THE MARINE BENTHIC FLORA
OF
SOUTHERN AUSTRALIA

Part IIIC

by

H.B.S. WOMERSLEY
Cover photograph:

The beach at Bridgewater Bay, Victoria, with drift of *Amoenotheumann planktonicum*, April 1954.
THE MARINE BENTHIC FLORA OF SOUTHERN AUSTRALIA

RHODOPHYTA — Part IIIC

Ceramiales – Ceramiaceae, Dasyaceae

H.B.S. Womersley
The Botanic Gardens of Adelaide and State Herbarium, and the Department of Botany, University of Adelaide, South Australia

with various co-authors

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To

my wife, Alleyne

in appreciation
PREVIOUS PARTS

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PREFACE

Part IIIC of this Marine Benthic Flora of southern Australia covers 2 families (Ceramiaceae and Dasyaceae) of the large order Ceramiales, leaving the families Delesseriaceae and Rhodomelaceae to be covered in Part IIID.

Part IIIC is arranged similarly to previous parts, of which Part I included introductory chapters on the collection and preservation of marine plants, the history of phycology in southern Australia, and general aspects of their ecology and biogeography.

Parts I, II and IIIA included maps of the southern Australian coast showing most localities mentioned in the text, and should be referred to for specimen localities in IIIC, which as before are listed from west to east.

Co-authors of sections of Part IIIC are past monographers of taxa who have been able to read and comment on the present manuscript, which has been compiled largely by HBSW. They include:

**Mr Robert N. Baldock**, c/o Centre for Environmental and Recreational Management, University of South Australia, The Levels, S. Australia 5095 (as co-author of Bornetieae and sole author of Griffithsieae).

**Dr John M. Huisman**, School of Biological and Environmental Sciences, Murdoch University, Perth, W. Australia 6150 (Monosporeae).

**Dr Murray J. Parsons**, Herbarium, Landcare Research, P.O. Box 69, Lincoln, New Zealand (Dasyaceae).

**Dr Elise M. Wollaston**, 50 Knox Terrace, Skye, South Australia 5072 (various tribes of Ceramiaceae).
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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 Carolyn Ricci, and in 1996–1998 by Sarah Hotchkiss, to whom appreciation is expressed for technical assistance, especially herbarium curating, slide preparation, manuscript and herbarium checking, and photographic processing.

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 (SA Museum, Adelaide), Mr John Lavers (Penneshaw, Kangaroo Island) and Dr G.E. Edgar (Department of Zoology, University of Tasmania)]. 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 extensive collections to AD.

Much of the manuscript of Ceramiaceae has been read and commented on by Dr Gerald Kraft (University of Melbourne). Dr Christine Maggs (The Queen’s University, Belfast, N Ireland) advised concerning some of the species here ascribed to Callithamnion, and Dr Paul Silva advised on previous use of new names.

The text of Part IIIC was entirely set up on word-processor by Miss Tina Eadsforth (State Herbarium), and Latin diagnoses were kindly provided by Mrs Mary Marlow.

Illustrations are by the author unless otherwise stated. Some illustrations have been re-used (by courtesy of the Editor or Manager) from the following journals: Australian Journal of Botany; Australian Journal of Marine and Freshwater Research; Transactions of the Royal Society of South Australia; Botanica Marina; British Phycological Journal; Pacific Science (University Hawaii Press); and Phycologia. In each case permission has been obtained from the Editor or the publisher, and the relevant captions refer to the original author(s) followed by the journal, and the references give full details of the publication.

H.B.S. Womersley
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INTRODUCTION

Part IIIC of the Rhodophyta continues the accounts of Part I on the Chlorophyta and seagrasses (Womersley 1984), Part II on the Phaeophyta (Womersley 1987), and Parts IIIA (1994) and IIIB (1996) on the Rhodophyta (excluding Ceramiales) and includes the Ceramiales, families Ceramiaceae and Dasyaceae, as listed in the Synopsis (pp. 9, 10). Part IIID will cover the remaining two families, Delesseriaceae and Rhodomelaceae.

The layout of Part IIIC is similar to that of previous Parts. In descriptions, ranges of dimensions apply to mature parts, and cell dimensions include the cell wall or sheath; in citing specimens the standard herbarium abbreviations (Holmgren et al. 1990) are used; most of these are listed in Part I. All names applying to southern Australian taxa are referenced, but names in minor checklists and ecological accounts are not included. Several species, probably undescribed but without adequate reproductive material, have not been included. Unless otherwise stated in the captions, all figures are by the author (H.B.S.W.) with herbarium photographs mostly taken by Carolyn Ricci or Sarah Hotchkiss.

Sets of “Marine Algae of southern Australia” continue to be distributed from the State Herbarium to herbaria listed in Part II (p. 11).

Identification of many Rhodophyta, especially Ceramiaceae and Dasyaceae, is far from easy. As well as abundant collections of good reproductive specimens (at least of female-cystocarpic and tetrasporangial plants) and microscopic facilities, experience, time and patience are necessary. The similarity in form of many species in different tribes is often confusing, and details of their reproduction requires careful study; many tribes of the Ceramiaceae are separated on details of the female reproductive systems. Only rarely can certain identifications be made on general appearance and form, or on sterile material. Staining of nuclei has been by the Wittman (1985) method.

Due to these difficulties, keys to tribes, and often genera, are frequently not fully comprehensive and have to be modified as knowledge develops. This Flora is (as previous parts) a step forward in our understanding of the Rhodophyta, and much research is still necessary as indicated in the accounts of many taxa; in particular, differences between some of the tribes merit further study.
CERAMIALES
ORDER CERAMIALES Oltmanns 1904: 683

Thallus usually erect, occasionally prostrate wholly or basally, much branched to foliose, branches terete to compressed or flat, branching radial to distichous, attached by loose rhizoids or a rhizoidal disc. Growth terminal. Structure uniaxial, the axial cells producing (centrally or distally) 2–20 periaxial or pericentral cells in whorls, or with single uniseriate determinate laterals, and in many taxa developing a filamentous or pseudoparenchymatous cortex on the axial cells. Trichoblasts present or absent. Pit-plugs with no cap layers. Rhodoplasts discoid, often in chains in larger cells, or ribbon like.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes usually dioecious, occasionally monoecious; procarpic. Carpogonial branches normally 4-celled, borne on a supporting cell (in some taxa with sterile groups) which after fertilization usually cuts off an auxiliary cell (rarely with development directly from the supporting cell). Fusion between the fertilized carpogonium and auxiliary cell direct or via a connecting cell, the carposporophyte with or without a basal fusion cell, then producing branched gonimoblast filaments with all cells or terminal cells (or chains) forming carposporangia. Carposporophyte naked or surrounded by a pseudoparenchymatous pericarp one to a few cells thick, developed from pericentral or cortical cells adjacent to the procarp. Spermatangia produced singly or in clusters from cells of whorl branchlets, or as surface layers on male stichidia (on trichoblasts) or branchlets.

Tetrasporangia (rarely polysporangia or monosporangia) produced on whorl-branchlets or determinate laterals, or in stichidia or branchlets where they are cut off from pericentral or cortical cells, tetrahedrally or cruciate/decussately divided.

The Ceramiales is usually regarded as the most advanced order of the Rhodophyta, characterised by uniaxial structure, presence of pericentral or periaxial cells, and especially by the formation of the auxiliary cell directly from the supporting cell post-fertilization.

This Order includes over half the genera and species of Rhodophyta on southern Australian coasts.

KEY TO FAMILIES OF CERAMIALES

1. Branches uniseriate and without pericentral cells, periaxial cells usually present as a loose investment of the axes and only partially covering the axial cells unless they produce corticating filaments. Colourless trichoblasts usually absent. Carposporophyte naked with a gelatinous cover (in a few taxa with a few discrete surrounding filaments), but in some with loose protective vegetative filaments. Tetrasporangia lateral or terminal, naked or partially involucrate, borne on periaxial cells, filaments, or cortical cells .............................................................................................................. CERAMIACEAE

1. Branches uniseriate but with close, coherent, pericentral cells, with or without further cortication. Colourless (or pigmented) trichoblasts usually present, absent in Dasyaceae. Carposporophyte enclosed by a coherent, ostiolate pericarp formed of erect filaments from cells adjacent to the supporting cell. Tetrasporangia cut off from pericentral (or cortical) cells, enclosed within stichidia or branchlets .................................................. 2

2. Axes sympodially developed, pericentral cells produced in a spiral clockwise manner (Dasya) or in alternating sequence (Heterosiphonia, Thuretia); trichoblasts absent but rhodoplastic pseudolaterals present; branching with walls of upper cells basally attached. Spermatangia on stichidia-like branches of the pseudolaterals,
16

CERAMIACEAE

Tetrasporangia in stichidia on the pseudolaterals, cut off from whorls of pericentral cells .......................................................... DASYACEAE

2. Axes monopodially developed, pericentral cells produced in an opposite or alternating manner; trichoblasts absent or present; branching with walls of upper cells basally free. Spermatangia on branches of the trichoblasts or in sori on the branchlets. Tetrasporangia in stichidia or branches, cut off from pericentral or cortical cells .......................................................................................... 3

3. Thallus usually compressed to flat, with 2 or 4 pericentral cells, the lateral ones cut off first and usually developing further. Tetrasporangia in sori on the thallus or in lesser branches, cut off prior to their cover cells ...................................... DELESSERIACEAE

3. Thallus terete to compressed or foliose, with 4-20 pericentral cells which are developed in alternating sequence. Spermatangia produced on branches of trichoblasts or on the thallus surface. Tetrasporangia in lesser branches or stichidia, cut off after their cover cells .................................................................................................. RHODOMELACEAE

FAMILY CERAMIACEAE Dumortier 1822: 73, 100

Thallus erect, decumbent or prostrate, much branched laterally, subdichotomously or with whorl branchlets, with 1-8 periaxial cells from each axial cell, ecorticate or corticated by rhizoidal filaments, adventitious filaments or adherent small-celled filaments. Gland cells present or absent. Growth apical; synchronous laterals present in Griffithsia.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes dioecious or occasionally monoecious; procarpic. Carpogonial branches 4-celled, with or without a separate supporting cell, borne on axial or periaxial cells or filaments, in some taxa with a sterile group on the supporting cell; supporting cell usually producing an auxiliary cell post-fertilization. Fusion cell present or absent, the carposporophyte naked (or with a loose involucre), developing goniolithes with all cells, terminal cells, or chains of cells forming carposporangia. Spermatangial initials on outer cells of periaxial filaments or in specialised clusters or heads.

Tetrasporangia sessile or shortly pedicellate, solitary or in small clusters on periaxial cells or filaments, on cortical rhizoids or filaments or on outer cortical cells, tetrahedrally or cruciately/decussately divided, rarely dividing to octosporangia; polysporangia and propagules present in a few genera.

Mixed phase plants, with tetrasporangia and gametangia on the one plant, occasionally occur in some taxa.

The Ceramiaceae is a large family, well represented on southern Australia coasts with some 22 tribes, 65 genera and 159 species (several other species are known to occur but have not been adequately collected). It is distinguished by the uniseriate branches often with periaxial (but not pericentral) cells and the naked carposporophytes and tetrasporangia.

The following key to the tribes of Ceramiaceae should be used with some caution. While some tribes are characterised by vegetative features, in others knowledge of reproductive structures, especially of the female system, is essential. Some genera also do not fit clearly into the tribe in which they are currently placed.

KEY TO TRIBES OF CERAMIACEAE

1. Cortication absent or by lax to dense rhizoidal filaments of elongate cells usually arising from the basal cells of lateral branches/-lets at least several cells below the apices, when present usually covering the axial cells with discrete filaments .............................................. 2

1. Cortication from usually close to apices, nodal or complete, by closely appressed filaments, appearing pseudoparenchymatous, cortex generally bare of external filaments with most outer cells short and isodiametric ................................................................. 19
PLATE 1 fig. 1. Amoenothammnion planktonicum drift at Bridgewater Bay, Vic. (AD,A22270).

fig. 2. Griffithsia teges at Robe, S. Aust., Nov. 1997 (similar to AD,A27858). Photo: R.N. Baldock

fig. 3. Griffithsia pulvinata at Robe, S. Aust. (AD, A63203).

fig. 4. Griffithsia monilis at Robe, S. Aust. (AD, A63202).
PLATE 2 fig. 1. Anotrichium elongatum at Robe, S. Aust. (AD, A63206).


fig. 3. Ceramium rubrum at Cloudy Lagoon, SE Tas. (AD, A64230). Photo: G. Edgar.

2. Whorl-branchlets opposite or whorled on indeterminate axes, in some taxa obscured by dense rhizoidal cortication .............................................................. 3

2. Branchlets alternate or irregular throughout, not obscured by rhizoidal cortication, with no more than slight opposite or whorled arrangement [except for involucral branchlets below carpogonial branches in some Griffithsiaceae, e.g. Halirus, and also Ochmapexus (Radiathamnietae)] ........................................ 12

3. Main axes and branches heavily corticated by lax descending rhizoids, whorl-branchlets irregularly much branched and adjacent whorls overlapping, whorls often indistinct ............... 4

3. Main branches not or relatively slightly corticated, with clearly defined whorls (or opposite pairs) of whorl-branchlets closely adjacent or clearly separated ........................................ 6

4. Branching opposite on indeterminate axes, irregular in whorl-branchlets; gland cells present. Carpogonial branches scattered on cells of determinate or indeterminate branches, carposporogenous discrete, compact; tetrads quadrately or decussately divided .................................. WARRENIEAE (p.20)

4. Indeterminate axes and branches with 2 opposite whorl-branchlets (obscured behind apices) or (4-) 5 whorl-branchlets; gland cells absent; Carpogonial branches on successive axial cells or on pilose outer cortical filaments; carpogonial branches incorporating whorl-branchlet filaments or discrete; sporangia tetrads quadrately or decussately divided ........................................ 5

5. Indeterminate axes and branches with (4-) 5 irregularly branched whorl-branchlets per axial cell. Carpogonial branches borne on successive axial cells near apices of indeterminate branches; carpogonial branches incorporating terminal parts of fertile branches, with gonimoblast filaments intermingled with sterile whorl-branch filaments ............................................. WRANGELIEAE (p.23)

5. Indeterminate axes and branches with 2 opposite, alternately branched, whorl-branchlets per axial cell, opposite branchlets rapidly obscured by dense cortication. Carpogonial branches borne on branched pilose outer cortical filaments; carpogonial branches discrete, compact .................................................. LASIOTHAMNIEAE (p.37)

6. Whorls of whorl-branchlets usually closely adjacent on the indeterminate branches, forming more or less linear branches with even contours; gland cells present or absent ........................................................................................................... 7

6. Whorls of whorl-branchlets clearly separated on the indeterminate branches, giving irregular or moniliform contours; gland cells usually present, parallel or angled to the bearing cell and broadly attached to it ........................................................................... 8

7. Whorl-branchlets in whorls of 3 or 4, formed in spiral or opposite sequence ............................................................................................................... CROUANIEAE (p.42)

7. Whorl-branchlets in whorls of 5 or 6, formed alternately or in opposite groups of 3 .................................................................................................................. DASYPHILEAE (p.67)

8. Thalli usually 5–20 cm high; gland cells absent. Sterile procarp cells producing an inner involucre of free filaments around the carpogonial branch; carpogonial branch terminal on gonimoblast filaments; tetrads quadrately or polysporaneous .................. SPHONDYLOTHAMNIEAE (p.73)

8. Thalli usually 0.5–4 cm high (Macrothamnion and some Pterothamnietae 5–20 cm high); gland cells usually present. Sterile procarp cells not producing an involucre around the carpogonial branch; most cells of carpogonial branch forming carposporogenous; tetrads quadrately or cruciately or decussately divided ............................................ 9

9. Thalli usually ecoricate; gland cells absent or on short, 2-3-celled branchlets or terminal on rachides; whorl-branchlets when branched usually distichous. Carpogonial branches successive on basal cells of relatively normal whorl-branchlets below indeterminate branch
18  CERAMIACEAE

9. Thalli with lower axes corticate with rhizoids or ecorticate; whorl-branchlets usually not distichously branched (except in *Ballia*); gland cells absent or present but not on short 2–3-celled branchlets; carpogonial branches on basal cells of normal or reduced whorl-branchlets, carposporophytes with or without an involucre; tetrasporangia on cells of normal or reduced whorl-branchlets or on special branches thereof .......................... 11

10. Gland cells present, on short, 2–3-celled, branches or terminal on whorl-branchlets; whorl-branchlets distichous or decussate on indeterminate axes, usually branched; carpogonial branches on basal cells of normal whorl-branchlets; tetrasporangia mostly lateral on whorl-branchlets, cruciately or decussately divided .......................................................................................................................... ANTITHAMNIEAE (p.98)

10. Gland cells absent; whorl-branchlets always distichous on axes, simple or with few branches; carpogonial branches on opposite, shorter, whorl-branchlets; tetrasporangia mostly terminal on whorl-branchlets, irregularly tetrahedrally divided ......................................................................................................................... GYMNOTHAMNIEAE (p.127)

11. Thalli mostly relatively large (5–20 cm high), lower axes usually corticated with rhizoids, gland cells present (touching only the bearing cell) or absent; carpogonial branches on basal rachis cells of whorl-branchlets; carposporophytes with an involucre; tetrasporangia on cells of whorl-branchlets or on branch systems, decussately divided ............................................................................................................................................ PTEROTHAMNIEAE (p.132)

11. Thalli mostly relatively small, 0.2–4 (-10) cm high; lower axes ecorticate; whorl-branchlets usually not distichously branched; gland cells usually present, touching the bearing cell and often the next outer cell. Carpogonial branches on basal cells of reduced (2–4 cells long) whorl-branchlets, 1–3 (–4) on each of one or two axial cells near each indeterminate branch apex; carposporophytes without a distinct involucre; tetrasporangia on normal whorl-branchlets, tetrahedrally or obliquely divided ... HETEROTHAMNIEAE (p.156)

12. Cells relatively small, mostly < 150 μm in diameter (apart from older axial cells), uninucleate or multinucleate; propagules absent; procarps subapical on short or several-celled axes or on intercalary cells of normal axes .................. 13

12. Cells large, lower cells usually over (100-) 150 μm in diameter (except some Monosporeae), multinucleate; procarps subapical on short axes .......... 17

13. Thalli small (less than 2 cm high), ecorticate; propagules present (Monosporeae) or absent; procarps on subapical cells of short branches or on the basal cell of a short axial branch, with single auxiliary cells and carposporophytes ......................................................................................... 14

13. Thalli small to large, (1-) 2–20 (-30) cm high, ecorticate or corticate at least below; procarps on axial cells with twinned supporting and auxiliary cells and carposporophytes, or on subapical or lower cells of short apical or lateral branches ...................................................... 15

14. Thalli small, 0.5–2 (-7) cm high, epiphytic or epilithic, with prostrate and usually straight erect axes, simple or irregularly branched cells; cells multinucleate; branching irregularly lateral; spermatangia formed on initials in compact heads; tetrahedrally divided sporangia or polysporangia ................................ SPERMOTHAMNIEAE. (p.208)

14. Thalli minute (less than 3 mm high), epiphytic on *Laurencia*, or *Caulerpa* and other algae; with a single basal cell or complanate multicellular holdfasts; main axes curved, with unilateral laterals from the convex side; cells uninucleate; spermatangia formed directly from branch cells; tetrasporangia tetrahedrally divided ................................................................. RADIOTHAMNIEAE (p.225)

15. Thalli small to 20 cm high, ecorticate above and corticated or not on lower axes or branches; apical cell divisions transverse. Carpogonial branches on one of two periaxial (supporting)
cells on intercalary cells of indeterminate axes or laterals, with both periaxial cells producing auxiliary cells and “twinned” carposporophytes; procarps without sterile cells; spermatangia on branched filaments or small clusters ....... CALLITHAMNIEAE (p.231)

15. Thalli 5–20 (-50) cm high, heavily corticated from near the apices or below, or with a network of filaments; apical cell divisions more or less transverse or oblique and alternating; procarps with a single carpogonial branch and auxiliary cells, on the subapical or a lower axial cell or on special 3–8-celled lateral branches, with sterile cells or axial cells below the procarp producing an involucre of filaments around the carposporophyte; spermatangia on heads ........................................ 16

16. Branch apices usually emergent. Procarps (2–3) situated 2–5 cells below apices of few-celled lateral axes which may extend apically after fertilization, with sterile cells of procarp forming short branches around the carposporophyte or an involucre from lower cells but not becoming larger and rounded ... COMPSOTHAMNIEAE (p.270)

17. Asexual ovoid, 1-3-celled, propagules present; upper (and often lower) cells less than 200 μm in diameter; tetrasporangia or polysporangia present ........ MONOSPOREAE (p.300)

18. Synchronous lateral branches absent; female axes 5–6 (-8) cells long with successive functional (4-celled) and non-functional (2-celled) carpogonial branches; carposporangia on slender gonimoblast processes, terminal, clavate .............. BORNETIEAE (p. 313)

19. Branching usually pinnate, with alternate or opposite laterals lying in one plane, usually alternately developed; cortication filamentous to pseudoparenchymatous, irregularly developed on the axial cells ........................................ 20

20. Indeterminate axis cells with 2 or 4 periaxial cells, producing alternate or opposite distichous determinate branches. Tetrasporangia on ultimate, ecorticate branchlets ........................................ PTILOTEAE (p.354)

21. Cortication of indeterminate branches complete, consisting of alternating bands of long and short cells, longitudinally and transversely aligned; indeterminate branches bearing lateral or whorled (or single) elongate determinate ramelli with narrow nodal cortication only and bearing tetrasporangia at the nodes ................. SPYRIDEAE (p.371)

22. Cortication of all branches arising nodally, closing completely or leaving a clear gap; elongate determinate ramuli absent; tetrasporangia from periaxial or cortical cells ...................................................... CERAMIACEAE (p.381)
Tribe WARRENIEAE Schmitz 1889: 450
by E.M. Wollaston & H.B.S. Womersley

Thallus profusely branched with opposite, irregularly branched whorl-branchlets and
laterals, loosely corticated below with rhizoidal branches arising from the basal periaxial
cells; gland cells present. Cells multinucleate.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes dioecious. Carpogonial branches 4-celled, borne directly
on cells of determinate or indeterminate branches, that cell acting as the supporting cell.
Auxiliary cell cut off from the supporting cell, with post-fertilization diploid nucleus transfer
by means of a connecting cell, then forming three gonimoblast initials and lobes of
carposporangia. Sterile involucral branchlets develop from cells below the supporting cell,
loosely surrounding the carposporophyte. Spermatangia borne oppositely or in slight whorls
on short lateral branchlets.

