD.

Distribution: Point Peron, W. Aust., to Walkerville, Vic., and northern Tasmania.

Selected specimens: Point Peron, W. Aust., on *Amphibolis antarctica* (*Ducker*, 15.ix.1973; MELU, 22429). Head of the Great Australian Bight, S. Aust., drift (*Womersley*, 4.ii.1954; AD, A19198). D'Entrecasteaux Reef, S. Aust., 15–20 m deep (*Shepherd*, 27.iii.1980; AD, A52162). Egg I., Isles of St Francis, S. Aust., 32–38 m deep (*Shepherd*, 11.i.1971; AD, A38042). Pearson I., S. Aust., 22 m deep (*Rowland*, 29.iii.1988; AD, A58653). Althorpe I., S. Aust., 10–13 m deep (*Baldock*, 4.i.1964; AD, A27232). Marion Bay, Yorke Pen., S. Aust., 1 m deep (*Womersley*, 15.x.1988; AD, A59152). Yilki, Victor Harbor, S. Aust., drift (*Womersley*, 31.xii.1993; AD, A63248). Victor Harbor, S. Aust., drift (*Womersley*, 28.xii.1976; AD, A47838 —"Marine Algae of southern Australia" No. 152). Snug Cove, N coast Kangaroo I., S. Aust., 16–21 m deep (*Mitchell*, 16.ii.1960; AD, A24046). Stokes Bay, N coast Kangaroo I., S. Aust., upper sublittoral (*Womersley*, 15.i.1965; AD, A28940). Seal Bay, Kangaroo I., S. Aust., drift (*Womersley*, 21.i.1965; AD, A28594). Nora Creina, S. Aust., 3 m deep (*Kraft* 4442 & *Johnson*, 11.ii.1973; MELU). Double Corner Beach, Portland, Vic., drift (*Beauglehole* 462A, 22.vii.1951; AD, A21726). Walkerville, Vic., drift (*Sinkora* A1647, 23.ii.1972; AD, A43286). Erith I., Bass Strait, 5–7 m deep (*Riddle*, 20.ii.1990; AD, A60457). Bombay Rock, Tamar Est., Tas. (*Perrin*, April 1949; AD, A61900). Musselroe Bay, Tas. (*Perrin*, 7.ii.1948; AD, A47156).

D. hypneoides is a more robust species than *D. elegans*, differing in having branched, flexed, ramuli which soon lose their complanate branching.

3. **Delisea pulchra** (Greville)Montagne 1844: 158. J. Agardh 1852: 784; 1876: 671. Bonin & Hawkes 1988a: 627, figs 29–31. De Toni 1900b: 763. Guiler 1952: 85. Harvey 1849: 89, pl. 34 lower; 1858: pl. 16; 1859b: 305. Hooker 1847: 484. Huisman & Walker 1990: 399. Kützing 1849: 770; 1868: 24, pl. 68a–c. Lucas 1929b: 50. Lucas & Perrin 1947: 241, figs 105, 106. May 1965: 374. Millar 1990: 381, fig. 36. Millar & Kraft 1993: 34. Reinbold 1897: 55. Ricker 1987: 161, fig. 69. Silva 1957: 143. Sonder 1881: 30. Tisdall 1898: 512. Wilson 1892: 169. Womersley 1950: 163.

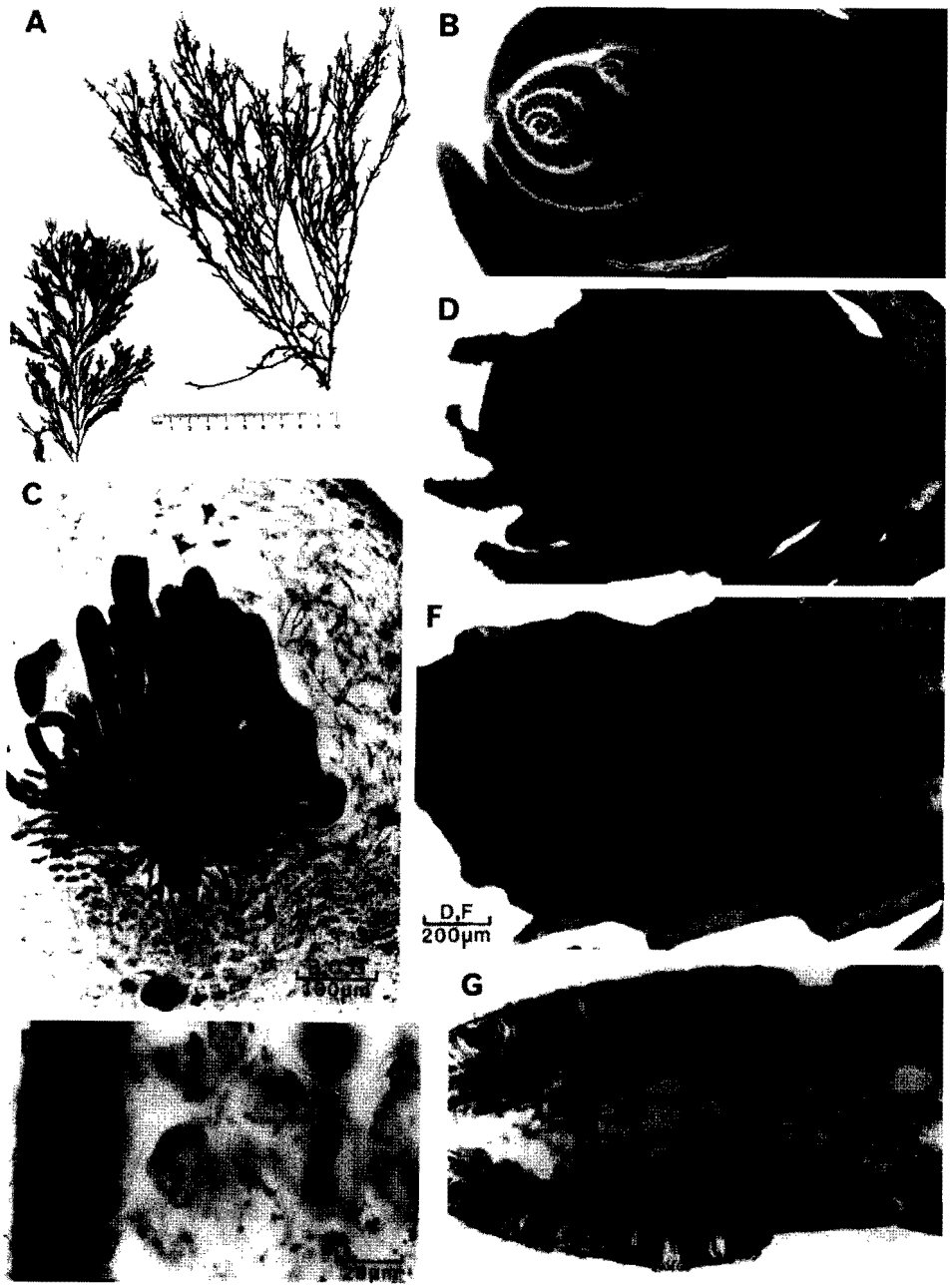


Fig. 154. *Delisea pulchra* (**A, C, G,** AD, A32467; **B,** AD, A63247; **D, E,** AD, A20766; **F,** AD, A43325). **A.** Habit. **B.** Branch apex. **C.** Carposporophyte with basal fusion cell, branched gonimoblast filaments and ovoid carposporangia. **D.** Branch end with spermatangial sorus. **E.** Transverse section of branch with spermatangial sorus. **F.** Tetrasporangial sorus on branch end. **G.** Transverse section of branch with tetrasporangial sorus.

Bowiesia pulchra Greville 1830: lvii. Kützing 1843: 408.
Calocladia pulchra (Greville)Greville *in* Lindley 1835: 436.
Bonnemaisonia pulchra (Greville)Endlicher 1843: 44.
Delisea fimbriata sensu J. Agardh 1852: 785; 1876: 672. Chapman 1969: 84, pl. 23. De Toni 1900b: 764. Kützing 1849: 771; 1868: 24, pl. 68d–l. Levring 1953: 521, figs 52–55A, B. J. Lewis 1984: 5. Montagne 1844: 158, pl. 11 fig. 1. Sonder 1881: 30. [NON *Fucus fimbriatus* R. Brown *ex* Turner (1811: 88, pl. 170) = *Vidalia fimbriata* (Turner)J. Agardh (1863: 1124), from northern Australia].
Delisea serrata Kützing 1849: 771; 1868: 24, pl. 69d, e. J. Agardh 1852: 784; 1876: 671. De Toni 1900b: 763. Guiler 1952: 85. Sonder 1881: 30.
Delesseria fimbriata Lamouroux 1813: 124, pl. 3 fig. 1.

FIG. 154

Thallus (Fig. 154A) medium to dark red-brown, fading to yellow-grey, 10–35 cm high, much branched complanately from the margins, branches compressed, axes 500–800 µm broad, with regular, alternate, evenly spaced, acute, compressed marginal spinous ramuli (0.5-) 1–2 (-3) mm long, basal width 250–400 µm, tapering evenly, axes becoming thickened and terete below, (1-) 2–3 mm in diameter near the holdfast, often denuded below. Holdfast discoid, 2–8 mm across, usually with a single stipe; epilithic. *Structure* uniaxial (Fig. 154B), with a small apical cell, the subapical cell(s) each cutting off two pairs of lateral and transverse periaxial cells, the first pair forming the more strongly developed lateral periaxial filament on alternate sides and developing into the lateral spinous ramuli, with the opposite lateral filament passing towards the sinus between spines and the transverse periaxial cells contributing to the cortex. Spinous ramuli closely adjacent near apices, becoming separated below. Main branches becoming 8–15 (-26) cells thick, the axial filament 50–140 µm in diameter with a surrounding sheath of small cells, the inner cortical cells ovoid, 25–50 µm in diameter and with intermixed small rhizoidal cells, outer cortical cells 4–6 µm in diameter, with scattered, larger, subsurface cells not covered by outer cells and appearing "gland like" in surface view with a rosette of outer cells. Rhodoplasts discoid, numerous per cell, often ribbon like in inner cells.

Reproduction. Gametangial thalli monoecious or dioecious. Carpogonial branches unknown. Carposporophyte (Fig. 154C) with a basal fusion cell, a tuft of branched, slender, gonimoblast filaments, and terminal elongate-ovoid carposporangia 20–45 µm in diameter. Cystocarps on the flat surface near branch ends, sessile, 0.5–1 mm in diameter, with a thick pericarp and an ostiole directed forwards and outwards. Spermatangial sori (Fig. 154D) on broadened branch ends, with the outer cortical cells each cutting off several elongate, tapering, spermatangia 2–3 µm in diameter (Fig. 154E).

Tetrasporangial plants with prominent, raised, nemathecia (Fig. 154F) 50–90 µm thick, near branch ends, tetrasporangia (Fig. 154G) elongate-ovoid, 30–55 µm long and 10–15 µm in diameter, obliquely divided, among elongate-clavate unicellular (rarely 2-celled) paraphyses 50–65 µm long and 6–11 µm in diameter; paraphyses often cutting off several small cells apically.