Tetrasporangia terminal on short branchlets on lower cells of lateral branchlets, ovoid,
cruciatey or decussately divided.

The Warrenieae includes the single genus and species Warrenia comosa (Harvey)Kützing.
Wollaston (1971, p. 297) regarded it as a phylogenetically primitive tribe of the family,
characterised by irregular and variable branching with most cells producing reproductive
organs; the cells of the lateral branchlets act as supporting cells and produce carpogonial
branchlets directly, with post-fertilization connection to the auxiliary cell via a relatively large
connecting cell, and with numerous sterile involucral filaments from cells below the supporting

Genus WARRENIA Harvey ex Schmitz & Hauptfleisch 1897: 492

With the characters of the tribe.

Type (and only) species: W. comosa (Harvey)Harvey ex Schmitz & Hauptfleisch 1897: 492.

Warrenia comosa (Harvey)Harvey ex Schmitz & Hauptfleisch 1897: 492. Kützing 1862: 13,
Callithamnion comosum Harvey 1844: 451; 1859b: 333; 1863, synop.: liii. J. Agardh
Phlebothamnion comosum (Harvey)Kützing 1847: 52.
Wrangelia comosa sensu Kützing 1849: 664 (NON Harvey in Hooker & Harvey
1847: 411).
Antiithamnion comosum (Harvey)J. Agardh 1892: 21.

FIGS 1, 2A–F

Thallus (Fig. 1A) erect, 5–30 (-35) cm high, profusely and irregularly branched with
the main branches bearing opposite indeterminate branches and becoming corticated below
by entwined branched filaments. Structure. Growth by transverse divisions of the apical
cell, with series of short subapical cells (Fig. 2A) cutting off first one lateral whorl-branchlet
and later a second, so that each axial cell bears two opposite whorl-branchlets (Fig. 1B);
whorl-branchlets more or less determinate, becoming irregularly branched with 1–3 branches
per cell. cells 6–10 (-12) μm in diameter and L/D 3–10 (-20); axial cells enlarging greatly,
when mature 250–500 μm in diameter and L/D 1.2–2 (-3); corticating filaments (Fig. 1C)
developing upwards from the distal ends of periaxial cells and downwards from the proximal
ends, becoming dense around and completely covering the lower axial cells, often densest
around the ends of the axial cells giving a nodose appearance; gland cells (Fig. 2B) present
on lateral branchlets, more or less ovoid, 7–12 μm across. Cells multinucleate; rhodoplasts reticulate.

Reproduction. Gametophytes dioecious. Carpogonial branches (Fig. 2C) 4-celled, borne singly and directly on the lower part of any cell of a lateral branchlet, or occasionally on an indeterminate branch, lying upwards along the bearing (supporting) cell. Post-fertilization, an auxiliary cell is cut off from the upper end of the supporting cell, and fusion with the fertilized carpogonium occurs via a connecting cell, then producing three gonimoblast initials and lobes of carposporangia. Sterile involucral branchlets develop from cells below (and from) the supporting cell and loosely surround the carposporophyte (Fig. 2D) which is 100–400 μm across. Spermatangia are borne oppositely or in slight whorls on short branches (Fig. 2E) of 5–8 cells borne adaxially on the whorl-branchlets; spermatangia ovoid, 1.5–2.5 μm in diameter.

Fig. 1. Warrenia comosa (A, AD, A33412; B, C, AD, A64628; D, AD, A35266). A. Habit. B. Young branch with opposite whorl-branchlets. C. Older branch with whorl-branchlets and cortication on axial cells. D. Young branch with whorl-branchlets bearing tetrasporangia.
Tetrasporangia develop terminally on short branches (Fig. 1D, 2F) 1–3 (-6) cells long, borne on lower cells of the whorl-branchlets, ovoid, 18–28 \( \mu \text{m} \) in diameter, decussately (occasionally cruciately) divided.

**Type** from Georgetown, Tas. (Gunn); lectotype Gunn 1303 in Herb. Harvey, TCD (Wollaston 1971).

**Distribution:** Waldegrave I., S. Aust. to Walkerville, Vic., and around Tasmania.


**Tribe WRANGELIEAE Schmitz 1889: 439**

by H.B.S. Womersley

**Thallus** much branched radially or distichously, axial cells with 5 (rarely fewer) periaxial whorl-branchlets which are determinate and much branched irregularly; indeterminate laterals arising on basal cells of whorl-branchlets; cortication moderate to dense, by descending rhizoids from basal cells of whorl-branchlets; apical cells dividing by alternately slightly oblique divisions; gland cells absent; cells uninucleate.

**Life history** triphasic with isomorphic gametophytes and tetrasporophytes.

**Reproduction.** Gametophytes dioecious. Procarpic, supporting cells each with a 4-celled carpogonial branch, borne on successive axial cells near the spines of indeterminate branches, with a connecting cell transferring the diploid nucleus to the auxiliary cell, then forming a large fusion cell by union of lower gonimoblast cells, fertile axial cell and lower cells of sterile whorl-branchlets; gonimoblast branched, with the end cells forming carposporangia, growing between adjacent whorl-branchlets to form a diffuse carposporophyte. Spermatangia formed as outer cells of compact, sub spherical, pedicellate heads on lower cells of whorl-branchlets.

Tetrasporangia on lower cells of whorl-branchlets, scattered, tetrahedrally divided.

The Wrangelieae was first listed as a tribe of the Gelidiaceae by Schmitz (1889, p. 439) but is now recognised as a mono-generic tribe of the Ceramiaceae (Kylin 1956, p. 382; Gordon 1972, p. 13). It is distinguished by the presence of 5 whorl-branchlets, the diffuse gonimoblast with intermingled whorl-branchlets, and the compact spermatanigial heads.

This account is based largely on that of Gordon (1972).

**Genus WRANGELIA** C. Agardh 1828: 136

With the characters of the tribe.

**Lectotype species:** *W. penicillata* (C. Agardh) C. Agardh 1828: 136 (J. Agardh 1842: 79).

A genus of some 17 species, well represented in southern Australia with five species.
KEY TO SPECIES OF WRANGELIA

1. Ends of thallus branches more or less terete; whorl-branchlets subdichotomously to unilaterally branched; cortical rhizoidal cells not producing an outer layer of branchlets

.......................................................................................................................................... 2

1. Ends of thallus branches strongly flattened owing to greater development of lateral whorl-branchlets; whorl-branchlets alternately pinnate or subdichotomous; corticating rhizoid cells producing an outer layer of branchlets

.......................................................................................................................................... 4

2. Terminal cells of whorl-branchlets mucronate, L/D 1-2

3. Terminal cells of whorl-branchlets not mucronate, usually L/D more than 2

2. Terminal cells of whorl-branchlets mucronate, L/D 1-2

3. Terminal cells of whorl-branchlets not mucronate, usually L/D more than 2

2. Thallus 10-30 (-60) cm high; whorl-branchlets subdichotomously branched 2-3 times near the base, ultimate branches of 9-10 cells; tetrasporangia not surrounded by special small-celled involucral branchlets

.......................................................................................................................................... 1. W. abietina

3. Thallus (2-) 5-10 (-25) cm high; whorl-branchlets subdichotomously to unilaterally branched 5-8 times, ultimate branches of 2-4 (-6) cells; each tetrasporangium surrounded by 2-5 curved involucral branchlets of small cells

.......................................................................................................................................... 2. W. plumosa

4. First- and second-formed whorl-branchlets of each whorl formed on opposite sides of the axis, strongly developed and reaching 3 mm long, other whorl-branchlets shorter, terminal cells acute; outer cortical branchlets terminating in acute cells

.......................................................................................................................................... 4. W. nobilis

4. Whorl-branchlets formed in alternating sequence with the first- and second-formed of each whorl on the same side of the axis, alternating on successive axial cells, villose and reaching 4 mm long, other whorl-branchlets much shorter with terminal cells mucronate; outer cortical branchlets terminating in large spherical cells

.......................................................................................................................................... 5. W. australis


FIGS 2G, 3, 4

Thallus (Fig. 3A) medium to dark red brown, fading to grey-red, 10-30 (-60) cm high, alternately pinnately branched for 3-4 orders, lateral branches 1-20 cm long. Holdfast 1-4 mm across, rhizoidal; epilithic or epiphytic on Codium. Structure. Apical and subapical cells (Fig. 2G) small, dividing slightly obliquely and enlarging gradually to 400-700 (-900) μm in diameter and 2-3 mm long near the thallus base. Each axial cell with 5 whorl-branchlets, developed from periaxial cells usually cut off in alternating sequence, the first on alternate sides on successive axial cells. Mature whorl-branchlets (Fig. 4A) 1-2 mm long, overlapping, basally branched subdichotomously, ultimate (6-) 8-10 cells unbranched, tapering, mid cells (18-) 20-35 (-45) μm in diameter and L/D 4-7. Indeterminate lateral branches arise from basal cells of whorl-branchlets (Fig. 4A). Cortication by descending rhizoids from the basal cells of whorl-branchlets, forming a pseudoparenchymatous cortex of longitudinal filaments, 1-8 mm thick below and exposed between the whorl-branchlets. Cells uninucleate; rhodoplasts discoid to elongate, ribbon like in larger cells.

Reproduction. Gametophytes dioecious. Procarps (Fig. 4B) formed successively on the third to sixth axial cells of indeterminate apices, the supporting cell bearing a terminal sterile cell and a lateral 4-celled carpogonial branch. Post-fertilization two connecting cells are cut off from the carpogonium, and occasionally similar cells from lower carpogonial branch cells; one fuses with the auxiliary cell which produces 1-3 short gonimoblast filaments with the
Fig. 3. Wrangelia abietina (A, AD, A2938; B, D, AD, A30841; C, AD, A20089). A. Habit. B. Carposporophyte with carposporangia and intermixed vegetative filaments. C. Whorl-branchlets with spermatangial heads. D. Main and lateral branches with whorl-branchlets bearing tetrasporangia.
terminal cells becoming pyriform to clavate carposporangia 45–65 μm in diameter, with further carposporangia formed by lower cells. Lower gonimoblast cells gradually fuse and the carposporophyte (Fig. 3B) becomes intermixed with sterile whorl-branchlets (with smaller cells than in normal whorl-branchlets), the whole forming a compact hemispherical mass

Fig. 4. Wrangelia abietina (AD, A20089). A. A branch with whorl-branchlets, an indeterminate lateral arising from the basal cell, and early cortication of the axial cells. B. A female axis with mature and post-fertilization carpogonial branches, the latter with division of the sterile cell on the supporting cell. C. Longitudinal section of a spermatangial head. D. Apex of a branch with tetrasporangia. (All as in Gordon 1972, courtesy of Aust. J. Bot.)
600–800 μm across. Spermatangia are formed terminally on radiating filaments of subspherical heads (Figs 3C, 4C) 40–60 μm in diameter, borne on the lower 1 or 2 cells of whorl-branchlets, surrounded by curved involucral branchlets.

Tetrasporangia (Fig. 4D) occur on the lower 1–3 cells of unmodified whorl-branchlets (Fig. 3D), subspherical, 80–100 μm in diameter, tetrahedrally divided.

Type from Garden I., W. Aust. (Harvey, Trav. Set 270, not located in TCD); lectotype (Alg. Aust. Exsicc. 267) in Herb. Harvey, TCD.

Distribution: Yanchep, W. Aust., to Phillip Is., Vic.


Gordon (1972, p. 38) considered W. abietina close to W. princeps. They are now united here since the dimensions of the whorl-branchlet cells overlap considerably and the habit and whorl-branchlets are similar but distinct to those of W. plumosa. In describing W. princeps, Harvey (1862, pl. 234) recorded it from Garden I., W. Aust. (Clifton 23, Aug. 1856), but made no mention of his earlier (1855a) W. ?abietina, also from Garden I.

W. abietina is closely related to the type species, W. penicillata, differing (Gordon 1972, p. 21) in greater diameter of cells of whorl-branchlets, which are more densely branched, and in absence of curved involucral filaments around the tetrasporangia.

It appears to be a deeper water alga, commonly epiphytic on Codium galeatum on rough-water coasts.


FIGS 5A, B, 6

Thallus (Fig. 5A) purplish-red to yellow-red, (2-) 5–10 (-25) cm high, alternately pinnately branched for 3–4 orders, outline broadly pyramidal. Holdfast discoid, 2–8 mm across, rhizoidal; epilithic. Structure. Apical cells (Fig. 6A) dividing slightly obliquely and enlarging gradually to 400–500 μm in diameter and 1.5–2.5 mm long near the base. Each axial cell with 5 whorl-branchlets, developed from periaxial cells cut off usually in alternating order. Mature whorl-branchlets 1–2 mm long, overlapping only near branch apices, subdichotomously branched 5–8 times with ultimate branches 2–4 (-6) cells long, median cells (20) 40–70 μm in diameter and L/D (3.5–) 5–8, terminal cells 12–20 μm in diameter and L/D 2–6. Indeterminate lateral branches arising from basal cells of first-formed whorl-branchlets. Cortication by descending rhizoids from the basal cells of whorl-branchlets, forming a cortex up to 1 mm thick. Cells uninucleate; rhodoplasts discoid, in chains and reticulate in larger cells.
Reproduction. Gametophytes dioecious. Procarps (Fig. 6B) formed successively on up to 7 axial cells, supporting cell without a terminal sterile cell. Post fertilization development as in *W. abietina*, with usually only one carpogonophore per fertile axis, carpogonophore (Fig. 5B) with intermixed sterile whorl-branchlets, the whole subspherical and 450–900 (-1200) μm across. Spermatangia terminal on radiating filaments of subspherical pedicellate heads (Fig. 6C) 80–110 μm in diameter, clustered from axial cells with all but one whorl-branchlet reduced to fewer and shorter involucral cells.

Tetrasporangia are terminal on short filaments arising from lower cells of modified whorl-branchlets (Fig. 6D), each sporangium surrounded by 2–5 curved involucral branches; tetrasporangia 50–80 (-100) μm in diameter, tetrahedrally divided.

Type from Georgetown, Tas. (*Gunn*); lectotype (*Gunn 1315*) in Herb. Harvey, TCD.

**Distribution:** Shark Bay, W. Aust. (Huisman & Walker 1990) to Coffs Harbour, N.S.W. (Millar 1990), and around Tasmania.


*W. plumosa* is common in lower eulittoral or uppermost sublittoral habitats, in contrast to the deeper water *W. abietina*. It differs from the latter in having median cells of whorl-branchlets 40–70 μm in diameter (25–30 μm in *W. abietina*) with the ultimate branches of 2–4 (-6) cells (9–10 cells in *W. abietina*) and in having small-celled involucral branches around the tetrasporangia.

*W. plumosa* is recorded from Coffs Harbour, N.S.W., by Millar (1990, p. 401) who comments on the absence of reduced involucral branches around the tetrasporangia; further comparisons are necessary.


**FIGS 5C, D, 7**

*Thallass* (Fig. 5C) medium to dark brown-red, 3–16 cm high, irregularly branched for 2–3 orders, branches terete, 1–2 mm in diameter, diverging widely, usually widely spaced, often unequal in length. Holdfast 3–7 mm across, rhizoidal; epitheca (as short plants 3–6 cm high)
or epiphytic on Amphibolis (larger, deeper water plants). Structure. Axes with small apical and sub-apical cells, enlarging to 200–300 μm in diameter and 400–500 μm long near the base. Each axial cell with 5 whorl-branchlets, developed from periaxial cells with the first formed often produced unilaterally, the first 3 in sequence around the axial cell, the fourth and fifth alternating. Mature whorl-branchlets (Fig. 7A) 1–1.5 mm long, subdichotomous 7–8 times, ultimate parts 2–4 cells long, terminal cells mucronate and L/D 1–2, median cells (40–) 55–90 μm in diameter and L/D 2–6. Indeterminate laterals arising on basal cell of whorl-branchlets. Cortication by descending rhizoids (often spiral) from the basal cells of whorl-branchlets, cortex 0.5–1 mm thick below. Cells uninucleate; rhodoplasts discoid, in chains in larger cells.

Reproduction. Gametophytes dioecious. Procarps (Fig. 7B) formed on sub-apical cells as in W. plumosa, the supporting cell without a sterile cell. Post-fertilization development as in W. plumosa, with the carposporophyte (Fig. 5D) intermixed with sterile whorl-branchlets, the whole 700–1000 mm across; carposporangia clavate, 25–40 μm in diameter; axial cells below the fusion cell swelling and pit-connections enlarging. Spermatangial heads (Fig. 7C) developed as in W. plumosa, 45–125 μm in diameter.

Teietasporangia (Fig. 7D) borne as in W. plumosa, each surrounded by 1–2 small-celled involucral branchlets from the stalk cell, sporangia 45–90 μm in diameter, tetrahedrally divided.

Type from "occid. Nov. Holl." (Preiss); holotype in MEL, 15237.

Fig. 6. *Wrangelia plumosa* (AD, A27894). A. Apex of an indeterminate branch with developing whorl-branchlets. B. Female axis with developing carpogonia branches. C. Whorl-branchlet bearing spermatangial heads on basal cells. D. A modified whorl-branchlet bearing tetrasporangia. (All as in Gordon 1972, courtesy of Aust. J. Bot.)
**Wrangelia** WRANGELIEAE


*W. velutina* is distinct in its irregular, relatively sparse, branching. This is superficially similar to *Dasya divergens* but the two species are distinct in structure. Small plants of *W. velutina* occur just above or below low tide level on rough-water coasts, while larger plants are epiphytic on *Amphibolis* in deeper, less turbulent, water.

Weber van Bosse (1921, p. 222) recorded *W. velutina* from Borneo to Timor; these records need confirmation.


**FIGS 8A–C, 9**

Thallus (Fig. 8A) medium to dark red-brown, 10–35 cm high, alternately distichously branched for 3–4 orders, lateral branches spreading, unequal, often with flattened clavate ends, covered with overlapping whorl-branchlets. Holdfast discoid, 4–12 mm across, composed of entwined rhizoids from the axis; epilithic. **Structure**. Axes with small apical cells dividing more or less transversely, increasing in size to 300–400 μm in diameter and 800–1000 μm long below, subapical cells cutting off first two opposite periaxial cells then three more, with the third and fifth on the same side giving a dorsiventral arrangement and the first and second developing into larger whorl-branchlets producing a flattened branch; mature lateral whorl-branchlets 2–3 mm long, alternately pinnate, tapering to acute terminal cells, mid cells 35–90 μm in diameter and L/D (1-) 2–5 (–10). Indeterminate branches arising on the basal cell of lateral whorl-branchlets. Branches densely corticated (Fig. 9A) by descending rhizoids from the basal cells of whorl-branchlets, forming outwardly a thick mat of short, simple or furcate, branchlets; lower parts of branches becoming denuded of whorl-branchlets. Cells uninucleate; rhodoplasts discoid, in chains in larger cells.
Fig. 7. Wrangelia velutina (AD, A27325). A. A whorl-branchlet. B. Female axis bearing carpogonial branches on successive axial cells. C. A whorl-branchlet with clusters of spermatangial heads from lower cells. D. A tetrasporangial cluster from the base of a whorl-branchlet. (All as in Gordon 1972, courtesy of Aust. J. Bot.)
Reproduction. Gametophytes dioecious. Procarps (Fig. 9B) formed on axial cells near apices, usually 2 per axial cell; carposporangial branches 4-celled with each cell cutting off a small cell and a connecting cell between the fertilized carposporangium and the auxiliary cell. Post-fertilization stages as in *W. plumosa* with sterile whorl-branchlets intermixed with the carposporophyte (Fig. 8B) which bears clavate carposporangia, the whole subspherical and 560–800 (-1000) μm across. Spermatangial heads (Fig. 9C) subspherical, 70–100 μm in diameter, borne on reduced whorl-branchlets with short (2 or 3 small-celled) involucral branches from each stalk cell. Tetrasporangia terminal on cells of short, small-celled, laterals (Fig. 9D) on the basal cells of whorl-branchlets (Fig. 8C), 65–100 μm in diameter, tetrahedrally divided.

Type from Georgetown, Tas. (Gunn); lectotype (Gunn 1324) in BM.

Distribution: Waldegrave I., S. Aust., to Walkerville, Vic., and around Tasmania.


5. *Wrangelia australis* (J. Agardh) Gordon 1972: 35, figs 9, 10, 54B.

Endemic. Wrangelieae 33

Thallus (Fig. 8D) medium to dark red-brown, 10–22 cm high, largely complanately and alternately branched with long laterals 0.5–1 mm in diameter, fringed with short lateral branchlets 1–3 mm long surmounted by a tuft of filaments; lower branches 2–5 mm in diameter. Holdfast 2–6 mm across, rhizoidal; epitheca. Structure. Apical and subapical cells small, enlarging gradually to 200–250 μm in diameter and to 500 μm long near the base. Each subapical cell cutting off 5 periaxial cells in alternating sequence, developing into pseudodichotomous whorl-branchlets 2–4 mm long, branched 5–6 times, median cells 45–65 μm in diameter and L/D 1.5–2 (–3), terminal cells mucronate; first and second whorl-branchlets become villose (Fig. 10A) and alternately pinnate, forming the terminal tufts on the short lateral branches. Indeterminate lateral branches arise from the basal cells of second-formed whorl-branchlets and are thus distichous on alternate sides of the main branches. Cortication by descending rhizoids from the basal cells of whorl-branchlets, developing below an outer cortex (Fig. 10B) of branched anticlinal filaments (Fig. 10C) 45–60 μm in diameter with subspherical terminal cells 90–125 μm in diameter; lower axes often denuded of whorl-branchlets in older plants, leaving only the cortex of anticlinal filaments. Cells uninucleate; rhodoplasts discord.

Reproduction. Gametophytes dioecious. Procarps (Fig. 10D) formed as in *W. nobilis*, carposporangial branches 4-celled (rarely 5-celled), formed on successive subapical cells. Carposporophyte with intermixed sterile whorl-branchlets, the whole 1–1.8 mm across, carposporangia clavate, 45–120 μm in diameter. Spermatangial heads (Fig. 8E) subspherical, 100–180 μm in diameter, borne on 1–2-celled stalks (Fig. 10E) on lower cells of the whorl-branchlets on young indeterminate branches with much reduced involucral branches 1–2 cells long on the stalk cell.
Tetrasporangia are terminal on 1–3-celled stalk cells on the lower 1–2 cells of whorl-branchlets (Fig. 10F), with short, curved, involucral branches on the stalk cell; sporangia 120–140 μm in diameter, tetrahedrally divided.