Type from "Novam Hollandiam" (*Fraser*); holotype in Herb. Greville, E. (See also Millar 1990, p. 382 and Ricker 1987, p. 161).

Distribution: Dongara, W. Aust., around southern Australia and Tasmania to Caloundra, Qld.

New Zealand; Subantarctic Islands; Antarctic Peninsula.

Selected specimens: Dongara, W. Aust., drift (*Wood*, 2.x.1960; AD, A24556). Torpedo Rocks, S of Yallingup, W. Aust., drift (*Royce* 574; AD, A15488). Cannan Reefs (S of Isles of St Francis), S. Aust., 20–25 m deep (*Branden*, 21.i.1991; AD, A61193). Hopkins I., S. Aust., 25 m deep (*Branden*, 17.xi.1990; AD, A60844). Amphitheatre Rock, West I., S. Aust., 19–23 m deep (*Shepherd*, 1.i.1969; AD, A33247). Port Elliot, S. Aust., drift (*Womersley*, 31.xii.1993; AD, A63247). Seal Bay, Kangaroo I., S. Aust., drift (*Womersley*, 24.i.1957; AD, A20766). South West Rock, S of Kangaroo I., S. Aust., 15–36 m deep (*Branden*, 18.vi.1991; AD, A61433). Cape Buffon, S. Aust., 5 m deep (*Kildea & Collings*, 27.ix.1992; AD, A61769). Port MacDonnell, S. Aust., drift (*Kraft* 3863, 2.ix.1971; MELU). Portland, Vic., 10–13 m deep (*Kraft* 6327, 30.xii.1976; MELU). Dinghy Cove, Lady Julia Percy I., Vic., 8–11 m deep (*Shepherd*, 3.i.1968; AD, A32467 —"Marine Algae of southern Australia" No.

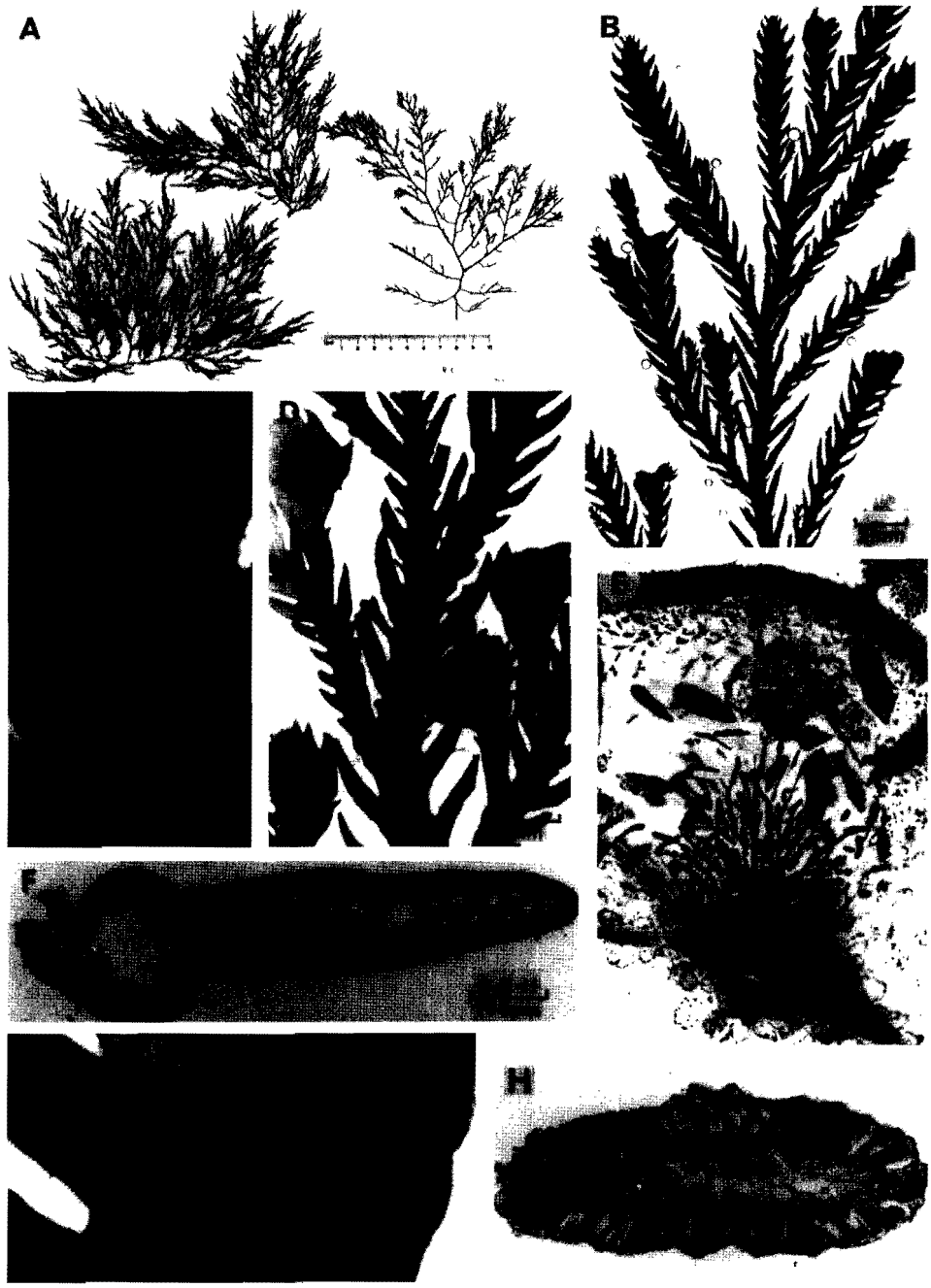


Fig. 155. *Delisea plumosa* (**A, B, D–F,** AD, A63353; **C,** AD, A58491; **G, H,** AD, A58490). **A.** Habit. **B.** Branches showing arrangement of laterals and ramuli. **C.** Surface view of branch with gland cells. **D.** Branches with cystocarps. **E.** Section of a cystocarp with carposporophyte. **F.** Transverse section of a branch with spermatangial sorus on left. **G.** Branch with tetrasporangial sorus. **H.** Transverse section of branch with a tetrasporangial sorus.

77a). Gabo I., Vic., 13 m deep (*Shepherd*, 14.ii.1973; AD, A43325). Bluestone Bay, Freycinet Pen., Tas., 6 m deep (*Brown & McGeary*, 4.xi.1982; AD, A56272). Pebbly Beach (N of Batemans Bay), NSW., upper sublittoral pools (*Womersley*, 15.i.1964; AD, A28038). Byron Bay, N.S.W., 6 m deep (*Silvester*, 21.vii.1973; AD, A43879). Stradbroke I., Qld., 10–25 m deep (*Watson*, 24.viii.1975; AD, A46546). Caloundra, Qld., drift (*McKeon*, 30.iv.1949; AD, A16628).

Delisea pulchra is a common species on southern Australian coasts, and tetrasporangial plants are not uncommon (A28038, A32467, A56272, A56608 and A61769 above). Only a few male plants (e.g. A20766, *Kraft* 3863) have been seen.

D. pulchra is superficially similar in habit to species of *Phacelocarpus* in the *Gigartinales* and to *Rhodocallis* in the Ceramiaceae but distinct in structure.

D. pulchra (as *D. fimbriata*) has been recorded from Japan (see Chihara 1962, p. 27, figs 20–22, 23–27 and Chihara & Yoshizaki 1971, p. 149, figs 1, 2) but these authors show that the Japanese species lacks a tetrasporophyte and the life history thus differs from the southern hemisphere plants. The Japanese species had been renamed as *D. japonica* by Okamura (1908, p. 139, pl. 39) and this is supported by Bonin & Hawkes (1988a, p. 631) and by Yoshida *et al.* (1990, p. 288).

4. **Delisea plumosa** Levring 1955: 427, fig. 13. Bonin & Hawkes 1988a: 627, figs 22, 23. Chapman 1969: 83, pl. 22.

FIG. 155

Thallus (Fig. 155A, B) dark red-brown, 12–30 cm high, complanately and regularly branched with alternate indeterminate branches separated by usually four (sometimes 2 or 6) determinate ramuli (Fig. 155B), evenly spaced with two on each side, alternating but with occasional to frequent very short spinous ramuli opposite the longer ones; ramuli mostly remaining on lower branches. Branches compressed, (300-) 500–700 µm broad above, 500–1000 (-1400) µm broad below, thickened to 1 mm near the base. Ramuli near branch apices compressed, tapering, 250–1000 (-1500) µm long and basally 100–250 µm broad, on lower branches becoming subterete, 1–2 (-3) mm long and basally 150–300 µm broad. Holdfast discoid, 1–2 mm across, bearing 1–3 fronds; epilithic. *Structure* uniaxial, the subapical cells with lateral and transverse periaxial cells, the lateral ones producing alternate ramuli with some opposite periaxial filaments forming the very short spines. Branches 8–15 cells thick, the axial filament 35–60 µm in diameter, with a slight sheath of small cells, inner cortical cells ovoid, 40–100 µm in diameter, outer cortical cells angular in surface view, 4–8 µm across, with frequent, scattered, subsurface gland cells (Fig. 155C) with a rosette of outer cells. Rhodoplasts discoid, in chains in inner cells.

Reproduction. Gametangial thalli dioecious or monoecious. Carpogonial branches unknown. Carposporophyte (Fig. 155E) with a small basal fusion cell and a surrounding nutritive tissue, and a tuft of slender, branched, gonimoblast filaments with terminal, elongate-ovoid carposporangia 25–55 µm in diameter. Cystocarps (Fig. 155D) on the flat surface near branch ends, sessile, 500–900 µm across, with a thick pericarp and an ostiole directed forwards and outwards. Spermatangial sori (Fig. 155F) raised, often appearing pustular, near branch apices, with the outer cortical cells each cutting off several elongate initials and spermatangia 2–3 µm in diameter.

Tetrasporangial nemathecia (Fig. 155G) on upper branches or ramuli, 50–80 µm thick, with the outer cortical cells producing elongate-clavate unicellular paraphyses and ovoid to clavate tetrasporangia (Fig. 155H) 40–60 µm long and 15–25 µm in diameter, obliquely divided.

Type from Stewart I., New Zealand (*Lindauer*, 7.i.1946); holotype in Herb, Levring, Göteborg (Levring 1955, fig. 13).

Distribution: Stewart I. and Otago, N.Z.
SE and SW Tasmania.