Type from Port Elliot, S. Aust. (Hussey 190); holotype in Herb. Agardh, LD, 35852.


Fig. 9. Wrangelia nobilis (A, AD, A21622; B, AD, A27885; C, AD, A27900; D, AD, A24383). A. Transverse section of a lower corticated axis. B. Female axis with carpogonial branches on axial cells. C. Whorl-branchlet with spermatangial heads. D. Transverse section of an axis with whorl-branchlets bearing tetrasporangia. (All as in Gordon 1972, courtesy of Aust. J. Bot.)

W. australis is distinguished by its largely complanately branched thalli, with short distichous branches along long laterals, and by the outer cortex of filaments with subspherical, swollen, terminal cells.

It appears to be a deeper water alga on moderate to rough-water coasts.

Tribe LASIOTHALIEAE Womersley, tribus nov.

by E.M. Wollaston & H.B.S. Womersley

Thallus erect, conspicuous, irregularly branched with distinct axes and laterals, heavily corticated with an inner entwined rhizoidal layer and an outer pilose layer of mostly unbranched filaments, occasional ones developing as indefinite lateral branches. Young axes with opposite whorl-branchlets, soon obscured by the cortication, whorl-branchlets alternately branched; gland cells absent. Cells uninucleate.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes dioecious. Procarps borne on potentially indeterminate filaments in the pilose layer, usually on several successive cells, with the basal cell of a short lateral branch acting as the supporting cell and bearing a 4-celled carpogonial branch. Post-fertilization a prominent fusion cell develops and successive rounded gonimolobes are produced; no special involucral branchlets occur but the carposporophyte is densely surrounded by the pilose filaments. Spermatangia occur on clusters on the pilose filaments and on lateral branchlets.

Tetrasporangia occur on short lateral branches on the pilose filaments, sessile or pedicellate, subspherical, tetrahedrally divided.

Thallus erectus, irregularim ramosus, grave corticatus, strato interiore implicato rhizoideali et strato exteriore piloso filamentorum haud ramosorum, aliquot crescentes tamquam ramos laterales indefinitiosae. Axes iuvenes ramulis oppositis verticillatis alterne ramosis.


Tetrasporangia in ramulis brevibus lateralibus in filamentis pilosis, sessilia vel pedicellata, subsphericalia, tetrahedraliter divisa.

Type genus: Lasiothalia Harvey 1855a: 558.

The structure and reproduction of Lasiothalia (with the single species, L. hirsuta) was clarified by Wollaston (1990), who suggested it was allied to the Antithamnieae. However, restriction of this tribe to genera bearing gland cells on reduced branchlets, with opposite or whorled branchlets throughout, and with not or only slightly corticate thalli, precludes inclusion of Lasiothalia in this tribe. The elaborate cortex, with outer pilose filaments among which
filaments bearing reproductive structures occur, appears to warrant placing *Lasiothalia* in its own tribe.

**Genus LASIOTHALIA** Harvey 1855a: 558.

With the characters of the tribe.

*Type species:* *L. hirsuta* Harvey 1855a: 558.

While several species have been placed in *Lasiothalia*, probably only the type species now remains in the genus. Other previously accepted species were *L. plumigera* and *L. superbiens*, now placed in *Dasythamniella* (Compsothamnieae) and *L. formosa*, now *Hirsutithallia formosa* (Callithamnieae).


**FIGS 11, 12A–C, 13A–E**

*Thallus* (Fig. 11A) erect, red brown to grey brown, 10–20 (-30) cm high, with irregularly branched, densely corticated axes, with an inner entwined rhizoidal layer and an outer pilose layer (Fig. 11C) of unbranched filaments, ecorticate near the apices only (Fig. 11B, D). Holdfast rhizoidal, 3–8 (-12) mm across, epilithic. *Structure.* Axial cells 100–250 μm in diameter and L/D 2–6 in mid thallus, to L/D 10–20 in lower parts, each cell bearing first a single and later an opposite (usually less well developed) lateral branchlet (Fig. 11B), each furbate several times and usually with a smaller basal cell; these branchlets soon obscured by the cortication. Rhizoidal filaments from the lower cells of branchlets form a dense cortical layer, often anastomosing, with each cell producing a determinate, simple, outwardly projecting filament which is curved upwardly (Fig. 13A), 8–20 μm in diameter, 150–700 μm long, cells L/D 1–2.5. Denuded plants, without growing tips and pilose filaments, are frequent; gland cells absent. Cells uninucleate; rhodoplasts discoid in smaller cells, ribbon like in larger axial cells.

*Reproduction.* Gametophytes dioecious. Procarps (Fig. 13C) borne near the tips of pilose cortical filaments (Fig. 13B), single or on several successive cells with the uppermost procarp usually on the third cell from the apex; the supporting cell, which bears the 4-celled carpogonial branch, is the basal cell of a short lateral branch 3–4 cells long, borne on the axial cell of the pilose filament. Post-fertilization the supporting cell cuts off an auxiliary cell and the carposporophyte (Figs 12A, 13D) consists of successive rounded groups 120–180 μm across of ovoid carposporangia 12–25 μm in diameter; the supporting cell, axial cell of the pilose branchlet and part of the lower axial cell fuse, but no involucral branchlets are produced. Spermatangial heads (Figs 12B, 13E) are borne on pilose cortical filaments and on lateral branchlets, each ovoid and 20–40 μm in diameter, L/D 1.5–2.5, with a basal pedicel and axis of 3–6 cells bearing whorls with terminal spermatangia 1–2 μm in diameter. Tetrasporangia (Fig. 12C) are borne on short lateral branches of the pilose filaments, sessile or usually on 1–2-celled pedicels, subspherical, 35–55 μm in diameter, tetrahedrally divided.

*Type* from Cape Riche, W. Aust.; holotype in TCD (Harvey, Trav. Set 321).

*Distribution:* Cape Riche, W. Aust., to Robe, S. Aust., and N coast of Tasmania.

*Selected specimens:* Investigator Strait, S. Aust., 41 m and 33 m deep (Watson, 14.i.1971 and 24.i.1971; AD, A38157 and A41090 respectively). Brighton, S. Aust., drift (Bienert, 12.xi.1965; AD, A29666). Port
As Silva et al. (1996, p. 416) point out, the De Toni & Forti (1923, p. 56) reference to *Lasiolithalia hirsuta* from Geraldton, W. Aust., may not apply to this species, which is otherwise known only east of Cape Riche.
Tribe CROUANIEAE Schmitz 1889: 451

by E.M. Wollaston & H.B.S. Womersley

Thallus erect, with or without a prostrate base, branches terete or compressed, with or without rhizoidal cortication. Axial cells with closely adjacent whorls of 3 or 4 whorl-branchlets formed in spiral or opposite sequence, branched several times; growth monopodial or with lower branches over-growing upper branches occasionally or repeatedly in a sympodial manner; lateral branches arising from basal cells of whorl-branches or (in Crouania and Gattya) from axial cells; gland cells absent or present on the whorl-branchlets, situated at an angle to the bearing cell and pit-connected to it.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes dioecious. Procarps borne in place of whorl-branchlets or on the basal cell of whorl-branchlets, with apical growth ceasing after initiation, with a supporting cell bearing a 4-celled carpogonial branch; carposporophyte with terminal and lateral gonimolobes, surrounded by whorl-branchlets usually in rounded or clavate branch ends. Spermatangia terminal on cells of whorl-branchlets.

Tetrasporangia sessile on cells of whorl-branchlets, subspherical, tetrahedrally divided.

A tribe of 5 genera, all known from southern Australian coasts. Wollaston (1968, p. 402) divided the genera into two groups, dependent on the branching, whether there are 3 or 4 whorl-branchlets per axial cell, and the position of tetrasporangia on the whorl-branchlets.

KEY TO GENERA OF CROUANIEAE

1. Whorl-branchlets in whorls of 3. Lateral branch initials arising on axial cells and basal cells of whorl-branchlets and forming a chain of 10–20 cells before initiation of whorl-branchlets; gland cells absent. Carposporophyte developed in club-shaped branch apices with the first gonimolobe developed terminally on a rounded central cell. Tetrasporangia on basal cells of whorl-branchlets ................................................................. 2

1. Whorl-branchlets in whorls of 4. Lateral branch initials arising on basal cells of whorl-branchlets and forming a chain 2–5 cells long before initiation of whorl-branchlets (except Gulsonia); gland cells present or absent. Carposporophytes lateral on long or short branches with the first gonimolobes developed laterally on a transversely elongate central cell. Tetrasporangia on basal to outer cells of whorl-branchlets (never on basal cells only) ........................................................................................................ 3

2. Axes of thallus terete. Axial branches (1 or 2) developed at irregular intervals unilaterally near branch apices .............................................. CROUANIA

2. Axes of thallus flattened. Axial branches developed singly, regularly and bilaterally forming pinnate thallus segments ................................. GATTYA

3. Axes of thallus flattened with indeterminate and determinate branches alternately-distichously arranged ........................................ EUPTILOCLADIA

3. Axes of thallus terete with a more or less alternate-distichous arrangement of indeterminate lateral branches (irregular in Ptilocladia australis and Gulsonia); determinate short branches scattered irregularly over thallus (absent in P. australis) ........................................ 4

4. Thallus spongiose and somewhat firm (flexuous in Ptilocladia australis). Branch initials 2–5 cells long before initiation of whorl-branchlets ....... PTLILOCLADIA

4. Thallus slimy-mucilaginous and flexuous. Branch initials 16–20 cells long before initiation of whorl-branchlets ........................................... GULSONIA
**Genus CROUANIA** J. Agardh 1842: 83

*Thallus* erect, often from prostrate basal filaments, much branched with lateral branches arising from axial cells below apices and basal cells of whorl-branchlets and often developing more strongly, axial cells each with 3 whorl-branchlets branched 4–8 times and covering the axis or with axial cells exposed between whorls; laterals 10–20 cells long before initiation of whorl-branchlets; attachment by rhizoidal holdfasts; gland cells absent. Cells uninucleate.

**Reproduction.** Gametophytes dioecious. Procarps borne in place of whorl-branchlets near branch apices, with a supporting cell bearing a 4-celled carpogonial branch. Post-fertilization the auxiliary cell cuts off a terminal and then lateral gonimolobes, the carposporophyte being surrounded by whorl-branches in a rounded to clavate end of a branch. Spermatangia are cut off from outer cells of whorl-branchlets.

Tetrasporangia are borne on basal cells of whorl-branchlets, sessile, subspherical, tetrahedrally divided.

**Type species.** *C. attenuata* (C. Agardh) J. Agardh 1842: 83.

A genus of numerous species, world-wide in distribution.

### KEY TO SPECIES OF CROUANIA

1. Thallus slimy, enveloped in mucilage. Terminal cells of whorl-branchlets small, rounded
   -.................................................................................................................. 1. *C. mucosa*

2. Plants less than 4 cm high. Erect axes arising from a prostrate base. Terminal cells of whorl-branchlets mostly rounded, L/D 1–2
   -................................................................................................................. 3

3. Axial cells elongate, not increasing in L/D in central to lower thallus. Whorl-branchlet whorls becoming separated at maturity to form distinct rings; lower whorl-branchlets some times shorter
   -................................................................................................................. 2. *C. shepleyana*

4. Thallus usually 4–15 cm high. Whorl-branchlets (150–) 200–300 (–400) μm long, horizontal to slightly upwardly directed (form sometimes distorted by growth conditions, presence of epiphytes or preservation). Axial cells clearly visible throughout. Whorl-branchlets usually adjacent or almost so
   -................................................................................................................. 4. *C. robbii*

5. Thallus up to 4 cm high. Whorl-branchlets 200–450 μm long usually with their outer part directed upwards. Axes slender with widely separated whorls of whorl-branchlets
   -................................................................................................................. 5. *C. brunyana*


**FIGS 12D, 13F–L**

*Thallus* (Figs 12D, 13F) medium to dark red-brown, fading to grey-red, 2–9 cm high, very mucoid, much branched irregularly with lax, often slightly curved branches of varying length, branches terete or slightly annular, usually basally constricted, smooth surfaced, tapering slightly from 1–1.5 mm in diameter in mid thallus to 400–600 μm just below apices. Holdfast discoid, 2–8 mm across with several axes; epilithic or occasionally epiphytic. **Structure.** Apices 10–20 cells long before initiation of whorl-branchlets, cells near apices (20–) 25–30 μm in diameter and L/D 0.7–1.2, increasing to 200–300 μm in diameter and L/D 1.2–2 in lower
axes, with only slight cortication by rhizoids from the basal cells of whorl-branchlets; apices of axes often replaced and overtopped by apices from below; lateral branches arising from axial cells or the basal cell of whorl-branchlets. Whorl-branchlets 3 (Fig. 13L) per axial cell, 300–500 \( \mu m \) long, formed in spiral sequence, with 5–8 orders of (tri-) or quadrichotomies, with basal cells 20–30 \( \mu m \) in diameter and L/D 1.5–2, tapering to ovoid terminal cells 5–8 \( \mu m \) in diameter and L/D 1–1.5, often bearing a hair; terminal cells forming a continuous surface layer. Cells uninucleate; rhodoplasts discoid to elongate.

Reproduction. Gametophytes dioecious. Procarps (Fig. 13G) borne in succession near the apices of young lateral branches, replacing whorl-branchlets, with the supporting cell bearing a 4-celled carpogonial branch. Post-fertilization a connecting cell is cut off the carpogonium to connect with the auxiliary cell, which enlarges to form a foot cell and upper gonimolobe (Fig. 13H), surrounded by whorl-branchlets. Spermatangia (Fig. 13I) are borne terminally on outer cells of whorl-branchlets, elongate and dumb-bell shaped, 2–3 \( \mu m \) in diameter. Tetrasporangia (Fig. 13K, L) occur on the basal cells of whorl-branchlets, sessile, subspherical, 50–80 \( \mu m \) in diameter, tetrahedrally divided.

Type from Robe, S. Aust., lower eulittoral (Womersley, 30.viii.1949); holotype and isotypes in AD. All 088-"Marine Algae of southern Australia" No. 95.

Distribution: Elliston, S. Aust., to Port Phillip, Vic., and N Tasmania.


C. mucosa is a distinctive species, being highly mucilaginous and occurring mainly in shallow water on wave-swept rock platforms.

2. Crouania shepleyana Wollaston 1968: 241, fig. 4, pl. 2.

FIGS 12E, 14A–E

Thallus (Figs 12E, 14A) mid to dark red-brown, 1–3 cm high, erect, slender and much branched irregularly, branches terete, flexuous and annular, branch apices pointed, axes ecorticate, not mucilaginous, with 3 whorl-branchlets (Fig. 14E) per axial cell. Base prostrate, attached by multicellular rhizoids; flexuous and annular. Structure. Apices 3–10 cells long before initiation of whorl-branchlets, apical cells 10–14 \( \mu m \) in diameter and L/D 0.5–1, increasing to 80–120 (-180) \( \mu m \) in diameter and L/D 1–2 throughout lower axes; lateral branches arising from axial cells. Whorl-branchlets appearing banded on axes, 90–140 \( \mu m \) long (sometimes shorter below), branched 4–6 times, basal cells 10–15 \( \mu m \) in diameter and L/D 1–1.5, tapering to ovoid terminal cells 5–9 \( \mu m \) in diameter and L/D 1–1.5 (-2). Cells uninucleate; rhodoplasts discoid.

Reproduction. Gametophytes probably dioecious. Procarps (Fig. 14B) produced near apices of young branches, with a supporting cell bearing a 4-celled carpogonial branch. Post-fertilization the carpogonium connects to the auxiliary cell via a connecting cell and a narrow lower foot cell and upper gonimoblast cell are formed, the latter developing a terminal lobe (Fig. 14C) and later lateral lobes 250–400 \( \mu m \) across of ovoid carposporangia 30–50 \( \mu m \) in diameter, the carposporophyte being protected by surrounding whorl-branchlets (Fig. 14D). Spermatangia unknown.

Tetrasporangia (Fig. 14E) are borne on inner cells of whorl-branchlets, sessile, subspherical, (25-) 40–50 \( \mu m \) in diameter, tetrahedrally divided.
Crouania

CROUANIEAE

Type from Port Willunga, S. Aust., in drainage channels on reef (Womersley, 25.x.1964; AD, A28382).


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CROANAIEAE

Crouania


C. shepleyana is a small species, only 1–3 cm high.

3. Crouania destriana Wollaston 1968: 244, fig. 5A–D.

**FIGS 14F–H, 15A, B**

**Thallus** (Fig. 14F) medium red-brown, 5–15 (–20) mm high, slender, much branched irregularly, branches terete, apices obverse and rounded, axes ecorticate, not mucilaginous, with 3 whorl-branchlets per axial cell. Base creeping on host, attached by rhizoids from numerous axial cells; epiphytic on coralline algae (especially Metagoniolithon). **Structure.** Apices 2–4 cells long before initiation of whorl-branchlets, cells near apices 7–10 μm in diameter and L/D 0.6–1, increasing to 150–250 μm in diameter and L/D 1–1.2 in lower axes; lateral branches arising from axial cells. Whorl-branchlets closely adjacent along branches (Fig. 15A), near horizontal, 180–250 μm long, branched 6–7 times di- to quadrichotomously, basal cells 12–22 μm in diameter and L/D (1.2–) 1.5–2, tapering to ovoid terminal cells 4–6 μm in diameter and L/D 1–2. Cells uninucleate; rhodoplasts discoid.

**Reproduction.** Gametophytes dioecious. Procarps (Fig. 14G) developed in place of whorl-branchlets several axial cells below apices, with apical growth ceasing and new branches developing below the carpogonial branch. Post-fertilization a connecting cell fuses with the auxiliary cell and a terminal gonimolobe (Fig. 14H) develops, followed by 1–2 lateral gonimolobes 140–280 μm across, of ovoid carposporangia 25–40 μm in diameter; carposporophytes are surrounded by whorl-branchlets in rounded branch ends (Fig. 14F). Spermatangia (Fig. 15B) are cut off from terminal cells of whorl-branches, ovoid, 2–3 μm in diameter.

Tetrasporangia (Fig. 15A) occur on mid cells of whorl-branchlets, sessile, subspherical, 40–70 μm in diameter, tetrahedrally divided.

**Type** from D’Estrees Bay, Kangaroo I., S. Aust., drift on Metagoniolithon stelliferum (Wollaston, 23.viii.1963; AD, A27035).

**Distribution:** Tiparra Reef, Spencer Gulf and Kangaroo I. to Cape Northumberland, S. Aust. (probably more widespread).

**Selected specimens:** Tiparra Reef, S. Aust., on Metagoniolithon, 5 m deep (Shepherd, 20.viii.1971; AD, A39466) and on Amphipora acuta, 7 m deep (Shepherd, 11.i.1978; AD, A49399), Praunshaw, Kangaroo I., S. Aust., on non-geniculate coralline algae on Heterozostera, 7 m deep (Lavers, 12.vii.1996; AD, A65917), Cape Northumberland, S. Aust., on Spirodictyon, 2–3 m deep (Edyvane, 5.vi.1982; AD, A55305).

This small species of Crouania appears to be confined to the surface of coralline algae, with prostrate axes attached to the host and producing erect branches.

4. Crouania robbii Wollaston, sp. nov.

**FIG. 15C–F**

Thallus (Fig. 15C) light to medium red, erect, 4–15 cm high, slender, with terete axes bearing irregular, often pectinate, lateral branches, branch apices tapering to rounded, axes ecorticate except for slight rhizoidal cortication (Fig. 15E) on lower parts, usually not mucilaginous, with 3 whorl-branchlets per axial cell. Base prostrate, attached by rhizoids from the basal cells of whorl-branchlets; epilithic, on shells or Posidonia. **Structure.** Apical cells 5–7 μm in diameter and L/D 1–1.5, enlarging to 150–250 μm in diameter and L/D 1.5–2 (–4) in the lower axes, axial cells clearly visible throughout the thallus; lateral branches arising from axial cells. Whorl-branchlets (150–) 200–300 (–400) μm long, with 5–8 di- or trichotomies, almost horizontal or slightly upwardly directed near branch apices, outer parts almost adjacent in side view of thallus, often nodose below; basal cells of whorl-branchlets 9–16 μm in diameter and L/D 1.5–2, tapering to terminal cells 5–7 μm in diameter and L/D
Crouania (2–3–4, often with a hair. Lower axes sparsely corticated (Fig. 15E) by a few multicellular rhizoids 8–15 μm in diameter, arising from the basal cells of whorl-branchlets, not obscuring the axial cells. Cells uninucleate; rhodoplasts discoid in small cells, becoming ribbon like and branched in larger cells.

Reproduction. Gametophytes dioecious. Procarps developed in place of a whorl-branchlet on 1–3 successive subapical cells, with a supporting cell bearing a 4-celled carpogonial branch. Mature carposporophytes (Fig. 15F) have 1–3 rounded groups 200–350 μm across of ovoid carposporangia 20–35 μm across, protected by enlarged surrounding whorl-branchlets in a clavate branch end. Spermatangia occur in whorls of 2–4 cells on terminal cells of whorl-branchlets.

Tetrasporangia (Fig. 15D) occur on basal and next cells of whorl-branchlets, sessile, subspherical, 45–55 μm in diameter, tetrahedrally divided. Thallus erectus, 4–15 cm altus, tenuis; axes tereti cum ramis irregularibus, saepe pectinati, lateralibus, ecorticati praeter corticationem in partibus inferioribus exiguam rhizoidalem, haud mucilaginosam, cum 3 ramulis verticillatis per cellulum axialem. Basis prostrata, per rhizoidea e cellulis basalis ramulorum verticillatorum affixa; epithelicius in conchis, vel Posidonia. Structure. Cellulae apicales 5–7 μm diametro et L/D 1–1.5, crescentes ad 150–250 μm diametro et L/D 1.5–2 (-4) in axibus inferioribus, cellulae axiales perspicue manifestae; rami laterales e cellulis axialibus orientes. Ramuli verticillati (150–200–300 (-400) μm longi, cum 5–8 di-vel trichotomatibus, paene horizontales, partibus exterioribus paene contiguis, saepe infra nodosi; cellulae basales ramorum verticillatorum 9–16 μm diametro et L/D 1.5–2, ad cellulas terminales 5–7 μm diametro et L/D (2-) 3–4 decrescentes. Cellulae uninucleatae; rhodoplasta discoidalia in cellulis parvis, taeniformia et ramosa in cellulis majoribus.


Tetrasporangia in cellulis basi et proximis ramulorum verticillatorum, sessilia, subspericatia, 45–55 μm diametro, tetraedrice divisa. Type from 5 km W of Port Noarlunga, S. Aust., 21 m deep on shells (Ottaway, 8.xii.1980); holotype (carposporangial) and isotype (tetrasporangial) in AD, A52115.


An early collection of this species was made from the wreck of the “John Robb”, after which it is named.

5. Crouania brunyana Wollaston, sp. nov.

Thallus (Fig. 16A) 2–4 cm high, erect, axes terete, straight to slightly flexuous, irregularly branched, eocorticate apart from very sparse cortical filaments on lower axes, not mucilaginous, with the whorls and each of the 3 whorl-branchlets in each whorl (Fig. 16A) separated, exposing the axial cells (Fig. 16B), with the outer part of the whorl-branchlets directed upwards. Base erect, attached by rhizoids from lower axial cells; epizoic or on shells. Structure. Apical and subapical cells 5–8 μm in diameter and L/D 0.7–1.5, enlarging below to 80–100 μm in
diameter and L/D 3–7, and to 150–250 μm and L/D 2–3 near the base; lateral branches arising from axial cells. Whorl-branchlets (Fig. 16A, B) 200–450 μm long, with 4–6 (-8) di-or trichotomies, basal cells 15–25 μm in diameter and L/D (1-) 1.5–2, tapering to elongate terminal cells (3-) 5–7 μm in diameter and L/D 2–4 (-6), usually with a terminal hair; corticating rhizoids (Fig. 16C) very sparse, arising from basal cells. Cells uninucleate; rhodoplasts discoid, becoming ribbon like and lying lengthwise in older cells.

Reproduction. Gametophytes unknown.

Tetrasporangia (Fig. 16D) borne on lower cells of whorl-branchlets, sessile, ovoid, 22–40 μm in diameter, tetrahedrally divided.

*Thallus* 3–4cm altus, erectus; axes teretes, recti et leviter flexuosi irregulari ramosi, eocortica praeter filamenta sparssissima eocorticataque in axibus inferioribus, haud mucilagini cum 3 ramulis verticillatis separatis per cellulam axialem cellululas axiales exponentibus. Basis erecta, per rhizoidea e cellulis inferioribus axialibus affixa; epizoica vel in conchis. *Structura.* Cellulae apicales subapicalesque 5–8μm diametro et L/D 0.7–1.5, infra crescentes ad 80–100μm et L/D 3–7, et ad 150–250μm et L/D 2–3 prope basin; rami laterales e cellulis axialibus orientes. Ramuli verticillati 200–450μm longi, cum 4–6 (-8) di vel trichotomibus, cellulase basales 15–25μm diametro et L/D (1-) 1.5–2, attenuates ad cellulases elongatas et terminales (3-) 5–7μm diametro et L/D 2–4 (-6). Cellulae uninucleatae; rhodoplasta discoidea, taeniforma crescentes et in maturiores celluluses longistrorsum iacentes.

*Reproduction.* Gametophyta ignota.

Tetrasporangia in celluluses inferioribus ramulorum verticillatorum portata, sessilia, ovoidea, 22–40μm diametro, tetraedrice divisa.

*Type* from Simpson Bay, Bruny I., Tas., on coralline algae on bryozoan?, 11 m deep (Shepherd, 11.ii.1972); holotype in AD, A41616.

*Distribution:* Only known from the type specimen and from Tinderbox, Tasmania.

*Selected specimens:* Tinderbox, Tas., on coralline algae on bryozoan?*, 11 m deep (Kraft 10141 and 10142 & Sanderson, 7.xii.1993; MELU, K10141 and AD, A66990, A66991 respectively). C. *brunyana* is named from the type locality, Bruny I.

C. *brunyana*, from the holotype and Tinderbox collections, differs from C. *robbii* in having longer mid-thallus axial cells and usually shorter whorl-branchlets well separated throughout the thallus.

**Genus GATTYA** Harvey 1855a: 555

*Thallus* erect from a prostrate base, with pinnate axes, branches compressed in plane of branching, constricted at intervals related to new growth phases, sympodially branched, axial cells with 3 whorl-branchlets, closest adjacent with outer cells cohering lengthwise in a firm gelatinous sheath, lateral branches originating from axial cells, becoming 10–20 cells long before initiation of whorl-branchlets; gland cells absent. Cells uninucleate.

*Reproduction.* Gametophytes dioecious. Procarps borne in place of whorl-branchlets near branch apices, with a supporting cell bearing a 4-celled carpogonial branch. Post-fertilization connection to the auxiliary cell is via a connecting cell and an erect, rounded gonimolobe develops followed by lateral gonimolobes, surrounded by whorl-branchlets in swollen branch ends. Spermatangia are cut off from terminal cells of whorl-branchlets.

Tetrasporangia occur on basal cells of whorl-branchlets, sessile, subspherical, tetrahedrally divided.

*Type species:* G. *pinnella* Harvey 1855a: 555.

A genus of 2 species, the type and G. *obtusa* Itono (1977: 14) from Japan. Gattya has whorls of 3 whorl-branchlets as in Crouania, but differs in its complanately branched thallus with compressed branches and sympodial development of axes.
Euptilocladiaceae


**FIGS 16E, 17**

**Thallas** (Figs 16E, 17A) medium red-brown, 2–10 cm high, firm, with alternately pinnate erect axes arising from prostrate lower parts, branches sympodially branched, compressed in the plane of branching with constrictions depending on new growth phases, branches with a gelatinous sheath. Attachment by rhizoids; epiphytic on Amphibolis or larger algae.

**Structure.** Apices with a row of 3–9 short cells 6–9 μm in diameter, axial cells enlarging below to 60–90 μm in diameter and L/D 1/2, basal axial cells lightly corticated with rhizoids; lateral branches arising from axial cells. Each axial cell with 3 (rarely 4) whorl-branches 250–450 μm long, closely adjacent, branched di- or trichotomously several times, basal cells 12–25 μm in diameter and L/D 1–2, adjacent cells L/D 5–6, tapering to subspherical terminal cells 5–8 μm in diameter. Cells uninucleate; rhodoplasts ovoid in smaller cells, elongate in larger cells.

**Reproduction.** Gametophytes dioecious. Procarps (Fig. 17B, C) produced in place of a whorl-branchlet near apices, with a large supporting cell bearing a 4-celled carpogonial branch. Post-fertilization the carpogonium connects with the auxiliary cell via a connecting cell and produces an erect rounded gonimolobe and later lateral gonimolobes, each with ovoid carposporangia 25–35 μm in diameter. Carposporophytes (Fig. 17D, E) occur in swollen branch ends. Spermatangia (Fig. 17F) are cut off from terminal cells of whorl-branchlets, ovoid, 2–3 μm in diameter.

**Tetrasporangia** (Fig. 17G, H) occur on basal cells of whorl-branchlets, produced successively, sessile, subspherical, 45–60 μm in diameter, tetrahedrally divided.

**Type** from Rottnest I., W. Aust. (Harvey); lectotype in Herb. Harvey, TCD (Trav. Set 223).

**Distribution:** Houtman Abrolhos, W. Aust. (Huisman 1997), to Westernport Bay, Vic., and N Tasmania.


**Genus EUPTILOCLADIA** Wollaston 1968: 269

Thallas erect, 5–15 cm high, much branched complanately and alternately distichously for 3–5 orders, with an axial filament bearing 4 whorl-branchlets from each cell, axes corticated below with rhizoids from the basal cells of whorl-branchlets. Lateral whorl-branchlets slightly longer than transverse ones, successively branched 3–5 times and with terminal unbranched filaments of short cells. Lateral branches arising from basal cells of whorl-branchlets, 2–5 cells long before initiation of whorl-branchlets; gland cells absent. Cells uninucleate.

**Reproduction.** Gametophytes probably dioecious. Procarps borne in place of a whorl-branchlet, with a supporting cell bearing a 4-celled carpogonial branch, and the carposporophytes...
Fig. 17. Gattya pinnella (AD, A28254). A. Habit of plant on Amphibolis. B. Branch apex with relatively large supporting cell bearing a 4-celled carpogonial branch. C. Supporting cell with a carpogonial branch. D. Carposporophyte surrounded by whorl-branchlets from lower axial cells. E. Branch with carposporophytes in clavate branch apices. F. Outer cells of a whorl-branchlet with spermatangia. G. Branch with tetrasporangia. H. Tetrasporangia on basal cells of whorl-branchlets. (All as in Wollaston 1968, courtesy of Aust. J. Bot.)
with gonimolobes on a transversely elongate central cell, situated at the apices of short
determinate lateral branches and surrounded by whorl-branchlets. Spermatangia unknown.

Tetrasporangia sessile on mid cells of whorl-branchlets, tetrahedrally divided.

Type species: *E. spongiosa* Wollaston 1968: 269.

A genus of 3 species, two from southern Australia and *E. magruderi* Abbott & Norris
(1993, p. 451) from the Hawaiian Islands, distinguished by the complanately branched thalli
with 4 whorl-branchlets, 2 longer ones in the plane of branching, and terminal rows of short
cells to the whorl-branchlets.

**KEY TO SPECIES OF EUPITOCLADIA**

1. Whorl-branchlets with terminal rows of more-or-less isodiametric cells 8–10 μm in
diameter; tetrasporangia 35–60 μm in diameter ........................................... 1. *E. spongiosa*

1. Whorl-branchlets with terminal rows of cells with L/D 1–1.5 and 14–22 μm in diameter;
tetrasporangia 80–130 μm in diameter ........................................... 2. *E. villosa*


*Ptilocladia pulchra* sensu J. Agardh 1851: 113; 1876: 89. Bastow 1899: pl. 2 fig. 62.

**FIGS 18A, 19A–F**

*Thallus* (Fig. 18A) medium to dark red-brown, 5–18 cm high, spongiose, more or
less alternately distichously branched (Fig. 19A) throughout, usually with a single main
axis, much branched above for 4 or 5 orders, axes compressed, 1–4 mm broad, decreasing
gradually to lesser branches 0.5–1 mm broad; main branches usually with numerous
short, distichous, terete laterals (Fig. 19A) 1–5 mm long; branches completely covered
by whorl-branchlets. Holdfast conical, rhizoidal, 1–3 mm across; epilithic or occasionally
epiphytic. **Structure.** Axes with small apical cells enlarging to 90–150 μm in diameter and
L/D 1–1.5, each cell with 4 whorl-branchlets (Fig. 19B) initiated very close to apices of
axes, with 2 opposite longer branchlets 400–650 μm and 10–14 cells long, branched 6–8
times with terminal rows of 3–8 cells, and 2 opposite shorter branchlets 180–300 μm and
8–10 cells long; lower cells of whorl-branchlets thick walled, 50–90 μm in diameter and
L/D 1–1.6, tapering to rows of small cells 8–10 μm in diameter and L/D 1–1.5. Lateral
branches arise from the basal cells of whorl-branchlets and the axial cells become heavily
corticated by rhizoids from the basal and inner cells of whorl-branchlets (Fig. 19C). Cells
uninnucleate; rhodoplasts discoid.

**Reproduction.** Gametophytes probably dioecious. Procarps (Fig. 19D) borne in place of
a whorl-branchlet several cells below apices, with a supporting cell bearing a 4-celled
carposporangial branch; post-fertilization the auxiliary cell forms a lower foot cell and a laterally
elongate cell which cuts off 2 gonimolobes (Fig. 19E) and later further ones, 90–120 μm
across with somewhat angular carposporangia 20–30 μm across. Mature carposporophytes
are surrounded by whorl-branchlets in short determinate branches (Fig. 19A). Spermatangia
unknown.

Tetrasporangia (Fig. 19F) are borne on central cells of the whorl-branchlets, sessile,
subspherical, 35–55 μm in diameter, tetrahedrally divided.

*Type from Robe, S. Aust., drift (Wollaston, 18.v.1964); holotype and isotypes in AD, A27925.*

**Distribution:** Houtman Abrolhos, W. Aust. (Huisman 1997), to Waratah Bay, Victoria.

2. Euptilocladia villosa Wollaston 1968: 275, figs 14I–P, pl. 5.

**FIGS 18B, 19G–I**

**Thallus** (Fig. 18B) medium to dark red-brown, 5–15 cm high, spongiose, more or less alternately distichously branched, with a branched main axis and strongly developed lateral branches, branched for 4 or 5 orders, axes slightly compressed, 1–2 mm broad, decreasing gradually to lesser branches 0.3–1 mm broad; main branches with numerous short, distichous, terete laterals 1–3 (-4) mm long; branches largely covered by whorl-branchlets except near apices where axial cells are visible between the whorls; lower branches heavily corticate with coarse rhizoids. Holdfast conical, rhizoidal, 1-4 mm across; epilithic. **Structure.** Axes with small apical cells, subapical cells 12–22 \( \mu \)m in diameter and L/D 1–1.5, enlarging to 200–350 \( \mu \)m in diameter and L/D 1–1.5 in lower thallus, each cell with 4 whorl-branchlets (Fig. 19H), thick walled, two opposite longer ones (in the plane of thallus branching) 0.5–1 mm and 7–11 cells long, subdichotomously branched 5–6 times with upwardly curved terminal rows of 3–7 cells, and 2 opposite shorter branchlets 250–500 \( \mu \)m and 5–6 cells long; basal cells of whorl-branchlets 60–90 \( \mu \)m in diameter and L/D 1.2–1.6, tapering to the terminal rows of short cells 14–22 \( \mu \)m in diameter and L/D 1–1.5. Lateral branches arise from the basal cells of whorl-branchlets and the axial cells become heavily corticated by entwined rhizoids 25–40 \( \mu \)m in diameter from inner cells of whorl-branchlets. Cells uninucleate; rhodoplasts elongate to ribbon like.

**Reproduction.** Procarps as in *E. spongiosa*, producing post-fertilization gonimolobes 200–500 \( \mu \)m across of ovoid carposporangia 16–25 \( \mu \)m in diameter, surrounded by whorl-branchlets in short determinate branches. Spermatangia unknown. Tetrasporangia (Fig. 19G, I) sessile on mid and outer cells of whorl-branchlets, subspherical when mature, 80–130 \( \mu \)m in diameter, tetrahedrally divided.

**Type** from Robe, S. Aust., drift (Wollaston, 6.v.1965); holotype in AD, A29282.

**Distribution:** Elliston to Cape Northumberland, S. Aust.


*E. villosa* is very similar in habit to *E. spongiosa* but differs in the whorl-branchlets having longer cells in the terminal rows, and in having larger tetrasporangia.

**Genus PTILOCLADIA** Sonder 1845: 52

**Thallus** erect, much branched irregularly radially with lateral branches arising from the basal cell of whorl-branchlets, axial cells with 4 equal length whorl-branchlets branched several times, the whorls either covering the axis or separated and exposing the axial cells; axes of branches densely, slightly or not covered by corticating rhizoids originating from the basal cells of whorl-branchlets and descending within the gelatinous sheath of the axial cells; lateral branches arising from basal cells of whorl-branchlets, 2-5 cells long before whorl-branchlet initiation; pyriform gland cells present or absent; attachment by rhizoids. Cells uninucleate.

**Reproduction.** Gametophytes dioecious. Procarps borne on the basal cell of whorl-branchlets which may or may not have further cells, with a supporting cell bearing a 4-celled carpogonial branch. Post-fertilization the auxiliary cell cuts off an upper cell which extends horizontally and produces 2 lateral gonimolobes, all cells becoming carposporangia, and often
later gonimolobes. The carposporophyte is protected by enlarged and surrounding adjacent whorl-branchlets. Spermatangia are cut off via initials from the outer cells of whorl-branchlets. Tetrasporangia are borne on mid cells of whorl-branchlets, sessile, ovoid to subspherical, tetrahedrally divided.

Type species: *P. pulchra* Sonder 1845: 52.


**KEY TO SPECIES OF PTILOCLADIA**

1. Thallus relatively robust (lower branches 1–2 mm in diameter), clothed with closely adjacent whorls of whorl-branchlets from the apices down, densely corticated with rhizoidal filaments within the gelatinous sheath of the axial cells; whorl-branchlets with terminal rows of 2–3 subspherical to ovoid cells ................................................. 2

2. Thallus slender (lower branches 0.5–1 mm in diameter), with the whorl-branchlet whorls mostly separated and exposing the axial cells between them, cortication absent or slight and starting well below the branch apices; whorl-branchlets with single, elongate (L/D 1.5–2.5) terminal cells .................................................................

3. Thallus mostly ecorticate, whorls of whorl-branchlets separated throughout thallus, gland cells present ................................................................. 3. *P. australis*

3. Thallus corticated below, whorls of whorl-branchlets distinctly to slightly separated, gland cells present or absent ................................................................. 4

4. Cortication relatively loose, spreading from the nodes, filaments largely outside the axial cell wall sheath; gland cells absent; tetrasporangia large, 80–100 μm in diameter ................................................................. 4. *P. gracilis*

4. Cortication compact, of appressed filaments within the axial cell wall sheath; gland cells present; tetrasporangia small, 20–30 μm in diameter ....... 5. *P. crouanioides*


Wollaston 1968: 255, figs 9F–S, 10, pl. 3.

*Wrangelia agardhiana* Harvey 1855a: 545.


*Ptilocladia agardhiana* (Harvey)Wollaston 1968: 261, fig. 9A–E.


**Thallus** (Figs 18C, 21A) medium to dark red-brown, 5–15 (-30) cm high, spongiose, branches terete, alternately subdistichous to irregular, usually pyramidal in form with long axes or lateral branches and progressively shorter second and third order laterals towards their apices; branches completely covered with whorl-branchlets; axes and lower branches 1–2 mm in diameter; decreasing gradually to 0.6–1 mm in diameter near branch apices. Holdfast rhizoidal, 1–3 mm across; epilithic. **Structure.** Axes with short apical cells 12–15 μm in diameter and L/D 0.5–1, increasing to 350–500 μm in diameter and L/D 1–2 in lower

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thallus, becoming densely corticate with entwined rhizoids from the basal cells of whorl-branchlets, with cells of the inner layer of rhizoids enlarging and the outer layer producing scattered, anticlinal, short filaments; lateral branches arising from the basal cell of whorl-branchlets. Whorl-branchlets in whorls of 4 (Fig. 21E) per axial cell, 300–450 μm long.

di- or trichotomous 5–7 times, basal cells 50–80 μm in diameter and L/D 1–1.5, tapering to terminal cells 10–15 μm in diameter and L/D 1–1.5, terminating in a short row of 2–3 ovoid cells, often with a hair; gland cells absent, mature axial cells often containing crystal-like inclusions. Cells uninucleate; rhodoplasts elongate, ribbon like in larger cells.

Reproduction. Gametophytes dioecious. Procarps (Fig. 21B) situated on the basal cell of shorter whorl-branchlets several cells below the apices of short determinate branches, with a supporting cell bearing a curved, 4-celled, carpogonial branch. Post-fertilization fusion with the auxiliary cell occurs via a connecting cell and the auxiliary cell divides to a lower foot cell and an upper cell which produces 2–3 successive, lateral, rounded gonimolobes (Fig. 21C). Tetrasporangia (Fig. 21E) occur on mid-cells of whorl-branchlets, sessile, subspherical to ovoid, 50–75 μm in diameter, tetrahedrally to subcucruciately divided.

Type from “Nov. Holl. austro occid.” (Preiss); holotype in MEL, 8445.

Distribution: Near Fremantle, W. Aust., to Queenscliff, Vic., and N Tasmania.


P. pulchra is often common in pools on rough-water coasts, extending to 13 m deep. P. agardhiana is identical in structure with P. pulchra, differing only relatively slightly in habit, being less pyramidal. It may be a more sheltered habitat form, and intergrades occur between typical P. pulchra and P. agardhiana; the two ‘species’ are here combined.


**FIGS 18D–F, 21F–I**

Thallus (Figs 18D, 21F) medium grey-red, 2–8 (~10) cm high, spongy, branches terete, irregularly to more or less alternately distichously branched, branches completely covered with whorl-branchlets except near active apices; axes and lower branches 1–2 mm in diameter, tapering to 150–300 μm near apices. Holdfast small, rhizoidal, 1–2 mm across; epiphytic on *Posidonia, Amphibolis* and various algae. Structure. Axes with short apical cells, enlarging to 20–25 μm in diameter and L/D 1–1.5 within a few cells, and increasing to 250–400 μm in diameter and L/D 2–2.5 in lower thallus, becoming corticate below (Fig. 21G) with rhizoids from the basal cell of whorl-branchlets, with anticlinal filaments from the rhizoids in older parts. Whorl-branchlets in whorls of 4, 150–500 μm long, directed obliquely upwards, branched several times, basal cells 25–35 μm in diameter and L/D 2–2.5, tapering to short chains of terminal cells 7–10 μm in diameter and L/D 1.5–3; pyriform gland cells common on the whorl-branchlets; lateral branches arising from the basal cell of whorl-branchlets. Cells uninucleate; rhodoplasts elongate in smaller cells to ribbon like and anastomosing in larger cells.
Reproduction. Gametophytes dioecious. Procarps (Fig. 21H) replacing whorl-branchlets near branch apices, with a supporting cell bearing a 4-celled carposporangial branch. Post-fertilization the auxiliary cell cuts off an upper cell which produces a rounded gonimolobe 200–500 μm across, with ovoid carposporangia 25–40 μm across, followed by later gonimolobes (Fig. 21H); the carposporophyte (Fig. 21F, I) lies on elongate branches, surrounded by adjacent whorl-branchlets. Spermatangia (Fig. 18E) are cut off from terminal cells of whorl-branchlets, ovoid, 3–4 μm in diameter. Tetrasporangia (Fig. 18F) occur on lower cells of whorl-branchlets, sessile, subspherical, 45–65 μm in diameter, tetrahedrally divided.

Type from Rottnest I., W. Aust., on "Zostera" (Posidonia) (Harvey); lectotype in Herb. Harvey, TCD (Trav. Set 338).


P. vestita appears to be usually epiphytic, especially on coralline algae often themselves on seagrasses or robust algae. It differs from P. pulchra in details of the rhizoidal cortication, in usually having abundant gland cells on the whorl-branchlets, and in the position of the carposporophytes.