Known specimens: Bicheno, Tas., 18–20 m deep (*Kraft* 9327, 18.xii.1992; MELU). Prosser Bay, Tas., 3–6 m deep (*Shepherd*, 10.ii.1970; AD, A35737). Eaglehawk Neck, Tas., 10 m deep (*Blackman*, 17.ii.1979; AD, A58491). North Point, Eaglehawk Neck, Tas., 12–15 m deep (*Kraft* 9636, 12.xii.1993;

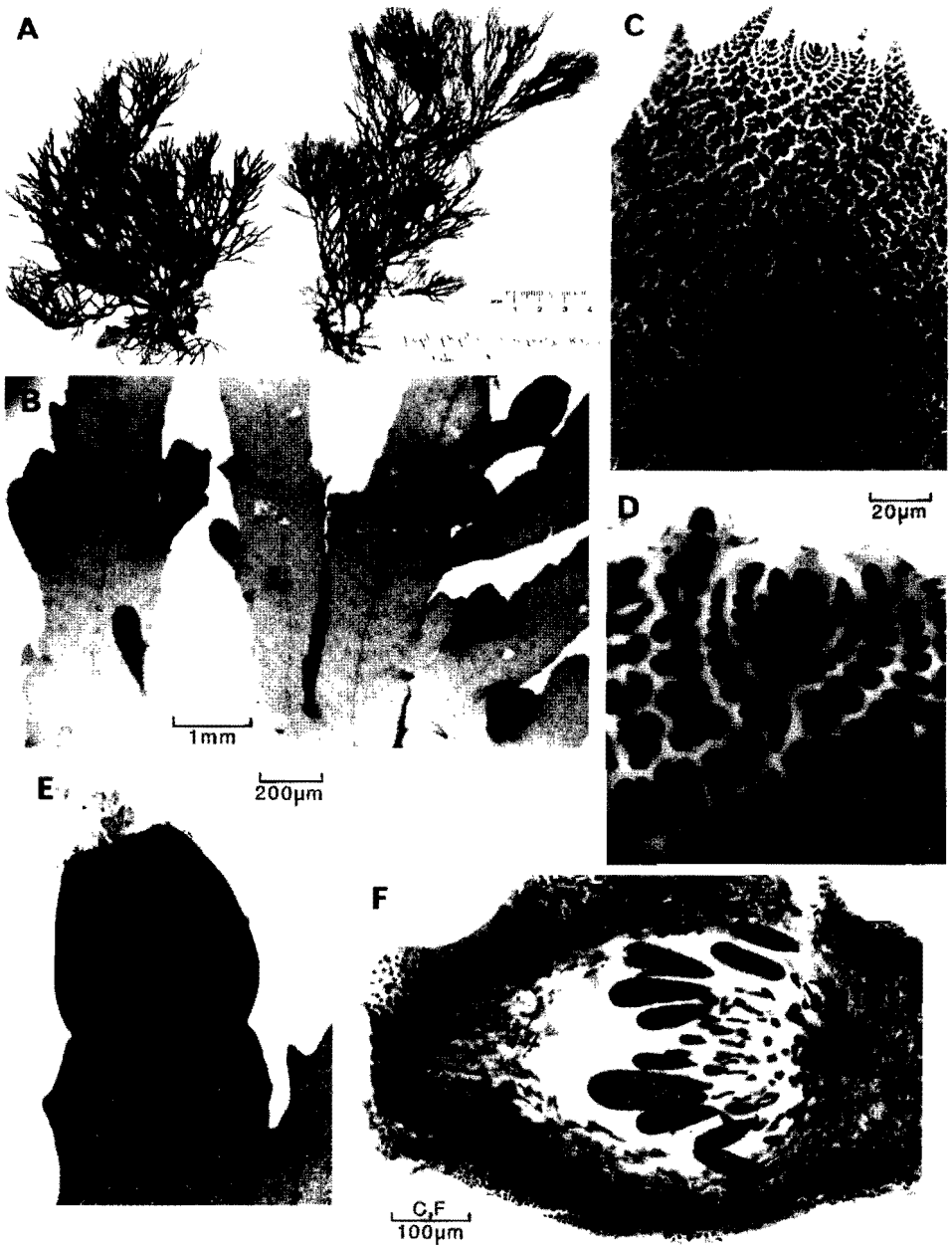


Fig. 156. *Leptophyllis conferta* (**A, B,** AD, A34873; **C–E,** AD, A63352; **F,** AD, A41514). **A.** Habit. **B.** Branches with cystocarps. **C.** Apex of branch. **D.** Apex showing development of lateral periaxial cells with no transverse periaxial cells. **E.** Cystocarp situated within the apex of a lateral. **F.** Section of a cystocarp with carposporophyte and carposporangia.

AD, A63353). Ninepin Point, D'Entrecasteaux Ch., Tas., 8 m deep (*Blackman*, 18.vi.1979; AD, A58490). Scotts Point, near Dover, Tas., 3–5 m deep (*Steane*, 8.v.1989; MELU). Southport, Tas. (*Stuart*; MEL 652928). Sarah I., Bathurst Ch., SW Tas., 2–5 m deep (*Edgar*, 11.iii.1995; AD, A64250).

The Tasmanian specimens agree very well in habit and structure with isotypes in AD (Lindauer 6937 and Alg. Nova-Zel. Exsicc. 192); A58490 and Kraft 9327 are tetrasporic while AD, A63353 is sexual. They are superficially similar to *D. elegans* but the latter has terete ramuli with irregular numbers of ramuli between the indeterminate lateral branches, and lacks the occasional minute ramuli opposite the normal ramuli in *D. plumosa*. The specimens from Scotts Point have an apparent pulvinate parasite.

Genus **LEPTOPHYLLIS** J. Agardh 1876: 674

Thallus erect, membranous, much branched more or less complanately and irregularly from the margins, branches flat, linear, 1–2 mm broad, with slight to distinct marginal serrations, basally constricted; axial filament present throughout forming a slight midrib, with opposite microscopic veins; holdfast discoid. *Structure* uniaxial, apical cell distinct, segmenting slightly obliquely, with each axial cell cutting off two opposite periaxial cells, one slightly prior to the other and alternating, with the first producing better developed abaxial tertiary rows with more cortical cells and the end protruding as the marginal serrations; each secondary cell cuts off four primary cortical cells which cut off further cortical cells and then the outer cortical layer; near the apex the flat surfaces show a slight gap above the axial cells, due to the lack of transverse periaxial cells, but this gap is closed as cortical cells are cut off from the first cells of the secondary filaments. Branches in sectional view with a prominent central axis and cortex 4–5 cells thick; gland cells absent.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli dioecious or monoecious. Carpogonial branches unknown. Carposporophyte with a basal fusion cell and a tuft of branched gonimoblast filaments with terminal ovoid carposporangia. Cystocarps urceolate, sessile on the surface of lesser branches, with a thick ostiolate pericarp. Spermatangia in sori near branch ends, cut off via initials from outer cortical cells.

Tetrasporangia in raised, mucilaginous, nemathecia on both sides of the midrib, accompanied by paraphyses of uniseriate cells, irregularly obliquely divided.

Type (and only) *species*: *L. conferta* (R. Brown *ex* Turner)J. Agardh 1876: 676.

Leptophyllis appears to be a member of the Bonnemaisoniales though the details of female reproduction need study. It differs from *Ptilonia* in habit, in formation of only lateral periaxial cells, and in having isomorphic gametophyte and tetrasporophyte generations. In these respects it appears adequately distinct from *Ptilonia* (see Bonin & Hawkes 1988b, p. 642).

Leptophyllis conferta (R. Brown *ex* Turner)J. Agardh 1876: 676. De Toni 1900b: 757. Guiler 1952: 85. Levring 1953: 526, fig. 55C–G. Lucas 1929a: 20. Lucas & Perrin 1947: 239. May 1965: 398. Sonder 1881: 30. Tisdall 1898: 512. Wilson 1892: 169.
Fucus confertus R. Brown *ex* Turner 1811: 116, pl. 184.
Delesseria conferta (R. Brown *ex* Turner)C. Agardh 1822: 177.
Dictymenia conferta (R. Brown *ex* Turner)Harvey 1847: 29, pl. 8.
Cladhymenia conferta (R. Brown *ex* Turner)Harvey 1859b: 306; 1860: pl. 144. Kützing 1864: 33, pl. 93a–d.

FIGS 156, 157

Thallus (Fig. 156A) medium red to red-brown, fading to yellow-brown, 5–15 cm high, essentially complanately and alternately marginally branched, branches flat, (0.5-) 1.5–2.5 (-3) mm broad, basally constricted, apices obtuse to pointed, with a slight midrib and opposite lateral veins, margin usually with small serrations; axes thickened and subterete near the base. Holdfast discoid, 2–4 mm across; usually epilithic, occasionally epiphytic. *Structure* uniaxial (Fig. 156A–D), apical cell usually distinct, each subapical cell with two opposite periaxial cells developing slightly more strongly alternately, the stronger producing

the small marginal serrations (Fig. 156C), with the axial filament forming the slight central midrib 45–75 μm in diameter and the periaxial filaments forming the opposite veins. Thallus 4–5 cells thick, inner cells ovoid, 30–80 μm in diameter, outer cells angular in surface view, 6–18 (-22) μm across and 8–17 μm thick (usually broader than thick). Rhodoplasts discoid.

Reproduction. Gametangial thalli dioecious or monoecious. Carpogonial branches unknown. Carposporophyte (Fig. 156F) with a small basal fusion cell, associated nutritive cells, and a tuft of branched gonimoblast filaments with slender elongate cells and terminal, ovoid to clavate carposporangia 40–80 μm in diameter. Cystocarps (Fig. 156B, E) sessile on the surface of branchlets, lying above the veins, urceolate, 500–800 μm in diameter, broadly ostiolate with a thick pericarp; inner pericarp cells elongate, often extruded with the carposporangia. Spermatangial sori near branch ends, with initials producing elongate spermatangia (Fig. 157A) 4–6 μm in diameter.

Tetrasporangia in raised nemathecia (Fig. 157B) on both sides of the midrib, ovoid to clavate, 20–30 μm in diameter, irregularly obliquely divided, among paraphyses (Fig. 157C) 3–5 cells long and 6–10 μm in diameter, with the outer cells short and branched, overarching the tetrasporangia.

Type from Kent Is (*Brown*); holotype in BM.

Distribution: Ward I., S. Aust., to Gabo I., Vic., and around Tasmania.

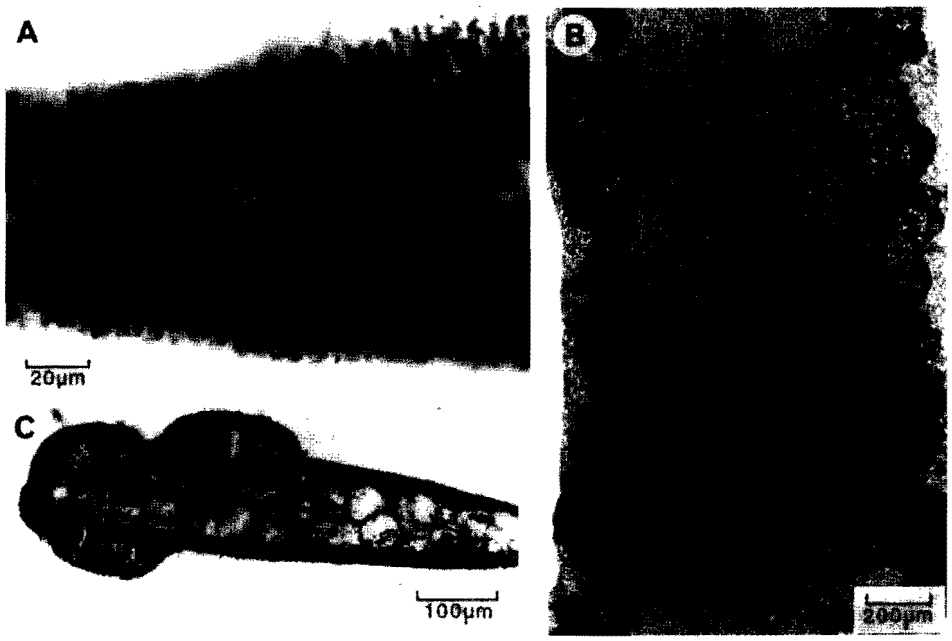


Fig. 157. A–C. *Leptophyllis conferta* (**A**, AD, A34873; **B, C**, AD, A59265). **A.** Section of branch with spermatangial sori. **B.** Surface view of branch with tetrasporangial sori. **C.** Transverse section of branch with tetrasporangial sori.

Selected specimens: Ward I., S. Aust., 30 m deep (*Graske*, 22.vi.1988; AD, A59265). Elliston, S. Aust., 20 m deep outside bar (*Shepherd*, 14.v.1971; AD, A38688). Toad Head, West I., S. Aust., 13–16 m deep (*Shepherd*, 15.i.1966; AD, A30330). 12 km S of Vivonne Bay, Kangaroo I., S. Aust., 50–70 m deep (*Latz*, 24.xi.1968; AD, A33005). Seal Bay, Kangaroo I., S. Aust., drift (*Womersley*, 29.x.1966; AD, A31025). Robe, S. Aust., drift (*Womersley*, 11.xii.1969; AD, A34873). Stinky Bay, Nora Creina, S. Aust., drift (*Gordon*, 26.i.1967; AD, A31629). Port Fairy, Vic., drift (*Womersley*, 24.i.1967; AD, A31496). Cape Woolamai, Vic., 15–18 m deep S side (*Sorokin*, 16.ii.1990; AD, A60195). Walkerville, Vic., drift (*Sinkora* A2354, 7.iii.1977; AD, A48358). Gabo I., Vic., 18 m deep (*Shepherd*, 17.ii.1973; AD, A43495). Eddystone (Point), Tas. (*Perrin*, 11.x.1942; AD, A8953). Eaglehawk Neck, Tas., 12–15 m deep (*Kraft*, 12.xii.1993; AD, A63352). Fluted Cape, Bruny I., Tas., 16 m deep (*Shepherd*, 10.ii.1972; AD, A41514).

Cladhymenia conferta var. β *foliifera* Harvey (1859b, p. 306), from Southport, Tas. (*Stuart*), illustrated by Kützing (1864, p. 33, pl. 93e) appears to be a plant with young, proliferous leaflets.

Genus PTILONIA (Harvey)J. Agardh 1852: 773

Thallus erect, much branched essentially complanately with alternate, compressed, branches, tapering slightly from base to rounded apices, margins entire, axes thickened below; holdfast discoid. *Structure* uniaxial with an inconspicuous apical cell and the subapical cells each cutting off two pairs of periaxial cells, the first two at right angles with the lateral one developing into a longer filament, then a second pair with the lateral opposite the first longer lateral remaining shorter; the transverse periaxial cells contribute to the cortex. Cortex pseudoparenchymatous, of rounded cells with adjacent air spaces, with a prominent axial filament throughout becoming surrounded by a layer of small (rhizoidal) cells; outer cortex with larger, usually clear, slightly sub-surface, gland cells. Older axes thickened, at first centrally, by a cortical meristem.

Life history apparently biphasic, with the gametophytes arising from a crustose stage; tetrasporophytes unknown.

Reproduction. Gametangial thalli monoecious or dioecious. Carpogonial branches 3-celled, borne near branch tips or on short laterals on periaxial (supporting) cells. Gonimoblast filaments arising from the fertilized carpogonium (or hypogynous cell), developing a basal fusion cell and a dense, much branched, erect to spreading tuft bearing terminal clavate to ovoid carposporangia. Pericarp thick, ostiolate with short, branched, filaments lining the pore. Cystocarps ovoid, sessile or stalked. Spermatangia in sori over ends of branches, cut off via initials from outer cortical cells.

Type species: *P. magellanica* (Montagne)J. Agardh 1852: 774.

Ptilonia includes six species, two from southern Australia, two from New Zealand (Bonin & Hawkes 1988b), one (the type) from the subantarctic and one from Japan (Chihara & Yoshizaki 1978). *Ptilonia* was first described as a section of *Plocamium* by Harvey (1847, p. 124). Chihara & Yoshizaki (1978) considered *Ptilonia* was not distinct from *Delisea*, but this was refuted by Bonin & Hawkes (1988b). *Ptilonia* differs from *Delisea* in habit, having entire, smooth margined, branches in contrast to the dentate or spinose branches of *Delisea*, resulting from the lateral adhesion of the determinate laterals in the former.

KEY TO SPECIES OF *PTILONIA*

1. Mid to upper branches 2–4 mm broad ..... 1. *P. australasica*
1. Mid to upper branches 0.5–1.5 mm broad ..... 2. *P. subulifera*

1. **Ptilonia australasica** Harvey 1859b: 305, pl. 190A. J. Agardh 1876: 674. De Toni 1900b: 759. Guiler 1952: 85. Levring 1953: 516, figs 44, 45B–E. Lucas 1929a: 20. Lucas & Perrin 1947: 240, fig. 102. May 1965: 398. Reinbold 1898: 48. Sonder 1881: 30. Tisdall 1898: 512. Wilson 1892: 169.
Delisea australasica (Harvey)Chihara *ex* Chihara & Yoshizaki 1978: 387.

FIG. 158

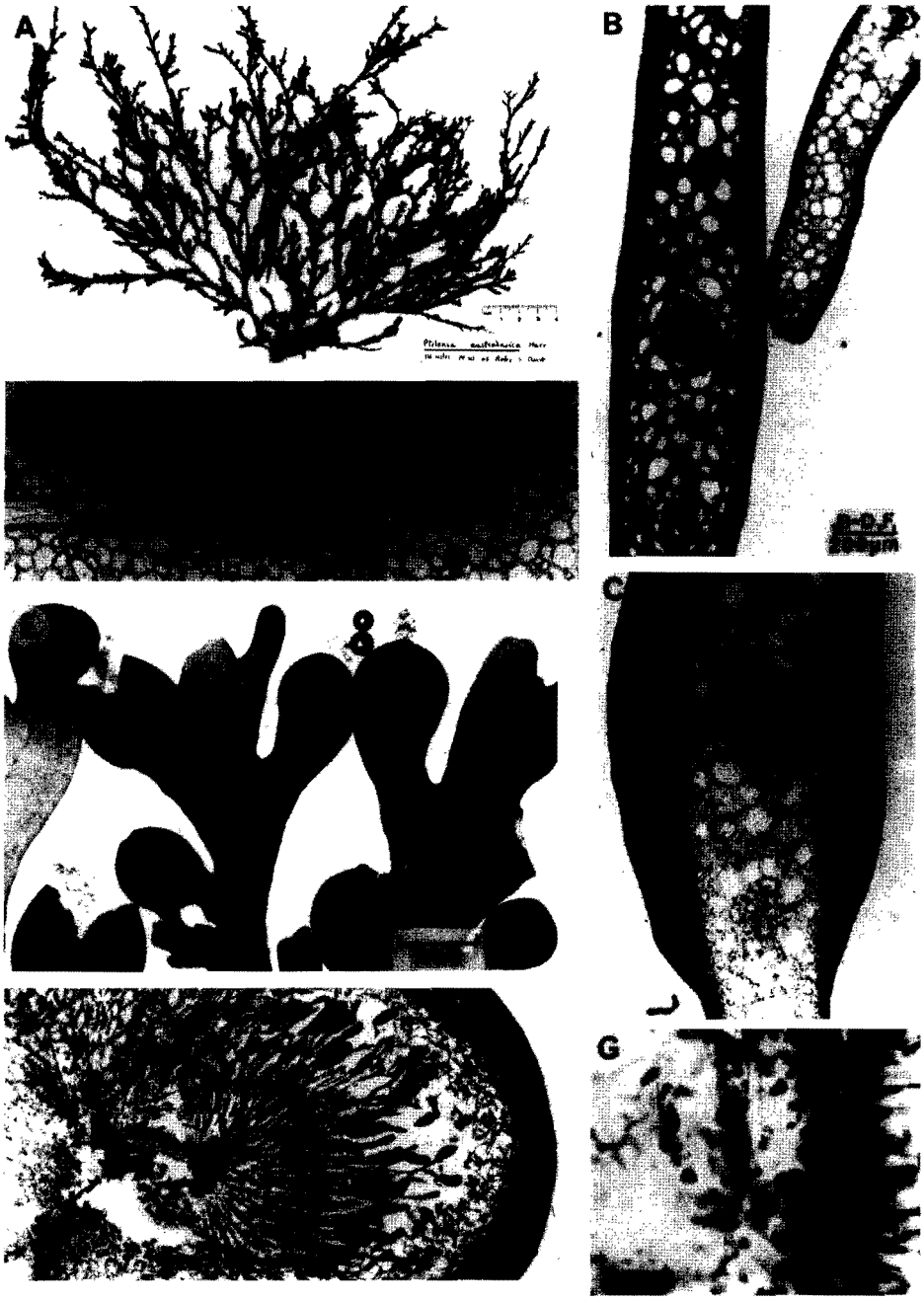


Fig. 158. *Ptilonia australasica* (**A, B, E,** AD, A33104; **C,** AD, A63194; **D, F,** AD, A60415; **G,** AD, A63988). **A.** Habit. **B.** Transverse sections of young and mid age branches. **C.** Transverse section of older branch with midrib. **D.** Longitudinal flat section of branch showing veins and parenchyma. **E.** Branches with cystocarps. **F.** Longitudinal section of cystocarp with carposporophyte. **G.** Section of branch with a spermatangial sorus.