FIGS 20A, 22A–F

Thallus (Figs 20A, 22A) light to dark red-brown, 3–8 cm high, slender, much branched irregularly, branches terete, with whorls of whorl-branchlets (Fig. 22A) distinctly separated over most of thallus leaving the axial cells exposed between them, in lower parts covering most of the axes, lower branches 0.7–1 mm in diameter, tapering to 150–360 μm near apices. Attachment by rhizoids from axial cells and basal cells of whorl-branchlets; mainly epiphytic on Posidonia and larger algae. Structure. Axes with short apical cells, enlarging within a few cells to 10–15 μm in diameter and L/D 1–1.5, and increasing to 150–300 μm in diameter and L/D 3–5 in mid and lower parts, often short (L/D about 1) near the base; axial cells mostly remaining ecorcite, older axes with slight rhizoidal cortication; lateral branches arising from basal cells of whorl-branchlets, Whorl-branchlets in whorls of 4, 120–270 μm long, outer parts curved upwards, branched several times, basal cells 15–25 μm in diameter and L/D 1.5–2, tapering to terminal cells 7–9 μm in diameter and L/D 1.5–2, often with a hair; pyriform gland cells (Fig. 22B) occur on the whorl-branchlets. Cells uninucleate; rhodoplasts discoid to elongate in smaller cells, ribbon like and orientated lengthwise in axial cells.

Reproduction. Gametophytes dioecious. Procarps (Fig. 22B, C) replacing whorl-branchlets, with a supporting cell bearing a curved 4-celled carpogonial branch (Fig. 22C), and with growth
of the branch axis continuing with further procarps. Post-fertilization the auxiliary cell divides and the upper cell produces lateral lobes (Fig. 22D) 150–300 μm across of ovoid carposporangia 25–35 μm in diameter, the carposporophyte (Fig. 22A) being protected by adjacent whorl-branchlets. Spermangia (Fig. 22E) are cut off from terminal cells of whorl-branchlets, ovoid, 2–3 μm in diameter.

Tetrasporangia (Fig. 22F) occur on lower cells of whorl-branchlets, sessile, subspherical, 30–70 μm in diameter, tetrabedrally divided.

Type from King George Sound, W. Aust. (Harvey); lectotype in Herb. Harvey, TCD (Alg. Aust. Exsicc. 485, isolectotype in AD, A18290).


P. australis is the most slender species of Ptilocladia in southern Australia, distinguished by the discrete, separated, whorls with the axial cells clear between the whorls. It is commonest as an epiphyte on Posidonia and some algae in sheltered waters.

Fig. 23. A–E. Ptilocladia crouanioides (A, AD, A48322; B, AD, A38377; C, AD, A37692; D, E, AD, A62191). A. Habit. B. Young branches. C. Young branch with gland cells on whorl-branchlets. D. Young branches with carposporophytes. E. Older corticated axis with young lateral bearing a carposporophyte. F. Gulsonia annulata (AD, A20059). Habit.


**FIG. 20B–F**

Thallus (Fig. 20B) 3–18 cm high, medium red to grey-red, slender, irregularly much branched, branches terete with distinct and separated whorls (Fig. 20C) of whorl-branchlets, branches 500–700 μm in diameter in lower thallus, tapering to 130–180 μm in diameter just below apices. Holdfast small (0.2–0.5 mm across), rhizoidal; probably epilithic. Structure. Axes with short apical cells 10–15 μm in diameter and L/D 0.5–1, in young branches axial cells 20–30 μm in diameter and L/D 3–4, increasing to 200–400 μm in diameter and L/D 1–2 in lower thallus, becoming corticate well below the apices but cortical filaments (Fig. 20E) relatively loose and outside the wall sheath, spreading from the nodes, 10–25 μm in diameter with long cells and numerous branched anticlinal filaments. Lateral branches originating from axial cells. Whorl-branchlets 4 per axial cell, 100–180 μm and 6–8 cells long, subdichotomous or trichotomous basally, basal cells 20–25 μm in diameter and L/D 1.2–1.5, tapering to terminal cells 6–10 μm in diameter and L/D 2–2.5; gland cells absent. Cells uninucleate; rhodoplasts discoid, in rows or ribbon-like in older cells.

Reproduction. Gametophytes dioecious. Procarps on axial cells, replacing a whorl-branchlet, with a larger, rounded, supporting cell bearing a 4-celled carpogonia branch. Post-fertilization the auxiliary cell produces a single gonimolobe 90–160 μm across of ovoid carposporangia 25–45 μm in diameter, surrounded by considerably longer whorl-branchlets (Fig. 20F) from lower cells. Spermatangia unknown. Tetrasporangia (Fig. 20D) occur mostly on basal cells of whorl-branchlets, sessile, subcylindrical, 80–100 μm in diameter, tetrahedrally divided.

**Type** from Tasmania (Gunn); holotype in Herb. Agardh, LD, 20269, isotype in MEL, 8438.

**Distribution:** N Tasmania and Investigator Strait, S. Australia.

**Selected specimens:** Investigator Strait, S. Aust., 33 m and 34 m deep (Watson, 20.i.1971; AD, A38585 and AD, A39208), 33 m deep (Watson, 4.i.1971; AD, A41083) and 31 m deep (Watson, 23.i.1971; AD, A41096).

*P. gracilis* is a slender species characterised by whorls of 4 whorl-branchlets, absence of gland cells, loose cortication with filaments at least largely outside the axial cell sheath, and very large tetrasporangia (80–100 μm in diameter). These features are shown in the type, which probably came from the north coast of Tasmania, and in the above deep-water specimens from Investigator Strait, though the latter are smaller (4–8 cm high) than the 18 cm high type specimen.


**FIG. 23A–E**

Thallus (Fig. 23A) medium red-brown, 2–8 cm high, erect, irregularly much branched, branches terete with distinct and slightly separated whorls of whorl-branchlets near apices (Fig. 23B), closely adjacent in mid thallus and separated on lower corticated parts, branches 500–850 μm in diameter below, tapering to 180–280 μm in diameter just below apices. Holdfast small, rhizoidal; epiphytic on *Posidonia*, *Amphibolis* or coralline or other algae. Structure. Axes with short apical cells 6–10 μm in diameter and L/D 1–1.2, axial cells in young branches 15–30 μm in diameter and L/D 2–3, increasing to 200–350 μm in diameter and L/D 1.5–2 in lower thallus, becoming corticate 10–20 cells below apices with compact cortical filaments (Fig. 23E) within the axial cell sheath, with many branched anticlinal filaments. Lateral branches originating from axial cells. Whorl-branchlets 4 per axial cell, 140–250 μm and 6–8 cells long, dif- (or tri-) or dichotomously branched, basal cells 20–30 μm in diameter and L/D 1–2, tapering to terminal cells 4–7 μm in diameter and L/D 1.5–2.5, often with hairs; gland cells (Fig. 23C) usually numerous near branch apices, pyriform to subcylindrical. Cells uninucleate; rhodoplasts discoid, ribbon like in larger cells.
Reproduction. Gametophytes dioecious. Procarps appear to be borne on mid cells of whorl-branchlets, with a supporting cell bearing a 4-celled carpogonial branch. Post-fertilization the auxiliary cell produces 1-3 gonimolobes 50-100 \( \mu \text{m} \) across of ovoid carposporangia 9-12 \( \mu \text{m} \) in diameter, loosely surrounded by whorl-branchlets (Fig. 23D, E). Spermatangia unknown. Tetrasporangia occur on mid cells of whorl-branchlets, sessile, subspherical, 20-30 \( \mu \text{m} \) in diameter, tetrahedrally divided.

**Type** from Tasmania (Stuart); holotype in MEL, 8458.

**Distribution:** Waldegrave I., S. Aust., to Walkerville, Vic., and N Tasmania.


**P. crouanioides** is similar to **P. vestita** but is generally slenderer, with whorls of whorl-branchlets separated throughout most of the thallus, and has distinctly smaller tetrasporangia than the latter. The procarp situation needs further study from fresh collections.

**Genus GULSONIA** Harvey 1855b: 334

**Thallus** erect, 5-30 cm high, very mucilaginous, irregularly much branched, branches terete with annihilations of the whorls of whorl-branchlets, whorls of 4 equal whorl-branchlets, branched several times often with terminal hairs and gland cells. Lateral branches arising from basal cells of whorl-branchlets, with long rows of cells before initiation of whorl-branchlets. Mature axes corticated with rhizoids from basal cells of whorl-branchlets, dense below. Cells uninucleate.

**Reproduction.** Gametophytes dioecious. Procarps borne singly or opposite on axial cells of short lateral branches which cease vegetative growth, with a supporting cell bearing a 4-celled carpogonial branch, developing post-fertilization one to a few rounded gonimolobes surrounded by whorl-branchlets from below. Spermatangia are cut off terminally from end cells of whorl-branchlets.

Tetrasporangia sessile on mid and outer cells of whorl-branchlets, subspherical, tetrahedrally divided.

**Type species:** *G. annulata* Harvey 1855b: 334.

A genus of 2 species, the type and *G. mediterranea* Kylin (1956, p. 373) from the Mediterranean, distinguished by the very mucilaginous thallus, whorls of 4 equal whorl-branchlets, lateral branches arising only from the basal cell of whorl-branchlets, and branch initials many cells long before initiation of their whorl-branchlets.


**FIG. 23F, 24**

**Thallus** (Fig. 23F) medium to dark red-brown, 5-20 (-30) cm high, very mucilaginous, much branched irregularly with one to a few main axes and long lateral branches with conspicuous annihilations (Fig. 24A) due to the whorls of whorl-branchlets; branches terete, 1-2.5 mm in diameter below, tapering to 0.2-0.5 mm in diameter shortly below apices. Holdfast
discoid, 1–5 mm across; epilithic. Structure. Apical cells 10–12 μm in diameter and L/D 0.5–1, increasing shortly below apices to 20–30 μm in diameter and L/D 1.2–1.5, and in

lower thallus to 250–500 μm in diameter and L/D 1.2–1.5. Lateral branches (Fig. 24B) originating from the basal cells of whorl-branchlets, becoming 16–20 cells long before initiating whorl-branchlets. Axial cells each with 4 whorl-branchlets of equal size (Fig. 24F), 350–750 μm long, forming annulations with the axial cells (or cortication) visible between them except near branch apices; whorl-branchlets branched 5–7 times di- or trichotomously, basal cells 35–75 μm in diameter and L/D 1–1.5, tapering to terminal cells 8–12 μm in diameter and L/D 1.2–2, often with terminal hairs; pyriform gland-cells (Fig. 24G) occur on mid cells of the whorl-branchlets, often with crystal-like inclusions. Mature axes are corticated by rhizoids from the basal cells of whorl-branchlets, becoming dense below. Cells uninucleate; rhodoplasts elongate, ribbon like in older cells.

Reproduction. Gametophytes dioecious. Procarps (Fig. 24C) single or opposite below the apices of short lateral branches which cease further growth; the supporting cell bears a curved 4-celled carpogonial branch, and post-fertilization a connecting cell is cut off and fuses with the auxiliary cell which forms a lower foot cell and an upper cell which develops successive rounded gonimolobes (Fig. 24D) 90–140 μm across of ovoid carposporangia 20–25 μm in diameter; lower whorl-branchlets surround the carposporophyte (Fig. 24D). Spermatangia (Fig. 24E) are cut off terminally on outer cells of the whorl-branchlets, ovoid or constricted, 3.5–5 μm in diameter.

Tetrasporangia (Fig. 24G) occur on third-order cells of the whorl-branchlets, sessile, subspherical, 60–120 μm in diameter.

Type from Phillip I., Western Port, Vic. (Harvey); lectotype in MEL, 517745. No type specimen could be located in TCD (1975), but the MEL specimen is labelled "396. Phillip I., Western Port, rare, W.H.H. Gulsonia annulata H. nov. gen."

Distribution: Hopetoun, W. Aust., to Phillip I., Vic., and N and E Tasmania.


G. annulata is a deep-water species known mainly from the drift, distinguished by its extremely mucilaginous thallus with prominent annular rings of the whorl-branchlets, though these are best seen in the mid thallus of most plants.

Tribe DASYPHILEAE Schmitz 1889: 450

by E.M. Wollaston & H.B.S. Womersley

Thallus erect, axes and laterals branched strictly alternately and distichously with a consistent pattern, apical cells of axes more or less transversely divided, cutting off subapically 5 or 6 whorl-branchlets (including lateral branches) in a modified alternating sequence, each branched 3–6 times trichotomously to laterally, whorls closely adjacent, axes corticated below with rhizoids; gland cells present or absent. Cells uninucleate.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes dioecious. Procarps borne on basal cells of whorl-branchlets, supporting cell cut off separately or a vegetative cell; gonimoblast with elongate, often branched, stalk cells bearing the lobes of carposporangia, and the lower part of the auxiliary
cell becoming pit-connected to the fertile axial cell. Spermatangia, where known, cut off from short lateral branches of the whorl-branchlets.

Tetrasporangia borne on the whorl-branchlets, sessile or terminal on short lateral branches, tetrahedrally divided.

A tribe of 2 genera, *Dasyphila* Sonder and *Muellerena* Schmitz (see Wollaston 1977a). Wollaston (1977a, p. 450) recognises the tribe Dasyphileae on the basis of its consistent branching pattern, whorls of 5 or 6 whorl-branchlets, and the elongate stalk cells to the carposporangial groups, together with the presence of a secondary pit-connection between the lower part of the auxiliary cell and the fertile axial cell. The 2 genera are regarded as advanced forms developed from the Crouanioidae.

**KEY TO GENERA OF DASYPHILEAE**

1. Axial cells with whorls of 6 whorl-branchlets; carposporophyte covered only by whorl-branchlets; tetrasporangia terminal on short pedicels .............................................. *DASYPHILA*

1. Axial cells with whorls of 5 whorl-branchlets; carposporophyte with involucral branchlets arising from sterile cells adjacent to the procarp; tetrasporangia sessile ...... *MUELLERENA*

**Genus DASYPHILA** Sonder 1845: 53

*Thallus* erect, 5–20 cm high, consistently alternately distichously branched, axes and branches terete, densely corticated below by rhizoids from basal cells of whorl-branchlets. Apical cells of axes dividing transversely or slightly obliquely, subapical cells developing whorls of 6 whorl-branchlets in largely alternating sequence, whorl-branchlets basally usually trichotomous and laterally branched above; gland cells absent. Cells uninucleate.

**Reproduction.** Gametophytes dioecious. Procarps borne on the basal (=supporting) cell of young whorl-branchlets, with a 4-celled carpogonial branch; the auxiliary cell divides to form a lower cell pit-connected to the axial cell and an upper gonioblast cell which develops successive groups of carposporangia, each with a long stalk cell and surrounded by whorl-branchlets from below but not a special involucre. Spermatangia are borne on short branches on outer cells of whorl-branchlets.

Tetrasporangia occur on outer cells of whorl-branchlets, terminal on short pedicels, tetrahedrally divided.

**Type species:** *D. preissii* Sonder 1845: 53.


**FIGS 25A, 26**

*Thallus* (Fig. 25A) mid to dark red-brown, 5–20 cm high, consistently distichously branched for 4–5 orders with alternate lateral branches (Fig. 26A) throughout, axes and branches terete or very slightly compressed, densely corticated with rhizoids from close to apices with the whorl-branchlets largely outside the cortication. Holdfast discoid, rhizoidal, 1–3 mm across; epilithic or epiphytic on larger algae. **Structure.** Apical cells dividing transversely or slightly obliquely, subapical cells cutting off 6 whorl-branchlets (Fig. 26B) in a largely alternating sequence, with lateral branches arising from the first or fourth formed whorl-branchlet (2–4) 4–6 axial cells apart. Axial cells enlarging from 6–10 μm in diameter and L/D 1.2 just below the apices to 300–400 μm in diameter and L/D 1.5–4 in lower parts, becoming corticated by descending rhizoidal filaments from the basal cell of whorl-branchlets, rhizoids 5–8 μm in
Diameter with cells L/D 4–8, forming a dense layer 200–500 (–800) μm thick. Whorl-branchlets 300–400 μm long, basal cells (becoming buried in cortex) 10–18 μm in diameter and L/D 1–1.5, branching above with usually 3 filaments then laterally branched with ultimate branches several cells long, 8–11 (–15) μm in diameter and L/D 1–1.3; gland cells absent. Cells uninucleate; rhodoplasts discoid.

Reproduction. Gametophytes dioecious. Procarps (Fig. 26C) borne on the basal cell (which acts as the supporting cell) of young whorl-branchlets, in succession as the apex elongates but

only one maturing at each tip. Carpogonial branches 4-celled, with an auxiliary cell cut off from the supporting cell and an upper gonimoblast cell which develops elongate stalk cells (Fig. 26D) each bearing a rounded group 90–200 μm across of carposporangia 10–15 μm in diameter, situated at branch apices and covered by adjacent elongate whorl-branchlets but not a special involucre. Spermatangia (Fig. 26E) are borne on short branches on outer cells of whorl-branchlets, ovoid, 3–5 μm in diameter.

Tetrasporangia (Fig. 26B) occur terminally on end cells of whorl-branchlets, subspherical, 25–35 μm in diameter, tetrahedrally divided.

Type from W. Aust. (Preiss); lectotype in BM (not located in MEL).

Distribution: Geraldton and Houtman Abrolhos, W. Aust., to Wilsons Prom., Vic., and N Tasmania.


Genus MUELLERENA Schmitz in Schmitz & Hauptfleisch 1897: 496

Thallus erect, 3–13 cm high, consistently alternately distichously branched, axes and branches terete, corticated with rhizoids from basal cells of whorl-branchlets. Apical cells of axes dividing transversely, lateral branches alternate, 2 cells apart, subapical cells developing whorls of 5 whorl-branchlets in alternating sequence, whorl-branchlets di- or trichotomous several times, with gland cells. Cells uninucleate.

Reproduction. Procarps on short special branches on basal cells of whorl-branchlets, with the supporting cell bearing a sterile cell and a 4-celled carpogonial branch. Diploidisation via a connecting cell with the auxiliary cell pit-connecting to the apical cell of the fertile axis and cutting off an upper gonimoblast cell which produces successive lobes of carposporangia on elongate stalk cells. Sterile cells adjacent to the procarp and on the supporting cell form loose involutional filaments around the carposporophyte. Spermatangia unknown.

Tetrasporangia borne on cells of the whorl-branchlets, sessile, tetrahedrally divided.

Type species: M. wattsii (Harvey) Schmitz in Schmitz & Hauptfleisch 1897: 496.

Muellerena wattsii has been described in detail by Wollaston (1972) and shown to belong to the Dasyphyllaeae by Wollaston (1977a. p. 450). The genus is probably monotypic.


FIGS 25B, 27

Thallus (Fig. 25B) mid to dark red-brown, 3–13 cm high, consistently distichously and alternately branched throughout for 4 (-5) orders, axes and branches terete. Holdfast discoid, rhizoidal, 1–2 mm across; epiphytic on larger algae or epilithic(?). Structure. Apical cells dividing transversely, cutting off from subapical cells whorls of 5 whorl-branchlets (Fig.
in alternating sequence, with lateral branches (curved when young) replacing one of the whorl-branchlets and arising alternately 2 axial cells apart (Fig. 27A). Axial cells enlarging from 15-30 μm in diameter and L/D 1–1.3 just below apices to 100–200 μm in diameter and L/D 1–1.5 in the lower thallus, becoming densely corticated by descending rhizoids (Fig. 27B) from the basal cells of whorl-branchlets, with short outward filaments. Whorl-branchlets (Fig. 27F) 90–140 μm long, 3–5 times di- or trichotomous, basal cells 25–40 μm

**Fig. 26. Dasyphila preissii** (AD, uncertain). A. Diagram of branch apex with main axis overtopped by laterals. B. Transverse section of branch with 6 whorl-branchlets bearing terminal tetrasporangia. C. Axial cells with carpogonial branches. D. Axial cells with several gonimolobes of a carposporophyte. E. Terminal spermatangia on filaments of a whorl-branchlet. (All as in Wollaston 1977, courtesy of Phycologia.)
in diameter and L/D 1–1.5, tapering to rounded end cells 8–12 μm in diameter and L/D 1–1.2, often with a hair; gland cells frequent on whorl-branchlets, ovoid to pyriform, 8–18 μm in diameter. Cells uninucleate; rhodoplasts discoid to ribbon-like and often reticulate in older cells.

Reproduction. Gametophytes probably dioecious. Procarps (Fig. 27C) borne on short, 2 (-3)-celled special branches borne usually on the basal cell of whorl-branchlets, with a supporting cell (which also cuts off a sterile cell) bearing a 4-celled carpogonial branch (Fig. 27D) as part of a whorl of 4 cells. Post-fertilization the 3 sterile cells, and the sterile cell on the supporting cell, enlarge and develop branched involucral filaments. A connecting cell occurs between the carpogonium and auxiliary cell which cuts off an upper gonimoblast cell and also pit-connects to the apical cell of the fertile axis. Several rounded gonimolobes (Fig. 27E) develop successively, becoming 50–150 μm across with carposporangia 10–15 μm across, surrounded by the involucral filaments. Spermatangia unknown.

Tetrasporangia (Fig. 27F) are borne on outer cells of the whorl-branchlets, sessile, subspherical, 20–28 μm in diameter, tetrahedrally divided.

**Type** from Warrnambool, Vic. (Watts, Sept. 1860); lectotype in Herb. Harvey, TCD (Alg. Aust. Exsiccat. 221).

**Distribution:** Seal Bay, Kangaroo I., S. Aust. to Point Roadknight, Victoria.


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**Fig. 27.** *Muellerena wattsii.* A. Branch apex with distichous laterals on alternate axial cells and development of lateral whorl-branchlets (transverse whorl-branchlets omitted). B. Descending cortical rhizoids from basal cell of a whorl-branchlet. C. Carpogonial branch on short special branch borne on basal cell of a whorl-branchlet. D. A carpogonial branch. E. Carposporophyte with 3 gonimolobes and fusion between auxiliary cell and axial cell. F. Transverse section of branch with 3 whorl-branchlets and terminal tetrasporangia. (All as in Wollaston 1972, courtesy of Roy. Soc. S. Aust.)
Tribe SPHONDYLOTHAMNIEAE Feldmann-Mazoyer 1941: 240
by H.B.S. Womersley

*Thallus* usually 5–20 cm high, much branched radially or distichously, axial cells with 2 to 5 whorl-branchlets, clearly separated on the indeterminate branches; indeterminate laterals formed directly on axial cells; cortication when present by descending rhizoids from basal cells of whorl-branchlets or from lower ends of axial cells; gland cells absent. Cells multinucleate.

*Life history* triphasic with isomorphic gametophytes and tetrasporophytes.