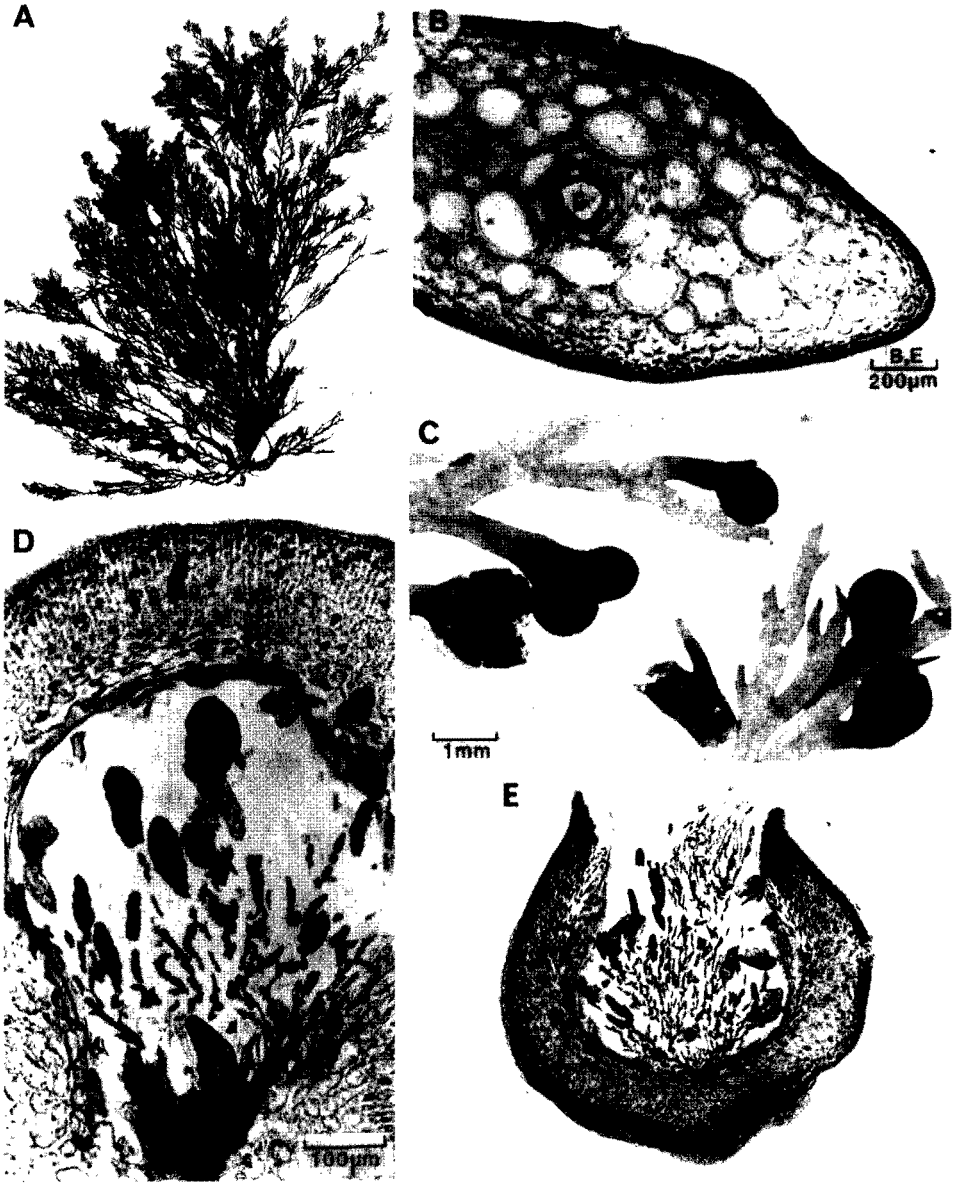


Fig. 159. *Ptilonia subulifera* (**A**, AD, A60747; **B, C,** AD, A25429; **D, E,** AD, A63931). **A.** Habit. **B.** Transverse section of thallus. **C.** Branches with cystocarps. **D.** Longitudinal section of a cystocarp showing basal fusion cell, gonimoblast filaments and pericarp. **E.** Longitudinal section of a cystocarp through the ostiole.

Thallus (Fig. 158A) medium red to dark red-brown, 10–30 cm high, essentially complanately and alternately marginally branched, axils rounded, apices obtuse; branches (1-) 2–4 (-5) mm broad, entire, often slightly basally constricted, older parts usually denuded. Holdfast discoid to lobed, 3–6 mm across, with one to several fronds; epilithic. *Structure* (Fig. 158B–D) uniaxial, apical cell inconspicuous, lateral periaxial filaments alternately longer and shorter on successive axial cells, axial filament prominent (Fig. 158C, D), becoming 60–90 (-200) µm in diameter, with a sheath of rounded to elongate rhizoidal cells; cortex compact, inner cells subspherical to ovoid, (25-) 50–100 µm in diameter, with intermixed smaller cells, outermost cortical cells 2–5 µm in diameter and L/D 1–2 in thallus section, with scattered larger, clear, gland cells in or just under the outer layer. Older axes with a secondary meristem (Fig. 158C), developing files of small cells from outer cortical cells, forming a midrib. Rhodoplasts discoid in outer cells, becoming ribbon like and branched in inner cells.

Reproduction. Gametangial thalli dioecious. Carpogonial branches unknown. Cystocarps (Fig. 158E) sessile on terminal leaflets or becoming stalked, ovoid, 1–2 (-3) mm in diameter, with a thick ostiolate pericarp. Carposporophyte (Fig. 158F) densely tufted, with a basal fusion cell, much branched gonimoblast filaments of slender, elongate, cells and single, terminal, clavate to elongate-ovoid, carposporangia 20–50 (-65) µm in diameter. Spermatangial sori near ends of branches, 1–2 mm across, with spermatangia (Fig. 158G) cut off from initials derived from outer cortical cells, elongate, 2–3 µm in diameter.

Tetrasporangia unknown (a doubtful record in Lucas & Perrin 1947, p. 239).

Type from Georgetown, Tas. (*Harvey*); lectotype in Herb. Harvey, TCD. (Alg. Aust. Exsicc. 244J).

Distribution: West I., S. Aust., to Walkerville, Vic., and around Tasmania.

Selected specimens: Amphitheatre Rock, West I., S. Aust., 13 m deep (*Shepherd*, 1.i.1969; AD, A33253). 22 km NW of Robe, S. Aust., 40 m deep (*Shepherd*, 20.xi.1968; AD, A33104). 1.3 km off Cape Northumberland, S. Aust., 15 m deep (*Turnbull*, 30.ix.1975; AD, A46612). 16 km NW of Cape Bridgewater, Vic., 80–100 m deep (*Watson*, 16.v.1969; AD, A34761). Cape Woolamai, Vic., 15–18 m deep, S side (*Sorokin*, 16.ii.1990; AD, A60198). Walkerville, Vic., drift (*Sinkora* A2316, 7.iii.1976; AD, A48379). Little Squally Cove, Deal I., Bass Strait, 15–28 m deep (*Houridis*, 12.iii.1993; AD, A63194). Granville Harbour, Tas. (*Blackman*, 28.i.1979; AD, A58501). Low Head, Tas., drift (*Perrin*, June 1943; AD, A8469). Bicheno, Tas., 17 m deep (*McCauley*, 26.ii.1990; AD, A60415). Bluestone Bay, Freycinet Pen., Tas., 6 m deep (*Brown et al.*, 4.xi.1982; AD, A56271). Marion Bay, Tas., 3–5 m deep (*Shepherd*, 13.ii.1970; AD, A35600). Arch Rock, E of Ninepin Point, Tas., 1–10 m deep (*Andrews*, 21.x.1994; AD, A64004); 0–5 m deep (*Sanderson*, 21.x.1994; AD, A63988). Fluted Cape, Bruny I., Tas., 16 m deep (*Shepherd*, 10.ii.1972; AD, A41522).

P. australasica is a deep-water species on rough-water coasts.

2. **Ptilonia subulifera** J. Agardh 1890: 46. De Toni 1900b: 759. Guiler 1952: 85. Levring 1953: 517, figs 45A, 46. May 1965: 398. Tisdall 1898: 512. Wilson 1892: 169.
Ptilonia intermedia Lucas 1913: 59; 1929a: 20. De Toni 1924: 364. Guiler 1952: 85. May 1965: 398.
Delisea subulifera (J. Agardh)Chihara *ex* Chihara & Yoshizaki 1978: 387.

FIG. 159

Thallus (Fig. 159A) medium to dark red-brown, 10–35 cm high, essentially complanately and alternately marginally branched, axils acute, apices narrowly rounded, branches compressed, 0.5–1 mm broad near apices, 1–1.5 mm broad in mid parts, 2–3 (-4) mm broad near the thickened (subterete) base, usually denuded below. Holdfast discoid-conical, 3–6 (-10) mm across, usually with a single stipe; epilithic. *Structure* uniaxial (Fig. 159B), apical cell inconspicuous, lateral periaxial filaments alternating slightly on adjacent axial cells, axial filament becoming 80–200 µm in diameter with a surrounding layer of rounded rhizoidal cells, cortex compact, inner cells subspherical to ovoid, 80–160 µm in diameter, with intermixed small rounded cells, outermost cortical cells 2–5 µm in diameter and L/D 1–1.5 in thallus section, with scattered, inconspicuous, larger gland cells. Older axes with a well-developed secondary cortex. Rhodoplasts discoid in outer cells, ribbon like and branched in inner cells.

Reproduction. Carpogonial branches little known (see Levring 1953, fig. 45A). Cystocarps (Fig. 159C) globular to ovoid, 1–1.5 mm in diameter, sessile on upper branchlets or appearing stalked, with a thick ostiolate pericarp (Fig. 159E). Carposporophyte (Fig. 159D, E) densely tufted, with a basal fusion cell, much branched gonimoblast filaments of slender elongate cells, and single, terminal, clavate to elongate-ovoid carposporangia 40–60 μm in diameter. Spermatangia unknown.

Tetrasporangia unknown.

Lectotype from Port Phillip, Vic. (*Wilson*, 18.i.1890); in Herb. Agardh, LD, 37493.

Distribution: 8 km S of West I., S. Aust., to Walkerville, Vic., and around Tasmania.

Selected specimens: 8 km S of West I., S. Aust., 20–25 m deep (*Edyvane*, 11.vii.1982; AD, A60747). Port Elliot, S. Aust., drift (*Womersley*, 26.xi.1961; AD, A25429). Robe, S. Aust., drift (*Womersley*, 20.iv.1969; AD, A34075). 11 km off Cape Northumberland, S. Aust., 48 m deep (*Shepherd*, 6.v.1975; AD, A46323). Off Barwon Heads, Vic., 20 m deep (*Macpherson*, 15.v.1963; AD, A28697). Cape Woolamai, Vic., 15–18 m deep, S side (*Sorokin*, 16.ii.1990; AD, A60199). Walkerville, Vic., drift (*Sinkora* A2566, 17.iii.1979; AD, A60984). Low Head, Tas., drift (*G. & F. Perrin*, May 1937; AD, A8985). Arch Rock, E of Ninepin Point, SE Tas., 5–8 m deep (*Sanderson*, 21.x.1994; AD, A63931).

P. subulifera is also a deep-water species found on rough-water coasts, differing from *P. australasica* in width of branches.

FAMILY NACCARIACEAE Kylin 1928: 11

Thallus (gametophyte) erect, profusely and irregularly radially branched, mucilaginous, branches terete. *Structure* uniaxial, axial filament conspicuous throughout, with 2 or 4 periaxial cells producing a cortex of ovoid cells and often with descending rhizoids. Rhodoplasts small, discoid, parietal.

Tetrasporophyte (where known) prostrate, of branched filaments.

Life history triphasic with heteromorphic gametophytes and tetrasporophytes.

Reproduction. Gametangial thalli monoecious or dioecious. Carpogonial branches 3–5-celled, borne on basal cells of laterals, with nutritive cells on the hypogynous or other cells. Fertilized carpogonia usually fusing with the hypogynous cell and producing gonimoblast filaments which ramify between the cortical filaments forming a diffuse (discrete in *Reticulocaulis*) carposporophyte with carposporangia terminal or in short chains; pericarp absent. Spermatangia formed on the outer cortex in superficial clusters.

Tetrasporangia (where known — Boillot & L'Hardy-Halos 1975) borne terminally or laterally on uniseriate filaments, tetrahedrally divided.

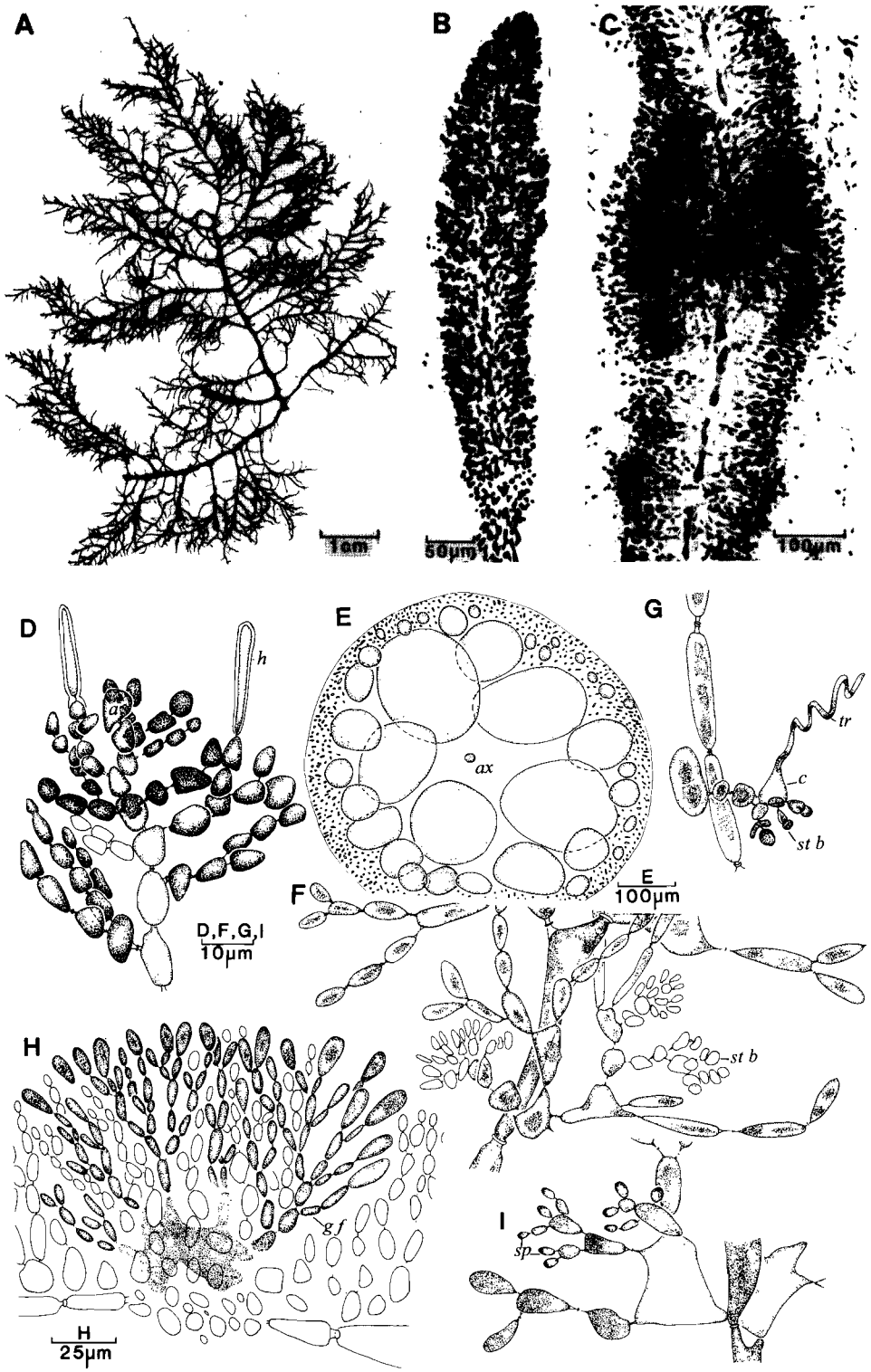
A family of three genera, *Naccaria* Endlicher with several species, *Atractophora* Crouan & Crouan (1848, p. 371) from Europe, and *Reticulocaulis* Abbott (1985) from Hawaii, differing from (and possibly not related to the Bonnemaisoniaceae) by the carposporophyte being (usually) diffuse, and lacking any pericarp.

Genus NACCARIA Endlicher 1836: 6

Thallus (gametophyte) erect, mucilaginous, much branched irregularly radially, branches terete, holdfast discoid. *Structure* uniaxial, with a conspicuous apical cell and each axial cell producing two opposite (and at opposite ends) periaxial cells, mainly on a ¼ spiral, then developing branched periaxial filaments which form a cortex of large inner cells and smaller outer cells; descending rhizoidal filaments formed from periaxial cells.

Tetrasporophyte prostrate, of branched filaments.

Fig. 160. *Naccaria naccarioides* (**A**, AD, A29627; **B–I**, AD, A29942). **A.** Habit. **B.** Lateral branch with periaxial filaments from central axis and rhizoids at base. **C.** Branch with a carposporophyte. **D.** Apex with periaxial filaments and hairs. **E.** Transverse section of older branch. **F.** Lateral filaments with accessory clusters. **G.** Carpogonial branch with accessory filament on hypogynous cell. **H.** Mature carposporophyte with intermixed vegetative filaments. **I.** Spermatangia on a determinate lateral.


A
1cm
B
50µm
C
100µm
D
h
D,F,G,I
10µm
E
ax
E
100µm
G
tr
c
st b
F
st b
H
gf
H
25µm
I
sp

Life history (where known) triphasic, with heteromorphic gametophytes and tetrasporophytes, or a filamentous stage giving the gametophyte directly.

Reproduction. Gametangial thalli monoecious or dioecious. Carpogonial branches 3- or 4-celled with the hypogynous cell bearing nutritive cells, borne on inner periaxial cells or upper cells of the rhizoidal filaments. Fertilized carpogonium fusing with the hypogynous cell and developing gonimoblast filaments which ramify between the cortical filaments forming a diffuse carposporophyte with terminal ovoid carposporangia, the whole swelling the branch; pericarp absent. Spermatangia in clusters, cut off from outer cortical cells.

Tetrasporophyte (of *N. wigghii* — Jones & Smith 1970) prostrate, minute, of branched filaments producing terminal, tetrahedrally divided, sporangia.

Type species: *N. wigghii* (Turner)Endlicher, from Europe.

A genus of about 5 species (Millar 1990, p. 378), with one present on southern Australian coasts.

Naccaria naccarioides (J. Agardh)Womersley & Abbott 1968: 177, figs 1–13, pl. 1. Millar 1990: 378, figs 33–35. Millar & Kraft 1993: 34.
Ardissonea naccarioides J. Agardh 1899: 99.
Neoardissonea naccarioides (J. Agardh)Kylin 1956: 127. May 1965: 385.

FIG. 160

Thallus (Fig. 160A) brown-red, mucilaginous, 4–14 cm high, much branched irregularly radially for 4–5 orders; branches terete, 100–200 μm in diameter near apices, 0.5–1 mm in diameter in main branches and 1–1.5 mm near the base. Holdfast discoid, 1–4 mm across, with one to a few axes; epilithic. *Structure* uniaxial (Fig. 160B–D), with a dome shaped apical cell dividing obliquely, subapical cells each cutting off first a periaxial filament (Fig. 160D) on an irregular spiral of ¼, and 8–10 axial cells from the apex cutting off a second, posterior and usually opposite, periaxial cell; periaxial filaments subdichotomous, directed towards branch apices, the inner cells becoming ovoid and in lower branches 40–80 μm in diameter, decreasing to the outer cortex with outermost cells ovoid and 4–6 μm in diameter; inner periaxial cells producing simple or branched rhizoids surrounding the axial filament which becomes 10–20 (-30) μm in diameter; older branches (Fig. 160E) pseudoparenchymatous in section, hairs common near apices; branches originate from periaxial cells. Rhodoplasts discoid, ribbon like in inner cells.

Reproduction. Gametangial thalli monoecious. Carpogonial branches (Fig. 160G) originating near branch apices, borne on inner cells of periaxial filaments or on the rhizoids, usually 4-celled with the hypogynous cell bearing dense clusters of nutritive cells, trichogyne spirally contorted; clusters of short branched filaments often present (Fig. 160F). Carposporophyte with a branched fusion cell producing clustered gonimoblast filaments between the cortical filaments (Fig. 160C, H), the terminal (and often subterminal) cells forming clavate carposporangia 8–12 μm in diameter; carposporophytes moderately discrete, slightly swelling the branches. Spermatangia (Fig. 160I) in patches on upper branches, cut off from outer cortical cells, ovoid, 2–3 μm in diameter.

Tetrasporophyte unknown.

Holotype from Western Port, Vic. (*Wilson*, 23.i.1893); in Herb. Agardh, LD, 31996.

Distribution: Gunyah Beach, Coffin Bay Pen., S. Aust., to Western Port., Vic., around Tasmania, and Coffs Harbour, N.S.W. (Millar 1990, p. 379).

Selected specimens: Gunyah Beach, Coffin Bay Pen., S. Aust., uppermost sublittoral (*Ricci*, 29.xi.1990; AD, A60806). Victor Harbor, S. Aust., drift (*Abbott*, 2.xi.1965; AD, A29627). Vivonne Bay, Kangaroo I., S. Aust., 0–6 m deep on jetty piles (*Kraft & Min-Thein*, 4.xii.1971; AD, A41421). Margaret Brock Reef, Cape Jaffa, S. Aust., 4–5 m deep in caves (*R. Lewis*, 29.xi.1972; AD, A42917). Cape Northumberland, S. Aust., 15 m deep (*Shepherd*, 1.ii.1978; AD, A49148). Rocky Cape, N Tas., drift (*Gordon*, 18.i.1966; AD, A29942). Taroona, Tas., 3–6 m deep (*Shepherd*, 4.ii.1970; AD, A35171).