*Reproduction.* Gametophytes dioecious. Procarps on the subapical cell of the female axis, enclosed in a gelatinous sheath together with associated sterile cells, with 1 or 2 auxiliary cells per procarp; fusion cell involving lower gonimoblast cells and usually (except *Drewiana*) the subapical cell of the female axis; carposporangia terminal; sterile cells associated with the procarp dividing post-fertilization to form an inner involucrum surrounded by an outer involucrum of branchlets from lower cells of the fertile axis. Spermatangia formed in compact glochular heads on cells of the whorl-branchlets.

Meiosporangia formed on cells of the whorl-branchlets, tetrahedrally or polyhedrally divided.

The tribe *Sphondylothamnieae* includes some 8 genera, 5 from southern Australia and *Sphondylothamnion* Naegeli, and probably *Vickersia* Karstakoff and *Dipiothamnion* Joly & Yamaguishi in Joly et al. (1966, p. 169) from the Northern Hemisphere and Brazil. The tribe is characterised by the habit of clearly separated whorl-branchlets, indeterminate laterals from axial cells, and procarps restricted to the subapical cell of axes, terminal carposporangia, and an inner involucrum of branchlets from sterile cells associated with the procarp.

The tribe was described in detail by Gordon (1972), on which this account is largely based

**KEY TO GENERA OF SPHONDYLOTHAMNIEAE**

1. Female axis 3 cells long, subapical cell with 2 pericentral cells; polysporangia present, with about 32 spores; corticating rhizoids often anastomosing by secondary pit-connections ................................................................. **INVOLUCRANA**

2. Procarps on the subapical cell of the female axis, enclosed in a gelatinous sheath together with associated sterile cells; terminal carposporangia, and an inner involucrum of branchlets from sterile cells associated with the procarp.

3. Indeterminate branches formed on axial cells in addition to whorl-branchlets; terminal cells of whorl-branchlets short and mucronate ........................................... **WOLLASTONIELLA**

4. Auxiliary cells 2 per procarp, fusion cell furcate and involving the hypogenous cell; whorl-branchlets distichous or orthostichous (when 4 per axial cell) ................................................................. **SHEPLEYA**

5. Auxiliary cell 1 per procarp, fusion cell not involving hypogenous cell, with up to 5 free gonimolobes; whorl-branchlets usually radial on axes or distichous if 2 per axial cell ............................................................. **MEDEIOTHAMNION**
Genus INVOLUCRANA Baldock & Womersley 1968: 214

**Thallus** erect, much branched with irregular long axes bearing first one then a second whorl-branchlet, largely distichously, on each axial cell, with some cells producing a third (rarely a fourth); indeterminate laterals developing from the first formed whorl-branchlet; whorl-branchlets relatively slightly branched; cortication of older axes by descending anastomosing rhizoids from the basal cells of whorl-branchlets. Cells relatively large, multinucleate.

**Reproduction.** Gametophytes dioecious. Procarpic with 3-celled fertile axes arising laterally on the subterminal cell of whorl-branchlets; subapical cells with 2 pericentral cells, one of which functions as the supporting cell and cuts off a sterile cell; carposporophyte with a central, lobed, fusion cell bearing branches with terminal clavate carposporangia, surrounded by an inner involucre of 3 branchlets arising from the apical cell of the fertile axis, the sterile pericentral cell and the sterile cell on the supporting cell; an outer involucre develops from the lower whorl-branchlets. Spermatangia borne on ovoid heads on reduced branch systems on lower cells of whorl-branchlets.

**Polysporangia**, with 20–32 spores, are borne terminally or laterally on lower cells of reduced branch systems on the lower cells of whorl-branchlets.

**Type species:** *I. meredithiana* (J. Agardh) Baldock & Womersley 1968: 215.

A genus of two species on southern Australian coasts.

**KEY TO SPECIES OF INVOLUCRANA**

1. Thallus branching irregular, subdistichous; whorl-branchlets often indistinct from indeterminate branches, 2–3 (-4) per axial cell, radial on main axes, 5–20 mm long, median cells 2–4 mm long ................................................................. 1. *I. meredithiana*

1. Thallus branching mostly distichous; whorl-branchlets nearly always distinct from indeterminate branches, distichous on main axes, 2 (-4) per axial cell, 2.5–4 mm long, median cells 0.7–1.2 mm long ................................................. 2. *I. crassa*


**FIGS 25C, 28**

*Thallus* (Fig. 25C) dark red-brown, 5–20 (-25) cm high, much branched with numerous long axes, lower cells of axes 400–500 μm in diameter and 2–4 mm long. Holdfast 2–10 mm across, rhizoidal; epilithic. **Structure.** Subapical cells forming first a periauxial cell alternately and subdistichously, then a second periauxial cell either unilaterally or suboppositely to the first, and usually a third on the left of the first, forming basally branched whorl-branchlets 5–20 mm long with ultimate branches 4–12 (-14) cells long, median cells 2–4 mm long and 250–400 μm in diameter, terminal cells rounded; indeterminate laterals arising by continued growth of the first formed whorl-branchlets. Cortication by descending and ascending rhizoids, sometimes anastomosing, developed from the lower end of axial cells and basal cell of whorl-branchlets. Cells multinucleate; rhodoplasts discoid to elongate.

**Reproduction.** Gametophytes dioecious. Female axes of 3 cells (Fig. 28A), arising from the subterminal cell of the first whorl-branchlet, the subapical cell producing 2 pericentral cells, the abaxial one being the supporting cell cutting off a sterile apical cell and a 4-celled carpogonial branch; fusion cell large, irregularly lobed, with terminal clavate carposporangia 45–90 μm in diameter, closely attached to the fusion cell; carposporophyte (Fig. 28B) 450–900 μm across; the apical cell, the sterile pericentral cell and the sterile cell on the supporting cell all divide post-fertilization to form an inner involucre of 3-celled, incurved, branches,
and an outer involucre develops from the hypogenous cell of the fertile axis, with 1–3 subdichotomous branches. Spermatangia (Fig. 28C) occur on sessile, ovoid, heads, 65–100 µm in diameter by 100–150 µm long, situated on short, lateral, branch systems on whorl-branchlets.

Polysporangia with 20–32 spores (Fig. 28D) occur on the inner side of short branch systems on whorl-branchlets, 150–220 µm in diameter.

**Type** from Orford, Tas. (Meredith); lectotype in Herb. Agardh, LD, 35383.

**Distribution:** Victor Harbor, S. Aust., to Port Phillip Heads, Vic., and E Tasmania.


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**Fig. 28. Involucrana meredithiana.** A. Branch with a mature procarp. B. A young carposporophyte with groups of sterile cells. C. A spermatangial head. D. A lateral branch bearing polysporangia. (All after Baldock & Womersley 1968, courtesy of Aust. J. Bot.)
Involucrana

1. *meredithiana* is a deep water species, often common on south-east coasts of South Australia.

2. **Involucrana crassa** (Hooker & Harvey) Gordon 1972: 105, figs 36, 61A.


**FIGS 25D, 29**

**Thallus** (Fig. 25D) dark red-brown, 5–20 cm high, branched alternately and distichously for 3–4 orders, with some long branches with hamate tips, erect axes arising from proximate basal branches or from a matted holdfast 2–10 mm across; epiphytic on larger algae or possibly epilithic. **Structure.** Subapical cells forming opposite, distichous pairs of whorl-branchlets (Fig. 29A), with occasionally a third and rarely a fourth opposite the third, axial cells 600–800 μm in diameter and L/D 2–5 below. Mature whorl-branchlets 2.5–4 mm long, spreading and overlapping, subpolyvotomous at their base and subtri- to dichotomous above, ultimate branches of 1–3 cells, ends of terminal cells rounded, median cells 200–300 μm in diameter and L/D 2.5–6; further laterals are produced from basal cells of whorl-branchlets in the lower thallus, obscuring the distichous arrangement of whorl-branchlets. Indeterminate branches arising in the position of whorl-branchlets on axial cells; on some branches the axial cells near apices bear reduced, or no, whorl-branchlets and the end becomes curved. Cortication of lower axes occurs by rhizoids from the lower ends of cells. Cells multinucleate; rhodoplasts discoid to elongate.

**Reproduction.** Gametophytes dioecious. Female axis (Fig. 29B) of 3 cells, arising distally and adaxially from the subterminal cell of a young whorl-branchlet, the subapical cell bearing two pericentral cells, one (the supporting cell) bearing a terminal sterile cell and a lateral carposporangia (Fig. 29C) 35–50 μm in diameter; carposporophyte 450–700 μm across; 3 inner involucral branchlets surround the carposporophyte, with an outer involucre from the lower whorl-branchlets. Spermatangial heads (Fig. 29D) ovoid, 80–100 μm in diameter, situated on reduced branch systems borne on lower to upper cells of whorl-branchlets.

Polysporangia with 27–32 spores (Fig. 29E), 100–220 μm in diameter, occur, borne terminally or laterally on lower cells of whorl-branchlets, surrounded by curved involucral filaments arising from the basal cell.

**Type** from Georgetown, Tas. (Gunn); lectotype in BM.

**Distribution:** Elliston, S. Aust., to Gabo I., Vic., and N and E Tasmania. Specimens from Freemantle, W. Aust. (Clifton, July 1858) and Kiama, N.S.W., are in BM. Millar & Kraft (1993, p. 41) comment on absence of any other N.S.W. records, and both these records need verification.


**Involucrana crassa** is a deep water alga, known mainly from drift specimens, on rough-water coasts; rarely it occurs in shallow, shaded, situations.
Involucrana SPHONDYLOTHAMNIEAE

Fig. 29. Involucrana crassa (A, AD, A31159; B, C, AD, A25467; D, AD, A31009; E, in NSW). A. Apex of indeterminate branch with whorl-branchlets. B. Mature procarp and associated cells. C. Part of fusion cell with carposporangia. D. Whorl-branchlet with spermatangial heads. E. Polysporangium with involucral branchlets. (All after Gordon 1972, courtesy of Aust. J. Bot.)
Genus DREWIANA Gordon 1972: 100

Thallus erect, much branched with distichous axes, each axial cell bearing 4–5 whorl-branchlets pinnately to subdistichously branched, terminal cells acute; indeterminate branches formed in position of whorl-branchlets; cortication of older axes by descending rhizoids from basal cells of whorl-branchlets; haptera without a terminal digitate disc. Cells multinucleate.

Reproduction. Procarps subapical on short lateral branchlets or laterals of whorl-branchlets, subapical cell with 3 pericentral cells, 2 sterile and the third (the supporting cell) bearing a terminal sterile cell and a lateral carpogonial branch; hypogenous cell elongate and without any laterals. Gonimoblast with a basal fusion cell and clavate carposporangia. Sterile cells associated with the procarp divide post-fertilization to form four inner involucral branchlets. Spermatangia unknown.

Tetrasporangia borne on lower cells of whorl-branchlets, adaxial, tetrahedrally divided.


Drewiana contains a single species, and is distinguished from related genera by the elongate hypogenous cell without any laterals, by the single auxiliary cell per procarp, and by the presence of pre-fertilization laterals on the sub-hypogenous cell.


FIGS 30A, 31A–D

Thallus (Fig. 30A) medium red to dark red-brown, 5–25 cm high, erect axes with distichous, alternate or opposite, branches (Fig. 31A), each axial cell with 4 or 5 whorl-branchlets. Holdfast 2–12 mm across, rhizoidal; epilithic. Structure. Subapical cells bearing 4 or 5 whorl-branchlets (Fig. 31D), overlapping only near branch apices, pinnately to subdichotomously branched 5–8 times, terminal cells acute, 18–24 μm in diameter and L/D 2.5–7; median cells 25–70 μm in diameter and L/D 2–6, basal cells 85–120 μm in diameter and L/D 1.5–2.5; axial cells 400–500 μm in diameter and L/D 4–6 below. Indeterminate branches arise on axial cells in position of whorl-branchlets. Cortication by rhizoids from basal cells of whorl-branchlets. Cells multinucleate; rhodoplasts discoid.

Reproduction. Gametophytes probably dioecious. Female axes 5–6 cells long, formed in position of a whorl-branchlet or a lateral thereof, the subapical cell bearing 3 pericentral cells, with one (the supporting cell) bearing a terminal sterile cell and a lateral carpogonial branch (Fig. 31B); the hypogenous cell is 2–3 times as long as the subapical cell. Post-fertilization 2 small connecting cells are formed each side of the carpogonium, and following fusion with the auxiliary cell the fusion cell produces a cluster of small gonimoblast cells, the lower ones fusing with each other, the auxiliary cell and the supporting cell, and the terminal ones forming clavate carposporangia (Fig. 31C) 20–25 μm in diameter; carposporophyte 240–500 μm across. The apical cell of the fertile axis, the 2 pericentral cells and the sterile cell on the supporting cell divide to form 4 inner involucral groups (Fig. 31C) around the carposporophyte. Spermatangia unknown.

Tetrasporangia (Fig. 31D) are borne terminally or laterally on the adaxial sides of lower cells of whorl-branchlets, 25–50 μm in diameter, tetrahedrally divided.

Lectotype from Rottnest I., W. Aust. (Harvey); in Herb. Harvey, TCD (Trav. Set 213).


Selected specimens: W of Geelvink Channel, Houtman Abrolhos, W. Aust., 60 m deep (Royce 1861, 12.x.1960; PERTH, 2664). W. Aust. (Clifton: AD, A18252). Nuyts Reef, S. Aust., 30 m deep (Shepherd,

*Drewiana nitella* is a deep-water species, superficially similar to *Sphondylothamnion multifidum* but differing in the much slenderer whorl-branchlets with acute but mostly non-spinous terminal cells.

Genus WOLLASTONIELLA Gordon 1972: 88

*Thallus* erect, branching sparse to dense, main branches irregularly to alternately subdistichous. Whorl-branchlets 3 or 4 per axial cell, each pseudodi- to trichotomous, median cells 90–200 μm in diameter, terminal cells short and mucronate. Indeterminate branches arising on axial cells in addition to whorl-branchlets. Cortication when present by descending rhizoids from lower ends of axial cells, adhering by haptera with a terminal digitate disc. Cells multinucleate.

**Reproduction.** Gametophytes dioecious. Procarps subapical on short lateral axes with 4 smaller terminal and subterminal cells, the subapical cell bearing 2 sterile pericentral cells and a supporting cell with a terminal sterile cell and a lateral carpogonial branch. A single auxiliary cell produces a fusion cell with lobes bearing clavate carposporangia, surrounded by an inner involucre developed from the apical cell of the female axis, the 2 sterile pericentral cells and the sterile cell on the supporting cell. The hypogenous and subhypogenous cells do not bear laterals. Spermatangial heads are subspherical, borne on cells of villose whorl-branchlets.

Tetrasporangia borne on lower cells of modified whorl-branchlets just below the apices of short lateral branches, tetrahedrally divided.

*Type species:* *W. myriophylloides* (Harvey) Gordon 1972: 89.

A genus of 2 species on southern Australian coasts, distinguished by the 4 relatively small cells of the female axis with only the subapical cell producing pericentral cell, and the single auxiliary cell per procarp. Vegetative features are the formation of indeterminate branches in addition to whorl-branchlets on axial cells, the short mucronate cells terminating the whorl-branchlets, and the formation of haptera from the proximal ends of rhizoidal cells.

**KEY TO SPECIES OF WOLLASTONIELLA**

1. Branching of thallus and whorl-branchlets divergent; whorl-branchlets (3-) 4 per axial cell, branched 3–4 times, median cells 120–200 μm in diameter and L/D 3–5; up to 4 indeterminate branches per axial cell; cortication present ............ 1. *W. myriophylloides*

1. Branching of thallus and whorl-branchlets fastigiate; whorl-branchlets 3 (-4) per axial cell, branched once or twice, median cells 90–160 μm in diameter and L/D 5–7; up to two indeterminate branches per axial cell; cortication absent ............ 2. *W. mucronata*


*Wrangelia myriophylloides* Harvey 1855a: 546; 1862: pl. 224; 1863, synop.: xxviii.


**FIGS 30B, 31E, F, 32**

*Thallus* (Fig. 30B) dark red-brown, fading to grey, 10–15 (-20) cm high, main branches irregularly alternate, often sparse and divergent, for 2–4 orders. Base of axes often prostrate and entwined, forming a matted holdfast attached by haptera; usually epiphytic on *Amphibolis*, fucoids or geniculate coralline algae. **Structure.** Subapical cells producing 3–4 whorl-branchlets (Fig. 31F) in circular sequence, axial cells enlarging to 300–350 μm in diameter and 2–3.5 mm long in lower axes; primary axes of whorl-branchlets 4 cells long, terminal cells maturing first and lower laterals produced basipetally; terminal cells short and mucronate, median cells 120–200 μm in diameter and L/D 3–5. Adjacent whorls (Fig. 31E) of whorl-branchlets become separated with 0.5–2.5 mm of the axial cell exposed between them. Indeterminate branches (up to 4 from each axial cell) produced in addition to whorl-branchlets (Fig. 31F). Cortication by rhizoids from lower axes, produced from lower ends of axial cells, forming haptera from the proximal ends of the rhizoidal cells (Fig. 32A). Cells multinucleate; rhodoplasts discoid.
Fig. 32. Wollastoniella myriophylloides (A, B, C, AD, A12732; D, AD, A32167; E, AD, A12731). A. Cortical rhizoids with haptera on an indeterminate axis. B. A fertile axis with the sixth axial cell bearing whorl-branchlets and 3 additional fertile axes. C. A mature carposporophyte with involucral and whorl-branchlets. D. A villose whorl-branchlet with spermatangial heads. E. Whorl-branchlets bearing tetrasporangia. (All as in Gordon 1972, courtesy of Aust. J. Bot.)
Reproduction. Gametophytes dioecious. Female axes (Fig. 32B) 5–6 cells long, up to 4 such axes alternating with whorl-branchlets on potentially indeterminate branches, with the last 4 cells relatively small and densely protoplasmic. The subapical cell bears 2 sterile pericentral cells and the supporting cell which bears a terminal sterile cell and a lateral carpogonial branch; the hypogenous and subhypogenous cells are without laterals (Fig. 32B). Post-fertilization, 2 connecting cells are formed and the auxiliary cell produces gonimoblast initials which divide and form clavate carposporangia 60–100 µm in diameter; carposporophyte (Fig. 32C) 450–1100 µm across; lower gonimoblast cells and sterile procarp cells fuse to form a relatively large multinucleate fusion cell, and the apical cell, the 2 sterile pericentral cells and the sterile cell on the supporting cell divide to form 4 inner involucral filaments. Spermatangial heads (Fig. 32D) are subspherical, 90–110 µm in diameter, sessile and adaxial on cells of villose whorl-branchlets.

Tetrasporangia (Fig. 32E) occur terminally and laterally on small cells of much branched whorl-branchlets, borne just below the apex of short indeterminate branches; tetrasporangia are 100-160 µm in diameter, tetrahedrally divided (rarely octosporangia).

Type from Rottnest Is, W. Aust. (Harvey); holotype in Herb. Harvey, TCD (Trav. Set 246).

Distribution: Port Denison, W. Aust., to Port Phillip, Victoria.


W. myriophylloides is a moderately deep water alga, usually epiphytic on Amphibolis or larger algae. The habit and robust glomerules of whorl-branchlets with mucronate end cells are distinctive.

2. Wollastoniella mucronata (Harvey) Gordon 1972: 97, figs 33C, D, 34, 59B.


FIGS 30C, 33

Thallus (Figs 30C, 33A) dark red-brown, 5–10 (-15) cm high, main branches fastigate, up to 5 orders, arising from entwined, prostrate, matted branches. Holdfast matted, 4–10 mm across, rhizoidal with haptera; epiththic. Structure. Subapical cells producing 3 (–4) fastigate whorl-branchlets (Fig. 33B), 1/3 to 2/3 the length of the axial cell above, pseudodi- or trichotomously branched once or twice, cells rigid, terminal cells small and mucronate, median cells 90–160 µm in diameter and 1/3D 5–7; lower axial cells 160–180 µm in diameter and 2–3.5 mm long. Up to 2 indeterminate branches formed on axial cells in addition to whorl-branchlets, apices occasionally villose in reproductive plants. Axes not corticated below. Cells multinucleate; rhodoplasts discoid.

Reproduction. Female axes (Fig. 33C) 6–7 cells long, the upper 4 cells small and densely protoplasmic, with the procarp, supporting and auxiliary cells and sterile cells as in W. myriophylloides, the carposporophyte (Fig. 33D) 350–550 µm across, producing clavate carposporangia 50–90 µm in diameter, surrounded by an inner involucre of 4 branches from the sterile procarp cells, with a loose outer involucrum from lower whorl-branchlets. Spermatangia unknown.
Fig. 33. *Wallastoniella* macronata (A, B, E, AD, A18987; C, D, MEL. 15322). A. Habit. B. Indeterminate apex with whorl-branchlets. C. Branch apex with a procarp. D. Young carposporophyte with fusion cell and part of inner involucrum. E. Axial cell with whorl-branchlets bearing tetrasporangia. (All as in Gordon 1972, courtesy of Aust. J. Bot.)
Tetrasporangia (Fig. 33E) are borne terminally or laterally on small cells of modified whorl-branchlets near apices of short indeterminate axes, 100–150 μm in diameter, tetrahedrally (rarely octahedrally) divided.

Type from Tasmania (Gunn) – probably N coast; holotype in Herb. Harvey, TCD.

Distribution: Cape Northumberland to Inverloch, Vic., and N coast of Tasmania.


W. mucronata is a distinctive but apparently rare species, with long branches bearing whorls of short branchlets with mucronate terminal cells. It often forms a turf in relatively shallow water.

Genus SHEPLEYA Gordon 1972: 69

Thallus prostrate or erect, branching subdistichous to irregular, bearing 2–4 (-5) whorl-branchlets per axial cell, distichous or orthostichous in opposite pairs, mostly adaxially branched with terminal cells of similar diameter to lower cells, ends rounded, median cells 55–85 μm in diameter. Indeterminate branches formed in position of whorl-branchlets. Cortication absent or by descending rhizoids from basal cells of whorl-branchlets, adhering by haptera with a terminal digitate disc. Cells multinucleate.

Reproduction. Gametophytes dioecious. Procarps subapical on short lateral branchlets 4–7 cells long, the last 3 cells smaller, the subapical cell producing a sterile pericentral cell, a fertile pericentral cell (which cuts the second auxiliary cell involved in the gonimoblast), and a supporting cell with a lateral carpogonial branch and a terminal sterile cell. The hypogenous cell bears no laterals, but is involved in the fusion cell which is furcate and produces terminal clavate carposporangia. Sterile procarp cells produce 2–3 inner involucral branchlets. Spermatangial heads sub-spherical to ovoid, borne adaxially on reduced branches of whorl-branches.

Tetrasporangia adaxial on small-celled branch systems on the whorl-branchlets.

Type species: S. wattsii (Harvey) Gordon 1972: 70.

A genus of 5 species, 3 from southern Australia, S. claviformis Gordon (1972, p. 83) from the west coast of Western Australia, and S. elixithamnia Gordon-Mills & Norris (1986) from South Africa.

Distinguishing features are the whorl-branchlets with large cells with rounded ends, the small hypogenous cell, without laterals, of the female axis, the 2 auxiliary cells per procarp, and the furcate fusion cell involving the hypogenous cell.

KEY TO SPECIES OF SHEPLEYA

1. Thallus prostrate, distichously branched, without erect axes; cortication absent; whorl-branchlets 2 per axial cell, median cells 55–85 μm in diameter; 2 inner involucral branchlets around the carposporophyte .............................................................. 3. S. australis

2. Thallus erect, 10–30 cm high; lower axes corticated with rhizoids; whorl-branchlets 2 or 4 per axial cell, median cells 130–300 μm in diameter; three inner involucral branchlets around the carposporophyte ............................................................ 2

3. S. wattsii
2. Whorl-branchlets 4 per axial cell, orthostichous, median cells 130–150 μm in diameter and L/D 3–5 ................................................................. 2. S. verticillata


**FIGS 30D, 34**

**Thallus** (Fig. 30D) medium to dark red-brown, 10–25 cm high, with numerous spreading subdistichous branches from every second to fifth axial cell of the main axes, branched for 3 or 4 orders; base of axes often prostrate. Holdfast 2–5 mm across, of entwined rhizoids with lateral haptera; epilithic. **Structure.** Subapical cells bearing 2 (-3) whorl-branchlets (Fig. 34A), first in opposite distichous pairs, with axial cells increasing in size to 200–500 μm in diameter and 1–1.5 mm long near the base; mature whorl-branchlets spreading, slightly incurved, branches only slightly tapering with rounded ends of terminal cells, median cells 180–300 μm in diameter and L/D 2–3; lower cells of whorl-branchlets with 2–4 simple laterals, upper cells with 1 or 2, orientated above and below the plane of branching and obscuring the distichous arrangement. Indeterminate branches arise in position of whorl-branchlets on axial cells. Cortication of the lower thallus is by rhizoids from the basal cells of whorl-branchlets, adhering of crowded whorl-branchlets of fairly even length.

**Reproduction.** Gametophytes dioecious, occasionally with mixed phase thalli. Female axes 4–6 (-8) cells long, the last 3 cells relatively short (Fig. 34B); subapical cell with 3 lateral haptera; epilithic.

**Distribution.** West Bay, Kangaroo I., S. Aust., to Port Phillip Heads, Vic., and SE Tasmania.


**Shepleya wattsii** is a deep-water alga on eastern South Australian and western Victorian coasts, often common in the drift. It is distinguished by relatively long branches with a fringe of crowded whorl-branchlets of fairly even length.

2. Shepleya verticillata Gordon 1972: 76, figs 25, 58A.

Fig. 34. Shepleya wattsii (A, B, D, F, AD, A27904; C, AD, A21262; E, AD, A31422). A. Indeterminate apex with whorl-branchlets. B. Apex with mature procarp. C. Fusion cell with 2 arms and immature carposporangia. D. Longitudinal section of a spermatangial head. E. Thallus with procarps and spermatangial heads. F. Small tetrasporangial branches on cells of whorl-branchlets. (All as in Gordon 1972, courtesy of Aust. J. Bot.)
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SPHONDYLOTHAMNIEAE

Shepleya

[= W. penicillata (C. Agardh) C. Agardh].

FIGS 35, 37A

Thallus (Fig. 37A) medium red-brown, fading to grey, 15–30 cm high, with alternate,
spreading, sparse to moderately dense branching for 3–4 orders; erect axes often basally
entwined, arising from prostrate axes (Fig. 35A). Holdfast rhizoidal, 3–8 mm across, attached
by haptera; epilithic.

Structure. Subapical cells bearing 4 orthostichous whorl-branchlets (Fig.
35B) in opposite pairs, the second pair initiated several cells below the first pair, with the
axial cells enlarging to 500–600 μm in diameter and 2–2.5 mm long near the base; mature
whorl-branchlets are slightly incurved, 1.4–2.2 mm and 4–5 cells long, tapers only
slightly, median cells 130–150 μm in diameter and L/D 3–5, the basal cell bearing 2–3 and
the next cell 1–2 adaxial branchlets, terminal cells with rounded ends. Indeterminate branches
arise in the position of whorl-branchlets on axial cells. Cortication of the lower thallus is by
rhizoids from the basal cell(s) of whorl-branchlets, adhering to the axis by haptera. Cells
multinucleate; rhodoplasts discoid to elongate.

Reproduction. Gametophytes dioecious, occasionally with mixed-phase thalli. Female
axis 4–7 cells long, in the position of, or on, whorl-branchlets, with the last 3 cells shorter;
procarp structure (Fig. 35C) as in S. wattsii, but the larger subhypogenous cell bearing only a
single lateral at fertilization. Carposporophyte 350–450 μm across, with a large furcate fusion
cell involving the hypogenous cell, carposporangia 45–60 μm in diameter, surrounded by an
inner involucrum of small-celled filaments from sterile cells of the procarp, and an outer
involucrum of 4 branchlets from the subhypogenous cell. Spermatanting heads (Fig.
35D) are slightly ovoid, 70–95 μm in diameter, borne adaxially on cells of whorl-branchlets.
Tetrasporangia (Fig. 35E) are sessile and adaxial on the upper ends of slightly smaller
whorl-branchlet cells, 100–160 μm in diameter, tetrahedrally divided.


Distribution: Gleeson Landing, Yorke Pen., and West Bay, Kangaroo I., S. Aust., to Western
Port, Victoria.

Brown Beach, Yorke Pen., S. Aust., 6–12 m deep (Shepherd, 14.iv.1963; AD, A26574). West Bay, Kangaroo
I., S. Aust., drift (Womersley, 6.i.1946; AD, A3257). Guichen Bay, S. Aust., 10–16 m deep (Womersley, 1.x.1949;
Aust., drift (Baldock, 19.v.1964; AD, A27886) and (Gordon, 15.v.1967; AD, A31420). Warmambool, Vic.,
(Kraft & Herrington, 19.xi.1989; AD, A67801). 1.3 km off Cape Northumberland, S. Aust., 15 m deep
(Shepherd, 17.v.1978; AD, A55203). Port Phillip Heads, Vic. (Wilson, 1.ii.1893; MEL, 15325).

Callithamnion australe J. Agardh 1841: 42; 1851: 26; 1876: 21; 1885: 2. Kützing 1849:
1968: 300.

FIG. 36

Thallus (Fig. 36A) red-brown, prostrate with axes creeping along the host (usually
Pterocladiina lucida) branches, branching opposite or alternate; attachment by haptera; epiphytic.
Structure. Subapical cells producing opposite, distichous pairs of whorl-branchlets (Fig. 36A),
axial cells enlarging to 180–190 μm in diameter and 400–500 μm long near the base; whorl-
branchlets 500–1000 μm long, oppositely and distichously branched in the plane of the host
surface, with the basal cell usually producing 1–3 more laterals in the plane of branching;
terminal cells with rounded ends, median cells 55–85 μm in diameter and L/D 2–4; haptera in
Fig. 35. Shepleya verticillata (A, AD, A31420; B, E, AD, A27886; C, MEL, 15325; D, AD, A10984). A. Prostrate axis bearing a young erect axis. B. Indeterminate axis with whorl-branchlets. C. Axis with a mature procarp. D. Whorl-branchlet bearing spermatangial heads. E. Axis and whorl-branchlets bearing tetrasporangia. (All as in Gordon 1972, courtesy of Aust. J. Bot.)
Fig. 36. *Shepleya australis* (AD, A31007). A. Indeterminate apex with whorl-branchlets and haptera. B. Apex with mature procarp. C. Fusion cell with carposporangia. D. Whorl-branchlet with spermatangial heads (one in section). E. Axis with whorl-branchlets bearing tetrasporangia. (All as in Gordon 1972, courtesy of Aust. J. Bot.)
opposite pairs from the lower ends of axial cells. Indeterminate branches develop by continued growth of whorl-branchlets. Cortication absent. Cells multinucleate; rhodoplasts discoid to elongate.

Reproduction. Gametophytes dioecious. Female axis (Fig. 36B) 4–12 cells long, arising at branch apices, with the last 3 cells shorter. Procarps as in S. wattsii with the subapical cell bearing a sterile pericentral cell, a fertile pericentral cell producing the second auxiliary cell, and the supporting cell with an apical sterile cell and lateral carposporial branch. The fusion cell (Fig. 36C) is furcate, cutting off small gonimoblast cells with ovoid to pyriform terminal (and subterminal) carposporangia 40–90 μm in diameter; the apical cell and sterile pericentral cell divide after fertilization to form 2 inner involucral branchlets while the subhypogenous cell bears 3 outer involucral filaments which together with the inner branches curve up and around the carposporophyte. Spermatangial heads (Fig. 36D) are slightly ovoid and 70–110 μm in diameter, borne on curved cells of the whorl-branchlets.

Fig. 37. A. Shepleya verticillata (AD, A26574). B. Medeiothamnion proterum (AD, A33180). C. Medeiothamnion halurus (AD, A30666). Habit for each species.
Tetrasporangia (Fig. 36E) are sessile on upper cells of whorl-branchlets where free from the host edge, 50–90 µm in diameter, tetrahedrally divided.

**Type** from Port Phillip, Vic. (Brown); holotype in Herb. Agardh, LD, 17960.


**Genus MEDEIOTHAMNION** Pujals 1970: 200

Thallus erect, usually with a prostrate base, branching of axes usually sparse, irregular to alternately subdistichous, whorl-branchlets 2–4 (-5) per axial cell, opposite or whorled, pinnately to subdichotomously branched, median cells 35–140 µm in diameter. Indeterminate branches arising in positions of whorl-branchlets. Cortication absent or by descending rhizoids from basal cells of whorl-branchlets, adhering by haptera with a terminal digitate disc. Cells multinucleate.

**Reproduction.** Gametophytes dioecious. Female axes several cells long with the last 2 cells small, the subapical cell bearing 2 sterile pericentral cells and a supporting cell bearing a terminal sterile cell and a lateral carpogonial branch, with the larger hypogenous cell usually bearing an adaxial, curved, involucral branchlet. One laterally elongate auxiliary cell per procarp, producing gonimolobes from each end, with short filaments producing terminal clavate carposporangia. Sterile procarp cells produce 3–4 inner involucral branchlets. Spermatangial heads subspherically ovoid, borne on cells of the whorl-branchlets. Tetrasporangia borne on reduced branches on lower cells of whorl-branchlets, tetrahedrally divided.

**Type species:** *M. santacrucense* Pujals 1970: 290.

A genus of five species, the type from Argentina, one from New Zealand and 3 from southern Australia (Gordon 1972, p. 49).

The distinguishing features of *Mediothamnion* are the comparatively elongate hypogenous cell of the female axis bearing (except in *M. santacrucense*) a single, adaxial, involucral branchlet, and the single auxiliary cell per procarp producing an elongate cell which cuts off gonimolobe cells at each end.

It is likely that *M. lyallii* (Harvey) Gordon (1972, p. 59, figs 16–18, 56A) also occurs in Victoria and Tasmania. (Gellibrand Pile Light, Port Phillip Bay, Vic., 5–8m deep (Kraft 5499 & O’Brien, 30.x.1975; MELU and AD, A67804) and Sarah L, Bathurst Channel, SW Tasmania, 2–5m deep (Edgar, 11.iii.1995; AD, A64258)). The Port Phillip record (Lewis 1983, pp. 262, 264) may be of an adventive. Female specimens are required to substantiate these records. Records of *Callithamnion flaccidum* Hooker & Harvey from Victoria and Tasmania (Harvey 1859b, p. 334; 1863, synop.:iv. Sonder 1881, p. 11) and Tasmania (Sonder 1853, p. 673) are probably not of this Cape Horn species (see also Wollaston 1968, p. 300), but may also apply to *M. lyallii*.

**KEY TO SPECIES OF MEDEIOTHAMNION**

1. Main axes prostrate, producing erect branches 1–5 mm high; axial cells 400–1000 µm long; rhizoidal cortication absent; epiphytic on *Cystophora* spp. .......... 3. *M. repens*
Medeiothamnion

SPHONDYLOTHAMNIEAE

1. Main axes erect, 4–30 cm high; axial cells becoming 2–3 mm long; rhizoidal cortication present but slight; epiphytic on algae or seagrasses ........................................................ 2

2. Whorl-branchlets subdi- or trichotomous, inwardly curved, adjacent whorls imbricate ........................................................ 2. M. halurus

2. Whorl-branchlets pinnate, not markedly inwardly curved, adjacent whorls imbricate only near branch apices ........................................ 1. M. protensum

1. Medeiothamnion protensum (Harvey) Gordon 1972: 51, figs 11–13, 55A.


Mazoyeria protensa (Harvey) Gordon 1970: 1498.

FIGS 37B, 38

Thallus (Fig. 37B) medium red-brown to grey-red, 4–30 cm high, branching irregularly alternate and subdistichous for 3 orders; main axes erect, arising from prostrate axes, with cortication by descending rhizoids, forming an entwined holdfast 2–3 mm across, attached by haptera; epithecid. Structure. Subapical cells bearing 3–4 (-5) whorl-branchlets (Fig. 38A, B) developed in an opposite sequence, overlapping only near branch apices, mature branchlets with pinnate or subdichotomous, divergent, branches, tapering markedly, median cells 35–40 μm in diameter and L/D 5–6.5, terminal cells 18–22 μm in diameter, ends rounded. Axial cells enlarging to 800–1000 μm in diameter and 2–3 mm long near the thallus base. Indeterminate branches arise in position of whorl-branchlets. Cortication by descending branched rhizoids from the basal cells of whorl-branchlets, adhering by haptera. Cells multinucleate; rhodoplasts discoid.

Reproduction. Gametophytes probably dioecious. Female axes 6–7 cells long, formed in position of young whorl-branchlets; apical and subapical cells small and densely protoplasmic, the hypogenous cell elongate. Subapical cell bearing 2 sterile pericentral cells and the supporting cell with a sterile apical cell and a lateral carpogonial branch (Fig. 38C), and the hypogenous cell bearing a 2-celled, curved, involucral filament. The auxiliary cell becomes laterally elongate and, following contact via a connecting cell with the fertilized carpogonium, cuts off small gonimolobe initials (Fig. 38D) at each end; these become multinucleate and on cells of the whorl-branchlets.

Tetrasporangia (Fig. 38F) occur terminally or laterally on cells of small branchlets on the lower cells of whorl-branchlets, 60–75 μm in diameter, tetrahedrally divided.

Type from Port Phillip, Vic. (Harvey); lectotype in Herb. Harvey, TCD (Alg. Aust. Exsic. 263F) – see Gordon 1972, p. 53.

Distribution: Port Turton, Yorke Pen., S. Aust., to Westernport, Vic., and N and E Tasmania.

Medeiothamnion

Medeiothamnion protensum occurs in conditions of slight water movement, either in shallow water (e.g. A26849, A46270) or in deeper water on rough-water coasts (e.g. A33180, A42157).


FIGS 37C, 39

Thallus (Fig. 37C) mid red-brown to (commonly) grey-red. 5-10-15 cm high, sparsely and irregularly branched, with prostrate axes attached by haptera (Fig. 39B); epiphytic, usually on Amphibolis. Structure. Sub-apical cells bearing 4-5 whorl-branchlets, when mature subdial- or trichotomously branched and incurved, with adjacent whorls (Fig. 39A) regularly imbricate along the whole axis often with trapped sand grains; branches tapering only slightly, axial cells 200-500 μm in diameter, and L/D 3-5, terminal cells with rounded ends, median cells 50-60 μm in diameter and L/D 3.5-5. Indeterminate branches arising in positions of whorl-branchlets. Cortication rare, only near base of thallus, rhizoidal. Cells multinucleate; rhodoplasts discoid.

Reproduction. Gametophytes dioecious. Female axes (Fig. 39C) with 2 short terminal cells and the longer hypogenous cell bearing a single involucral filament, with the subapical cell bearing 2 sterile pericentral cells and a supporting cell with a sterile apical cell, and a lateral carposporangial branch. Development as in M. protensum with the fusion cell (Fig. 39D) producing gonimoblast cells, carposporophytes 650-1100 μm across with terminal clavate carposporangia 30-40 μm in diameter; the sterile cells of the procarp produce 4 inner involucral branchlets (Fig. 39D). Spermatangial heads (Fig. 39E) are subspherical, 45-90 μm in diameter, terminal on short cells borne on cells of the whorl-branchlets.

Tetrasporangia (Fig. 39F) are formed terminally or laterally on small cells borne on lower cells of the whorl-branchlets, 50-60 μm in diameter, tetrahedrally divided.

Type from Fremantle, W. Aust., on Amphibolis (Harvey); holotype in Herb. Harvey, TCD (Trav. Set 127).

Distribution: Rottnest I., W. Aust. (Huismans & Walker) to San Remo, Vic., and Robbins I., N. Tasmania.


Medeiothamnion halurus is usually epiphytic on Amphibolis, rarely on algae.


FIG. 40

Thallus (Fig. 40A) red-brown, with prostrate main axes and erect branches 2-5 mm high, attached by haptera; epiphytic on receptacles (and vesicles) of Cystophora platylobium and C. siliquosa. Structure. Sub-apical cells of prostrate axes (Fig. 40B) bearing 3 (-5) whorl-
Fig. 40. Medeiothamnion repens (AD, A30665). A. Habit, on Cystophora platylobium. B. Prostrate axes with erect and prostrate whorl-branchlets, with tetrasporangia. C. Axis with a mature procarp. D. Mature carposporophyte and involucral branches. E. Longitudinal section of a spermatangial head, with a juvenile stage. F. Whorl-branchlets with tetrasporangia. (All as in Gordon 1972, courtesy of Aust. J. Bot.)
branchlets, 1 (or 2) of which are erect and to 5 mm high, the others prostrate and smaller, one on each side of the erect whorl-branchlet; erect whorl-branchlets (Fig. 40B) more or less pectinately and adaxially branched, median cells 60–140 μm in diameter and L/D 2.5–4; prostrate axial cells 180–200 μm in diameter and L/D 2–5. Indeterminate branches produced in position of prostrate whorl-branches. Cortication absent. Haptera produced in pairs from proximal ends of axial cells, often with additional small branchlets and haptera later. Cells multinucleate; rhodoplasts discoid.

**Reproduction.** Gametophytes dioecious. Female axes (Fig. 40C) developing in position of an erect whorl-branchlet, (4-) 6–9 (-14) cells long; procarps as for the genus, with the subapical cell producing 2 sterile pericentral cells and a supporting cell with a sterile cell and a carposporophylobranch (Fig. 40C), the larger subhypogenous cell with an involucral filament. Post-fertilization, the auxiliary cell fuses with adjacent cells and the fusion cell cuts off gonimoblast cells, with the carposporophyte (Fig. 40D) 450–680 μm across, carposporangia clavate and 25–65 μm in diameter. Three inner involucral filaments are formed from the apical cell, supporting sterile cell and one sterile pericentral cell. Spermatangial heads (Fig. 40E) are ovoid, 50–60 μm in diameter, and terminal on short laterals on the upper parts of erect whorl-branchlets.

Tetrasporangia (Fig. 40F) are sessile or stalked on the lower cells of erect whorl-branchlets, 80–100 μm in diameter, tetrhedraly divided.

**Type** from Kingston, S. Aust., on *Cystophora platylobium* (Womersley, 19.viii.1966; holotype in AD, A30665).

**Distribution:** Known from Elliston, SW Yorke Pen., the S coast of Kangaroo I., and Kingston, S. Aust; probably more widely distributed but inconspicuous.


*Medieothamnion repens* is an inconspicuous but distinctive epiphyte known from two species of *Cystophora*, but is probably of wider distribution.

**Tribe ANTITHAMNIEAE** Hommersand 1963: 330

by E.M. Wollaston & H.B.S. Womersley

*Thallus* erect, with or without prostrate basal filaments, erect branches ecorticate or loosely corticated with rhizoids, bearing usually clearly separated whorls of 2, 3 or 4 whorl-branchlets from each axial cell, unbranched or pinnately branched (when distinctly pinnate, often referred to as pinnae, branches as pinnules). Growth monopodial, lateral branches arising on basal cells of whorl-branchlets; gland cells usually present, situated on short lateral branches or terminal on rachides. Cells uninucleate.

**Life history** triphasic with isomorphic gametophytes and tetrasporophytes.

**Reproduction.** Gametophytes dioecious. Procarps produced successively on basal cells of whorl-branchlets at branch apices which then have limited growth, with the basal cell acting as the supporting cell and bearing a 4-celled carposporophylobranch. The auxiliary cell is cut off the supporting cell and after union with the fertilized carposporophyte forms an upper cell which produces one to several rounded gonimolobes, with fusions occurring between the axial cell, the lower whorl-branchlet cells and lower gonimoblast cell; carposporophytes without an involucre. Spermatangia are borne terminally on short branches on inner cells of the whorl-branchlets.
Tetrasporangia are usually sessile on cells of the whorl-branchlets or on small lateral branches of the whorl-branchlets, subspherical or ovoid, cruciately or decussately divided.

The Antithamnieae is regarded as a primitive tribe of the Ceramiaceae. It was first distinguished by Hommersand who included (1963, pp. 344, 345) 11 genera, but modified by Wollaston (1968, p. 405) who separated genera into the Heterothamnieae, Warreniae and Crouanieae and retained only 5 genera in the Antithamnieae. Athanasiadis (1996) further restricts the Antithamnieae in segregating the Pterothamnieae and Perithamnieae (the latter not accepted here).

The great variety in form of the genera previously included in the Antithamnieae, particularly Lasiothallia and Ballia, indicates that these genera are better placed in separate tribes.