N. naccarioides appears to be confined to rough-water coasts, occurring in summer months in shallow water.

APPENDIX: Change of name for *Hildenbrandia expansa*

Dr Paul Silva has pointed out that *Hildenbrandia expansa* Womersley (1994, p. 145) is a later homonym of *Hildenbrandia expansa* Dickie (1874, p. 357) from St Paul's Rocks in the tropical Atlantic Ocean.

Hildenbrandia patula Womersley is here proposed as a substitute name for *H. expansa* Womersley.

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GLOSSARY

abaxial: on the side of the branch facing away from the axis.
accessory: additional to the normal branches or structures.
acuminate: tapering gradually to a sharp point.
acute: with a pointed apex or a narrow axil.
adaxial: on the side of a branch facing the axis.
adventitious: an organ or structure arising in an abnormal position.
agar: a phycocolloid (a sulphated polysaccharide) occurring in the cell walls of Rhodophyta, especially Gelidiales and Gracilariales.
alternate: with branches arising at different levels along an axis.
amphoroid: in the form of an amphora, a vessel with handles (branches) from the upper sides.
anastomosing: union of cells or filaments laterally to form a network.
anterior: towards the front or apex of a structure.
anticlinal: cell division by a wall perpendicular to the surface of the tissue (usually the outer layer of the thallus).
apical: the tip of a branch or structure.
apical plug: a muciferous plug situated at the apex of a tetrasporangium or bisporangium and blocking or helping to block a conceptacle pore in certain genera of Corallinales.
apomeiotic: formation of reproductive cells without meiosis.
apomictic: reproduction devoid of karyogamy and meiosis.
applanate: flattened and horizontally expanded.
arborescent: tree-like; in non-geniculate Corallinales, a term for a thallus composed of a distinct holdfast and stipe bearing flattened, ribbon-like to fan-shaped branches.
asexual: reproduction which does not involve sexual fusion of gametes or the occurrence of meiosis.
assimilatory: filaments or cells which contain photosynthetic plastids.
assurgent: inclined upwards (usually curved) from its origin.
attenuate: tapering gradually.
auxiliary cell: a cell which produces the carposporophyte following transfer to it of the zygote nucleus or one of its diploid progeny.
axial: pertaining to the axis or central core of a branch.
axile: situated on the axis of an organ.
axis: the main stem or a major branch of a thallus, usually bearing laterals.

binomial: a two word scientific name for an organism, comprising a genus name and a species name.
biphasic: with two phases in the life history.
bipinnate: doubly pinnate.
bisporangium (-a): a sporangium containing two spores.
bispore: a spore from a sporangium bearing only two spores.

caducous: dropping off early.
calcified: with deposition of calcium carbonate in or on cell walls of the thallus.
calcified compartment: a structure in genera of Sporolithaceae (Corallinales) that is derived from the wall of a tetrasporangial initial and houses a tetrasporangium.
calcite: the hexagonal crystalline form of calcium carbonate.
canaliculate: with a channel along the length of the organ.
cap layer: one or two layers (polysaccharide) over each side of the pit-plug between two cells.
carpogonial branch/filament: the uniseriate branch, two to several cells long, which bears the terminal carpogonium.
carpogonium: the female reproductive cell (oogonium), usually bearing a trichogyne, in the Rhodophyta.

carposporangia: the reproductive cells produced by the carposporophyte, and which usually give rise to the tetrasporophyte.
carpospore: the diploid spore released from a carposporangium.
carposporophyte: the post-fertilization phase of the Florideophyceae, comprising gonimoblast filaments bearing carposporangia.
cartilaginous: firm and tough but somewhat flexible.
cell-fusion: linkage between cells of two vegetative filaments in which portions of the cell walls break down and the protoplasts then apparently fuse. Not to be confused with **fusion-cell.**
cheilosporoid: with segments as in *Cheilosporum*, compressed with two upper (usually acute) lobes.
chevron: the form of a broad inverted V.
clavate: club-shaped, broadest near the apex.
coherent: closely associated laterally.
columella: a structure formed from a group of persistent but often senescent sterile cells, arising from the floor of a tetrasporangial/bisporangial conceptacle in some Corallinaceae.
columnar: in non-geniculate Corallinales, an elongate vegetative cell in which the end walls (those possessing primary pit-connections) are much shorter than the side walls, and cell length is substantially more (usually 2–4 times) than cell diameter.
complanate: flattened or branched in one plane.
compressed: flattened but not strongly so, with an ovate cross section.
concavo-convex: division of cells so that the two resultant cells have concave and convex walls.
conceptacle: a flask-shaped cavity, opening to the surface, containing reproductive organs.
conceptacle primordium: a group of initials from which a conceptacle develops.
connecting filament: a filament, usually aseptate, through which the zygote nucleus is transferred from the carpogonium (or nearby cell) to the auxiliary cell.
contiguous: adjacent filaments or cells (e.g. in non-geniculate Corallinales) that are touching and aligned in a more or less parallel manner.
converging: approaching and finally merging together.
core: in non-geniculate Corallinales, the region of a monomerous thallus in which filaments or portions of filaments are orientated more or less parallel to the thallus surface.
coriaceous: leathery, somewhat tough.
cortex: the outer layer of cells or tissue of a thallus, outside the medulla.
corticate: covered with an outer layer, usually of smaller cells.
crenulate: scalloped, with small rounded teeth.
cruciate: divided into four by cross walls, visible as a cross (in tetrasporangia).
crustose: forming a firm to hard crust or layer on the substrate.
cuneate: wedge-shaped.
cystocarp: reproductive structure in Rhodophyta consisting of the carposporophyte and surrounding tissue (usually the pericarp).

decumbent: reclining or prostrate but with the apex or margin ascending.
decussate: divided into pairs alternately at right angles; a sporangium with cross walls in different planes.
dendroid: tree like, with a trunk and spreading branches above.
dentate: with marginal teeth.
determinate: having a fixed limit to growth.
diaphragm: a regular monostromatic partition across the branch (in *Champia*).
dichotomous: branching into two equal parts by equal division at the apex.
diffuse (growth): growth in almost any part of the thallus, not localised.
digitate: branched like the fingers of a hand.
dimerous: a type of thallus construction in non-geniculate Corallinales involving two distinct groups of filaments that are produced successively and are orientated more or less at right angles to one another.

dimorphic: with two forms.
dioecious: having the male and female gametes produced on different plants.
discoid: forming a flattened disc with a rounded outline.
discrete: separate, not joined or coalescent.
distichous: in two opposite rows along an axis or branch and thus lying in one plane.
divaricate: branching at wide angles.
dorsiventral: having distinct dorsal and ventral sides.

element: in nomenclature, a single (or more if small) specimen, illustration, or herbarium preparation (sheet, box, packet, jar, microscope slide) used for purposes of typification.
encrusting: crust-like; in non-geniculate Corallinales, a term for a thallus that is crustose and flattened or sleeve-like and devoid of protuberant or lamellate branches.
endophyte: an organism living within the tissues of a host plant.
epigenous: growing upon (but necessarily firmly attached to) a substrate.
epilithic: living attached to rock or stones.
epiphytic: living attached to a plant, but not parasitic.
epithallial cell: in the Corallinales, a cell formed outwardly from a division of a vegetative initial or from an asymmetric transverse division of a primigenous cell of a dimerous thallus.
epizoic: living attached to an animal.
eulittoral: the main intertidal zone between the sublittoral (usually dominated by large brown algae) and the littoral fringe (usually dominated by littorinid snails).

fastigiate: with branchlets clustered, erect and subparallel, but tapering above.
fibrous: divided into slender fibres.
filament: a long row of cells attached end to end, usually uniseriate, or a very elongate and narrow coenocytic cell or part thereof.
flanged: slightly projecting longitudinal rims on a branch.
flared: spread out or broadened above the base.
flexed: bent above its origin.
flexuous: axes or branches with zig-zag development, usually with alternate branches on each side.
foliose: broadly flattened and leaf-like; in non-geniculate Corallinales, a term for a thallus that consists of several to many flattened lamellate branches arranged at various angles to one another.
fragmentation: a mode of vegetative reproduction in which a thallus breaks into two pieces, both of which then continue to grow independently.
frond: the thallus or a main branch thereof.
fruticose: shrubby; in non-geniculate Corallinales, a term for a thallus that has protuberant branches that are usually branched and are mostly over 3 mm long.
furcate: divided into two, usually fairly equally, but not strictly dichotomous.
fusiform: spindle shaped, thicker centrally and tapering to both ends.
fusion cell: an enlarged, often irregular, cell formed from the zygote by fusion with other adjacent cells.

gametangium (-a): in red algae, a unicellular gamete-producing structure. Female gametangia are termed carpogonia; male gametangia are termed spermatangia.
gametophyte: the multicellular sexual (N) gamete-producing phase of the life history of a plant.
generation: one of the two phases (gametophyte or sporophyte) in the life history of a plant.
geniculate: possessing genicula.
geniculum (-a): the uncalcified segments between the calcified intergenicula in Corallinales.
gland cell: a small, usually subspherical, cell with highly refractive contents, darkly staining, which may function in secretion or storage.
globose (globular): nearly spherical.

globule: a globular inclusion in a cell.
gonimoblast filament: a filament, usually becoming multicellular and branched, produced by the zygote or fusion cell and which produces the carposporangia.

habit: the morphological form of a plant.
habitat: the environment in which an organism lives.
hair: elongate, unicellular or multicellular and uniseriate, extensions, not or only slightly pigmented, tapering or cylindrical.
hamate: hooked at the tip.
haustorium (-a): a specialised cell that is presumed to absorb nutrients for a host organism.
hemiparasitic: partially but not completely parasitic.
heteromorphic: with morphologically different gametophyte and tetrasporophyte phases.
heterotrichous: having a thallus composed of distinct prostrate and erect portions.
heterotypic synonyms: in nomenclature, synonyms based on different nomenclatural types.
holdfast: a basal attachment organ.
holotype: the single specimen or sheet on which an author bases the description of a new taxon.
homotypic synonyms: in nomenclature, synonyms based on the same nomenclatural type.
hypogynous cell: the cell immediately below the female carpogonium.

imbricate: overlapping, like tiles on a roof.
indeterminate: capable of unlimited growth.
inflexed: bent inwardly.
initial: the cell from which other specialised cells originate.
intercalary: situation or growth occurring between the apex and base.
intergeniculum (-a): the calcified segments between uncalcified genicula in branches of certain Corallinales.
isobilateral: capable of being divided into two similar halves in one plane only.
isodiametric: with approximately equal diameters or dimensions.
isomorphic: organisms with the gametophyte and sporophyte of similar morphology and size.
isotype: a duplicate specimen to the holotype.

janioid: branched as in *Jania*, subdichotomously with terete branches.

L/B: length divided by breadth.
lacerate: torn or irregularly cleft.
L/D: length divided by diameter.
lamellate branch: in non-geniculate Corallinales, a more or less flattened or curved branch that usually has a dorsiventral internal organisation.
laminate: flattened to form a lamina.
lanceolate: lance-shaped; long and narrow, tapering to both ends, especially to the upper.
lateral: from the edges of a compressed or flat structure.
layered: in non-geniculate Corallinales, a term for a thallus that consists of several to many lamellate branches arranged in horizontally orientated layers.
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 history: the sum of an organism's morphological, cytological and reproductive phases.
linear: narrow, with parallel sides and several times longer than broad.
longitudinal section: a thallus section cut along the axes of one or a parallel group of filaments.
lumpy: a thallus that has short, swollen protuberances that are usually unbranched and are often crowded or contiguous.

macroscopic: structures seen clearly with the unaided eye.
medulla: the central region of a thallus, internal to 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: delicate and often transparent.
meristem: a region of cells actively dividing.
microscopic: small structures only seen clearly with a microscope.
moniliform: arranged like a string of rounded beads.
monoecious: producing male and female gametes usually in separate structures but on the same individual.
monomerous: a type of thallus construction in non-geniculate Corallinales involving a single pseudoparenchymatous system of repeatedly branched filaments forming a core in which filaments are orientated more or less parallel to the thallus surface and a peripheral region in which portions of filaments become orientated more or less perpendicular to the thallus surface.
monopodial: growth by means of a continuous apical growing point.
monostromatic: single layered, usually only one cell thick.
mucilaginous (mucoid): slimy, with surface and/or internal mucilage.
multiaxial: a thallus formed of several to many axial filaments, all with apical or subapical growth.
multifid: cleft into many branches or segments.
multinucleate: with many nuclei in each cell.

nemathecium: a raised area on the thallus surface containing reproductive organs, often among paraphyses.
node: the position on an axis or branch where laterals arise.
nom. cons.: nomen conservandum, or a name conserved according to the International Code of Botanical Nomenclature.
nomenclatural type: the single specimen or other element of a taxon on which its name is based.
non-geniculate: lacking genicula.
nutritive cells (filaments): cells or filaments supplying nutrition to other cells (e.g. the developing carposporophyte), usually darkly staining.

obovoid: egg-shaped, but broadest near the upper end (a three-dimensional term).
obtuse: blunt or rounded at the apex.
orbicular: a flat structure with a circular outline.
ostiole: the pore-like surface opening to a reproductive structure (e.g. a cystocarp).
ovate: egg-shaped in outline, broadest near the base (a two-dimensional term).
ovoid: egg-shaped, often broadest near the base (a three-dimensional term).

palisade cells: rows or tiers of elongate cells, usually on the surface of tissues, with primary pit-connections on the short basal wall; however, in non-geniculate Corallinales, the term covers elongate vegetative cells in which the end walls (those possessing primary pit-connections) are much longer (usually 2–4 times) than the side walls, and cell length is substantially less than cell height or diameter.
paraphyses: sterile filaments, usually uniseriate, on the thallus surface or within conceptacles.
parasite: an organism growing on and dependent on the host for its nutrition.
parenchymatous: a tissue of thin-walled, more or less isodiametric cells, derived by division in different planes.
parietal: adjacent to the inner side of a cell or structure.

partition: a cross structure across an otherwise hollow branch, usually a few cells thick.
pedicel: the stalk of a reproductive organ.
pedicellate: with a cellular stalk, usually applied at the microscopic level.
percurrent: extending from base to apex of a thallus as one or more well-developed axes.
perennial: a thallus or part thereof which lasts for several years.
periaxial cell/filament: a cell or filament cut off from an axial cell but (shorter and) orientated obliquely or at right angles to it.
pericarp: the protective tissue around or outside the carposporophyte, derived from the cortex.
pericentral cell: a cell cut off from an axial cell and remaining similar in size and orientation to the axial cell.
peripheral region: in non-geniculate Corallinales, the region of a monomerous thallus in which filaments or portions of filaments become orientated more or less perpendicular to the thallus surface.
peripheral: surrounding, either inside or outside, a round tissue.
pinna(-e): a lateral of a distichous, regularly branched, frond.
pinnate: with laterals, ramuli or segments arranged along each side of an axis or branch.
pit-connection: a cytoplasmic strand connecting two adjacent cells through a pit in their wall.
pit-plug: a lens-shaped plug filling the pit-connection, consisting of a proteinaceous central core and often one or two polysaccharide caps.
plastid: the photosynthetic organelle within a cell, carrying chlorophyll and other pigments.
plumose: feathery.
polychotomous: division at one point into several subequal branches.
polyspore: one of many spores in a polysporangium, homologous to a tetrasporangium.
polystromatic: with several layers or stroma.
pore: the opening above a reproductive structure (Corallinales).
pore canal: a canal in a conceptacle roof through which spores or gametes pass.
pore-plate: the part of a multiporate conceptacle (Corallinales) containing the pores and pore canals.
postigenous filament: any of the filaments in a dimerous thallus that arise at right angles from cells of primigenous filaments.
primary: the first part developed.
primary pit-connection: a pit-connection between adjacent cells of the same filament.
primigenous filament: any of the filaments that are directly traceable to the germinating spore and collectively form the unistratose layer in a dimerous thallus.
procarpic: close association of the supporting cell, carpogonial branch, and auxiliary cell in the one branch system.
procumbent: lying along the substrate.
proliferous: bearing branchlets as irregularly placed offshoots.
propagule: a multicellular vegetative structure, usually of particular form, that is capable of growing into a new thallus after detachment from the parent plant.
prostrate: lying flat on the substrate.
protuberant: protruding or bulging out from an organ or thallus.
pseudolateral: a hair or branch system displaced to a lateral position.
pseudoparenchymatous: parenchyma-like due to lateral adherence or interweaving of filaments but without cell divisions in all planes.
pulvinate: hemispherical or cushion-shaped, with a broad base.
pustule: a blister or pimple-like structure.
pyriform: pear-shaped, attached at the narrower end.

radial: on the radii of the structure or around an axis.
ramulus(-i): lesser or ultimate branchlets.
reflexed: bent backwards or downwards.
refractive: contents of a cell which appear dense and uniform in transmitted light, usually darkly staining.

reticulum: in the form of a net.
retrorse: turned or projecting backwards.
rhizoid: a single- or few-celled (without differentiation) attaching or absorptive structure or produced from inner cells.
rhodolith: in the Corallinales, an unattached, commonly nodular thallus that develops as a result of fragmentation or envelopment of a stone or other object.
rhodoplast: the photosynthetic plastid of the Rhodophyta, with single thylakoids which bear the phycobilin pigments.
rosette: with a ring of small cells around the margin of a larger inner cell.
rostrate: with a beak, narrowed into a slender tip.

saccate: in the form of a sac or cavity.
schizogenous: developed by splitting of the tissue.
secondary pit-connection: a pit-connection between cells of two adjacent filaments.
secretory cell: a specialised cell which secretes mucilage.
secund: bearing laterals more or less in a row on one side of a branch.
segment: a unit of a constricted branch.
septate: with cross walls to the cells or filaments.
seriate: arranged in a series on an axis.
serrate: marginally toothed with teeth pointing forwards.
sessile: attached directly to the substrate without a distinct holdfast and stipe; not stalked.
sheath: the surrounding tissue of an organ.
simple: unbranched or undivided.
sinuous: with a wavy margin.
sinus: the recess between two structures.
solitary: single, only one from the same place.
sorus(-i): a cluster of reproductive organs, occurring as a surface patch or slightly raised group.
spathulate: elongate, with the end broader and tapering basally.
spermatangia: the cells which contain or cut off the spermatia.
spermatia: the non-motile male cells of the Rhodophyta, usually without a cell wall.
spine: a stiff, sharp-pointed projection on a cell or tissue.
splaying: spreading laterally or outwards.
sporangia: spore-producing cells or structures.
sporangial complex: in the Sporolithaceae, a reproductive structure consisting of a sporangium within a calcified compartment that in turn is enveloped by a group of filaments that differ in appearance from ordinary vegetative filaments.
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.
stellate: with the form of a star, with numerous projections from a central region.
stipe: the stalk, lying between the holdfast and the blade or frond of the thallus, or bearing the primary branches.
stolon: a prostrate or creeping axis, lying on the substrate, from which erect branches arise.
stoloniferous: stolon-like or stolon-bearing.
strut: in non-geniculate Corallinales, a branch that grows downward from the ventral surface of a thallus and aids in support.
subapical: shortly below the apex; one (or more) cells below the apex.
subdichotomous: almost dichotomous but not truly so.
subepithallial initial: in the Corallinales, a meristematic cell situated beneath an epithallial cell.
sublittoral: the photic zone below the eulittoral region, from about mean low tide level to the lower limit of algal growth.
subspherical: almost spherical.
supporting cell: the cell which bears one or more carpogonial branches.
synchronous: simultaneous growth of branches.

syntype: one of the specimens used by the author when no holotype was designated, separate from one selected as lectotype.

terete: cylindrical and usually slightly tapering.
terminal: the end cell (or tissue) of a chain.
tetrahedral: a four-sided figure, as in tetrahedrally divided tetrasporangia.
tetrasporangium: a meiosporangium containing four spores, usually in a distinctive arrangement.
tetrasporocyte: the protoplast within a developing tetrasporangium that divides to produce four spores.
tetrasporophyte: the diploid generation which produces tetrasporangia.
thallus: the relatively simple plant body of a non-vascular plant.
thylakoid: a flattened sac-like membranous structure associated with photosynthetic pigments, within the plastids.
tier: a regular row or series (of cells).
transverse: from the sides of a compressed or flat structure.
traversing nutritive cells: elongate cells (or filaments) between the carposporophyte and pericarp (in *Gracilaria*), darkly staining and probably nutritive in function.
trichocyte: in the Corallinales, a specialised, sometimes hair-producing cell that is usually larger in size or has thicker walls or more deeply staining contents as compared to other vegetative cells.
trichogyne: the slender prolongation from the carpogonium to which spermatia become attached.
trichotomous: branching equally in three's.
trimorphic: with three morphological forms.
triphasic: with three phases in the life history.
type: the specimen on which a species (or lesser category) is based (see holotype, isotype), or the species name which provides the basis of the genus; similarly for higher taxa.
typification: in nomenclature, the process of designating a nomenclatural type.

ultrastructure: the fine structure of cells as seen in the electron microscope.
unconsolidated: in non-geniculate Corallinales, a term for a thallus that consists partly or entirely of filaments that are not pseudoparenchymatously united.
uniaxial: with a single axis or central filament within the thallus.
unilateral: branched on one side of the axis or branch.
uninucleate: with a single nucleus in the cell.
uniporate: with a single pore.
uniseriate: arranged in a single row or series, not more than one cell broad.
unistratose: single-layered.
urceolate: shaped like an urn; hollow and contracted at the mouth.

verrucose: covered with wart-like growths.
verticillate: structures (usually branchlets) arranged in a ring or whorl around an axis.
vesicle: a sac- or bladder-like structure, often partly filled with gas, sometimes forming a floatation organ.

warty: verrucose; covered with wart-like protuberances.

zonate: with parallel cross walls dividing the spore or tissue into zones.
zygote: the diploid cell resulting from fusion of gametes.

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