KEY TO GENERA OF ANTITHAMNIEAE

1. Thallus usually 1–30 cm high, ecoricate or corticate on lower axes, whorl-branchlets in whorls of 3 (2 in M. acanthophorum) from each axial cell; gland cell branches also bearing spermatangial or tetrasporangial clusters ........................................ MACROTHAMNION
2. Thallus 0.5–4 cm high, ecoricate, whorl-branchlets in one or two pairs from each axial cell; gland cell branches not also bearing spermatangia or tetrasporangia ................... 2

2. Whorl-branchlets pinnate or irregularly branched, in single pairs per axial cell; gland cells on short 2-4-celled lateral branches on pinnules .......... ANTITHAMNJON
2. Whorl-branchlets pinnate, in two pairs per axial cell, similar or different in length; gland cells terminal on the end cell of the rachides .......... ACROTHAMNION

Genus ANTITHAMNION Nageli 1847: 202

Thallus usually 2–20 mm high, delicate, with prostrate and occasionally erect indeterminate axes, completely ecoricate, bearing determinate whorl-branchlets (often as pinnae) in opposite pairs, each with a small unbranched basal cell and other rachis cells bearing opposite, alternate or secund pinnules; gland-cells sessile on short 2–4-celled branchlets on the pinnules; attachment of prostrate axes by rhizoids with haptera; usually epiphytic. Cells uninucleate. Reproduction. Gametophytes usually dioecious. Procarps on the basal cells of whorl-branchlets near apices of indeterminate branches, with series of (4–) 8–20 developed successively; the basal cell acts as the supporting cell and bears a 4-celled carpogonial branch, and only a single carposporophyte matures per branch. Post-fertilization the auxiliary cell is cut off the supporting cell and divides to form a lower foot cell and upper gonimoblast cell which forms one or a few rounded groups of carposporangia; no involucral branchlets occur. Spermatangia occur in branched clusters on cells of the pinnules. Tetrasporangia occur on cells of the pinnules, usually sessile, cruciately divided.

Type species: A. cruciatum (C. Agardh)Nageli (1847, p. 202), from Europe.

Antithamnion is a large genus with species in all oceans of the world. Wollaston (1968) monographed the 7 then known southern Australian species and Athanasiadis has added 3 more.

KEY TO SPECIES OF ANTITHAMNION

1. Whorl-branchlets (pinnae) distichously arranged along axes. ........................................ 2
1. Whorl-branchlets decussately arranged along axes (irregularly decussately to distichously in A. uniramosum), usually slightly curved and facing the axes ........................................ 7

2. Thallus branching not entirely complanate, pinnules lax and often diverging, rachis cells L/D 1.5–2.5 ................................................................. 1. A. gracilentum
2. Thallus branching complanate, pinnae usually closely branched; rachis cells L/D mostly 0.5–1.5 (2–4 in A. pectinatum) ........................................ 3
3. Pinnae with only adaxial pinnules .................................................. 2. A. armatum
3. Pinnae with adaxial and abaxial pinnules ........................................... 4

4. Pinnae with alternate pinnules ....................................................... 3. A. verticale
4. Pinnae with opposite pinnules ....................................................... 5

5. Mature axial cells 90–250 μm in diameter and L/D 1.5–2, pinnae rachis cells mostly 30–55 μm in diameter and L/D 1–1.7 ......................................................... 6

6. Axial cells 120–250 μm in diameter, pinnae rachis cells mostly 35–55 μm in diameter, gland cells with markedly angled walls to 2 pinnule cells ............ 5. A. biarmatum
6. Axial cells 90–120 μm in diameter, pinnae rachis cells 30–45 μm in diameter, walls of pinnule cells alongside gland cells not markedly angled ...... 6. A. pinnafolium

7. Pinnae rigid, cells L/D 1–2, terminal cells mucronate ....................... 7. A. hanovioides
7. Pinnae (whorl-branchlets) relatively lax, cells L/D (1–) 2–4, terminal cells with rounded ends .............................................................. 8

8. Whorl-branchlets pinnate, complanately branched with distichous pinnules, tetratorangia sessile ...................................................... 9
8. Whorl-branchlets not distinctly pinnate, pinnules separated on rachis, lax; tetratorangia pedicellate ......................................................... 10

9. Pinnae 200–580 μm long, upwardly curved and shorter on prostrate axes and lower parts of erect lateral branches; pinnules opposite below for 1–3 pairs, alternate above, with 1 to several simple branches .................................................. 8. A. diminutum
9. Pinnae mostly 600–1200 μm long; pinnules alternate (or lowest 1–3 in opposite pairs), mostly unbranched ........................................ 9. A. delicatulum

10. Whorl-branchlets laxly branched, single above and in opposite pairs below, bearing only opposite pairs of short, simple, 1–2-celled pinnules; axial cells 20–80 μm in diameter and L/D 4–8, whorl-branchlet rachis cells 20–25 μm in diameter and L/D 4–6 .................................................. 10. A. uniramosum
10. Whorl-branchlets densely branched but lax, with opposite pinnules below, often unilateral above; axial cells 60–110 μm in diameter and L/D 2–4, whorl-branchlet rachis cells 23–35 μm in diameter and L/D 2–3 ..................... 11. A. craciatum


FIGS 41A–C, 42, 43A–C

Thallus (Fig. 42A) medium to dark red-brown, with branched prostrate axes bearing erect, opposite, distichous pinnae to 5 mm high, not entirely complanately branched, pinnae (Fig. 41B, C) with 3–8 lower pairs of opposite lax, often diverging pinnules, alternate above. Attachment by branched multicellular processes (Fig. 42D) with terminal haptera, arising from cells of prostrate axes; epiphytic (on Cystophora spp.). Structure. Apical cells 7–9 μm in diameter and L/D 1–2, increasing to 130–180 μm in diameter and L/D 1–2.5 (3) in mature axial cells. Pinnae (Fig. 42B, C) with a small isodiametric basal cell, cells of rachis 35–80 μm in diameter and L/D 1.5–2.5, decreasing in pinnules to 20–40 μm in diameter and L/D 1–2 several cells below their ends; gland cells (Fig. 42C) on special 2–4-celled branches on the lower sides of pinnule cells, 2–4 cells from pinnule base. Lateral branches arising regularly.
Fig. 42. Antithamnion gracilentum. A. Diagram of thallus branching of a prostrate axis with free tips and lateral branches on (usually) every third cell. B. Branch apex with young pinnae and lateral branch initials. C. Pinna with pinnules opposite below, alternate above, and bearing gland cells. D. Attachment rhizoids from basal cell of a pinna. E. Branch apex with successive carpogonial branches on basal cells of whorl-branchlets. (As in Wollaston 1968, courtesy of Aust. J. Bot.)
and alternately usually at intervals of 3 (–4) axial cells, directly from the axial cells. Cells uninucleate; rhodoplasts discoid, elongate in larger cells.

Reproduction. Gametophytes dioecious. Procarps (Fig. 42E) with a 4-celled carpogonial branch borne on the basal cell (supporting cell) of successive pinnae. Post-fertilization fusions occur (Fig. 43A) between the axial cell, supporting cell, and foot cell and upper cell from the auxiliary cell, and the upper cell forms the first gonimolobe 400–1000 μm across of carposporangia 40–70 μm in diameter; pinnae on axial cells below the carposporophyte enlarge and curve over the carposporophyte (Fig. 41A). Spermatangial heads (Figs 41B, 43B) occur on special branches on the adaxial side of lower cells of the pinnules, each head 35–55 μm in diameter and L/D 1–2, with an axis of 5–8 cells each bearing a whorl of 4 cells with terminal spermatangia.

Tetrasporangia (Figs 41C, 43C) occur adaxially on basal (to third) cells of pinnules, sessile, ovoid, 45–90 μm in diameter, decussately or cruciately divided.

Type from Rottnest I., W. Aust. (Harvey); holotype in Herb. Harvey, TCD (Trav. Set 327).


Callithamnion plumula sensu Lucas 1909: 51.

Callithamnion plumula forma y investiens J. Agardh 1876: 24.

Callithamnion simile sensu Harvey 1862, pl. 207 (in part, fig. 47).

FIGS 41D–F, 43D–G

Thallus (Figs 41D, 43D) medium red-brown, with prostrate branched axes bearing erect unattached, distichously branched, fronds 1–3 cm high, the axial cells bearing opposite, distichously arranged pinnae with single pinnules (Fig. 43D) on the upper side of each cell, just overlapping the pinna above. Attachment by rhizoids (Fig. 43E) from the basal (and second) cell of the pinnae, each 3–7 cells long with a digitate hapteron; epiphytic on various algae. Structure. Apical cells 6–10 (–15) μm in diameter and L/D 1–1.25, enlarging rapidly after a few cells, and to 130–300 μm in diameter and L/D 1–1.5 (–2) in mature axial cells. Pinnae (Figs 41F, 43F) 500–800 μm and 8–12 cells long, closely branched, rachis cells 50–90 μm in diameter and L/D 1–1.2, slightly shorter basally and tapering to a small mucronate cell, each cell bearing a single pinnule (longest centrally on the pinna) adaxially, unbranched apart from adaxial short branches often bearing gland cells or tetrasporangia; pinnae cells 35–50 μm in diameter and L/D 1–1.5, tapering above to small, mucronate terminal cells; gland cells frequent (Figs 41E, 43F), on short 2–3-celled branches, often on 2–4 successive cells near the base of the pinnules. Lateral branches arise near apices in place of pinnae. Cells uninucleate; rhodoplasts discoid to elongate, ribbon like in larger cells.

Reproduction. Gametophytes dioecious. Procarps borne in series of 4–8 on basal cells of pinnae at branch apices, with 4-celled carpogonial branches. Carposporophytes with 1–3 lobes, each 180–350 μm across, with ov oid carposporangia 25–45 μm in diameter. Spermatangia terminal on densely branched clusters (Fig. 41E) on the end of the short branches bearing gland cells.
Antithamnion

Tetrasporangia (Fig. 43G) borne on the lower side of special short branches which also bear the gland cells, sessile, ovoid, 45–75 μm in diameter, decussately or cruciately divided.

**Type** from "Novae Hollandiae"; lectotype in Herb. Agardh, LD, 18041.

**Distribution:** Shark Bay, W. Aust., to Stinky Bay, Nora Creina, S. Australia.


A. armatum is a distinctive species with its distichous pinnae with adaxial pinnules. In describing *C. armatum*, J. Agardh (1885, p. 3) apparently overlooked his C. *plumula* var. *investiens* J. Agardh (1876, p. 24) which was based on Harvey’s Alg. Aust. Exsicc. 543A (as C. *simile*) from near Fremantle, W. Aust. Harvey’s plate (1862, pl. 207) probable in part includes *A. armatum*, as for the W. Aust. specimens, but otherwise is of *Pterothamnion nodiferum*.


**FIG. 44A**

*Thallus* (Fig. 44A) light to medium red, with branched prostrate axes bearing erect branched fronds 1–3 cm high, axes with distichous pairs of opposite pinnate pinnae, lying in the same plane or divergent from it (probably depending on crowding). Attachment by branched rhizoidal clumps from basal pinna cells; epiphytic on various algae. **Structure.** Apical cells small, enlarging to 130–250 μm in diameter and L/D 1.2–1.5 in lower axes. Pinnae (Fig. 44A) closely and complanately branched, lying in the plane of thallus branching or twisted from this by crowding, with alternate, simple or once branched pinnae; rachis cells 45–75 μm in diameter and L/D 0.6–1.2, slightly flexuous, tapering over subterminal cells to 20–25 μm in diameter and L/D 0.5–1, terminal cells pointed; pinnule cells 35–45 μm in diameter and L/D 0.8–1.2, tapering over last few cells to pointed terminal cells; gland cells on short 3–4-celled branches on the pinnae, ovoid, covering 2–3 cells and 25–45 μm in diameter. Lateral branches probably arising from basal cells of pinnae. Cells uninucleate; rhodoplasts discoid.

**Reproduction.** Gametophytes unknown.

Tetrasporangia on lower pinnae cells, sessile, ovoid, 40–50 μm in diameter, decussately divided. **Type** from Garden I., W. Aust. (Harvey); lectotype in Herb. Harvey, TCD (Trav. Set 267).

**Distribution:** Rottnest I., W. Aust., to Warnambool, Victoria.

Athanasiadis (1996, p. 153) placed *A. verticale* and its synonyms as probable synonyms of *A. hanovioides*. The two species, however, are clearly distinct in that in *A. verticale* the pinnae are distichously arranged on the axes and the pinnules are distichous, in contrast to *A. hanovioides* with decussate pinnae.

   
   Athanasiadis 1996: 146, fig. 67.
   
   *Callithamnion pectinatum* Montagne 1842: 9.
   
   *Callithamnion applicatum* Harvey 1855c: 258.
   
   *Antithamnion applicatum* (Harvey)J. Agardh 1892: 21.

   **FIGS 44B, C**

   *Thallus* (Fig. 44B) with prostrate axes bearing erect axes 3–25 mm long, complanately branched with opposite, distichous, whorl-branchlets (pinnae) from each axial cell. Attachment by multicellular rhizoids with digitate haptera, arising from basal cells of pinnae; epiphytic. **Structure.** Apical cells 6–10 µm in diameter and L/D 1.5–2, enlarging to 50–90 µm in diameter and L/D (2-) 3–4 in mature axial cells. Pinnae closely branched, 300–550 µm and 10–12 cells long, rachis cells (apart from the basal) with opposite, distichous pinnules 90–270 µm and 8–12 cells long, simple or the larger ones with a branch; rachis cells 25–40 µm in diameter and L/D 2–4, the basal cell isodiametric, tapering to subterminal cells 8–12 µm in diameter and L/D 1–1.5, terminal cells with rounded ends; pinnule cells 10–14 µm in diameter and L/D (2-) 3–4 in mature axial cells.

   **Reproduction.** Gametophytes dioecious. Carpogonial branches borne on the basal cells of pinnae, one to several near apices; post-fertilization producing 1–3 gonimolobes 250–450 µm across, with ovoid carposporangia 25–55 µm across, surrounded by adjacent pinnae. Spermatangial heads (Fig. 44B) ovoid, sessile, on the basal (or next) cells of pinnules, 30–45 µm in diameter, with an axial row of 4–6 cells producing whorls of initials and outer spermatangia.

   Tetrasporangia (Fig. 44C) borne on the basal cells of pinnules, sessile, ovoid, 50–75 µm in diameter, decussately divided.

   **Type** from “Auckland” [almost certainly Auckland I., since the city of Auckland in New Zealand was not established until 1840 and the D’Urville (1940) expedition did not visit the site of Auckland]; holotype in Herb. Montagne, PC.

   **Distribution:** New Zealand; probably widespread (see Athanasiadis 1996, p. 147).

   In southern Australia, from Portland and Gabo I., Vic., and SE Tasmania.


5. **Antithamnion biarmatum** Athanasiadis 1996: 144, fig. 64.

   **FIG. 44D–F**

   *Thallus* (Fig. 44D) red-brown, with prostrate axes bearing erect axes 2–15 mm long, complanately branched with opposite, distichous, whorl-branchlets (pinnae) from each axial cell. Attachment by much branched rhizoidal clusters from basal cells of pinnae; epiphytic. **Structure.** Apical cells 8–11 µm in diameter and L/D 1–1.5, enlarging rapidly and to 120–250 µm in diameter and L/D 1.5–2 in mature axial cells. Pinnae (350–) 500–800 µm and 10–15
Fig. 44. A. Antithamnion verticale (AD, A27996). Axis with pinnae. B, C. Antithamnion pectinatum (AD, A63852). B. Pinnae and pinnules with spermatangial heads. C. Branches with tetrasporangia. D–F. Antithamnion biarmatum (AD, A41924). D. Axes with opposite pinnae and pinnules. E. Gland cells with angled attachment to two pinnule cells. F. Branch with tetrasporangia.
cells long, rachis cells (apart from the basal) each with opposite, distichous, pinnules (Fig. 44D) becoming 120–160 μm and 4–7 cells long; rachis cells 35–55 (–80) μm in diameter and L/D 1.2–1.7, the basal cell shorter, tapering to subterminal cells 15–20 μm in diameter and L/D 0.8–1.2, terminal cells with rounded ends; pinnule cells 20–28 μm in diameter and L/D 1–1.2; gland cells (Fig. 44E) single (–2) on the upper side of reduced or normal pinnules, in contact with 2 bearing cells with the common wall angled, 25–35 μm in diameter. Cells uninucleate; rhodoplasts discoid in small cells, ribbon like in larger cells.

Reproduction. Gametophytes dioecious. Carpogonial branches not observed. Carposporophytes with 1–3 rounded gonimolobes 150–450 μm across, with ovoid to angular carposporangia 30–60 μm across, without any involucral branchlets. Spermatangial heads borne on upper side of pinnule cells, elongate-ovoid, 25–35 μm in diameter and 40–80 μm long, with 5–7 axial cells each with several initials cutting off outer spermatangia. Tetrasporangia (Fig. 44F) borne on lower pinnule cells, sessile, ovoid, 70–90 μm in diameter, decussately divided.

**Type** from Split Rock, Bicheno, Tas., on Codium harveyi, 20–22 m deep (Kraft 9387, 18.xii.1992); holotype in OB, isotype in MELU.

**Distribution:** SE Tasmania and Gabo I., Victoria.

**Selected specimens:** Gabo I., Vic., on Plocamium costatum, 18 m deep (Shepherd, 17.ii.1973; AD, A43509). Bicheno, Tas., in kelp, 18–20 m deep (Kraft, 18.xii.1992; MELU, 40425). Fluted Cape, Bruny I., Tas., on Hymenaeophyceae (?), 23 m deep (Shepherd, 12.ii.1972; AD, A41924) and on Polyopes constrictus, 16 m deep (Shepherd, 10.ii.1972; AD, A41515).


**Thallus** (Fig. 45A) red-brown, with prostrate branched axes bearing erect laterals 5–15 mm high, pinnae opposite, distichous, with opposite pinnules (Fig. 45A) of equal development from each rachis cell above the basal cell. Attachment by clusters of branched rhizoids (Fig. 47C) arising from the basal cells of pinnae, each branch developing terminal branched haptera; epiphytic on various algae. **Structure.** Apical cells (Fig. 47A) 8–10 μm in diameter and L/D 1–1.5, enlarging to 90–120 μm in diameter and L/D 1.5–2 in mature axial cells. Pinnae (Fig. 47B) 500–1000 μm and 12–24 cells long, with a small rounded basal cell (without pinnules) and each rachis cell above bearing opposite pinnules, simple apart from frequent branches on the lower 1 or 2 pinnules (Fig. 47B). rachis cells 30–45 μm in diameter and L/D 1–1.5, pinnule cells 10–22 μm in diameter and L/D 0.7–1.3, decreasing slightly to terminal cells with rounded ends; gland cells (Figs 45B, 47B) on short, 3–6-celled, pinnules, ovoid, 15–20 μm in diameter. Lateral branches arising irregularly, 2–7 axial cells apart, from the basal cells of pinnae. Cells uninucleate; rhodoplasts discoid, elongate in larger cells.

Reproduction. Unknown.

**Type** from Stanley Beach, Kangaroo I., S. Aust., on Sargassum (Womersley, 2.ii.1957); holotype in AD, A29504.


**Selected specimens:** Eliot, S. Aust., on Rhodophyllis, drift (Womersley, 13.i.1951; AD, A13508) and on Calliophycus oppositifolius, 28 m deep (Shepherd, 23.x.1970; AD, A37478). 13 km S of Vivonne Bay, Kangaroo I., S. Aust., on Rhodymenia, 50–70 m deep (Latz, 24.xi.1968; AD, A33008).

*A. pinnafolium* appears to be a distinctive species of *Antithamnion* but reproductive features are still unknown.

*A. pinnafolium* was recorded with doubt from Natal by Norris & Aken (1985, p. 59).

**FIGS 45C–E, 46**

*Thallus* (Figs 45C, 46A) medium to dark red-brown, with branched prostrate axes with more or less erect unattached ends 1–3 cm long, densely covered with pairs of opposite, decussate, whorl-branchlets (pinnae) which are upwardly curved and overlap. Attachment by branched clusters of rhizoids (Fig. 46D) from the basal cells of pinnae, with terminal digitate haptera (Fig. 46E); epiphytic on *Posidonia*, *Amphibolis* and various larger algae. Structure. Apical cells 8–15 μm in diameter and L/D 1–1.5, densely surrounded by young whorl-branchlets, increasing to 100–300 μm in diameter and L/D 1–1.5 in mature axial cells which have prominent pit-connections. Pinnae (Fig. 45D, E) rigid, distichously branched, (0.5-) 1–2 mm long, rachis cells 35–70 μm in diameter, basal cells L/D 0.8–1.2, then cells L/D 1.2–1.6, each cell bearing a single, alternate, usually branched pinnule, lower cells 25–55 μm in diameter and L/D 1–2, tapering near their apices to a mucronate end cell; gland cells (Fig. 45D, 46B) prominent, ovoid, borne on short 2–3-celled branches of the pinnaules, 25–40 (-50) μm in diameter. Lateral branches occur irregularly, arising on the small basal cells of the pinnae (Fig. 46C). Cells uninucleate when small, probably multinucleate when larger; rhodoplasts discoid in small cells, becoming elongate and ribbon like in axial cells.

*Reproduction.* Gametophytes dioecious. Carposporangia (Fig. 46F, G) borne in series of 10–16 on basal cells of young pinnae, with axial elongation ceasing on development of the first carposporophyte, and pinnaules usually absent on the rachides. Post-fertilization carposporangia 25–45 μm in diameter and L/D 1–2, tapering near their apices to a mucronate end cell; gland cells (Fig. 45D, 46B) prominent, ovoid, borne on short 2–3-celled branches of the pinnaules, 25–40 (-50) μm in diameter. Lateral branches occur irregularly, arising on the small basal cells of the pinnae (Fig. 46C). Cells uninucleate when small, probably multinucleate when larger; rhodoplasts discoid in small cells, becoming elongate and ribbon like in axial cells.

*Type* from Gulf St Vincent, S. Aust.; holotype missing in MEL but Sonder’s drawings (labelled “No. 43, P. Adelaide”) and his description (as in 1853, p. 674) are present.

**Distribution:** Houtman Abrolhos, W. Aust. (Huisman 1997), to Barringjoey Heads, N.S.W., and around Tasmania.

Fig. 46. *Antithamnion hanovioides*. A. Diagram of thallus branching with decussate, upwardly curved pinnae. 
A. hanovioides is the most common species of Antithamnion on southern Australian coasts, epiphytic on a wide variety of larger algae and seagrasses. Callithamnion spinescens Kützing (1843, p. 373) from W. Aust. (Preiss) appears to be a distinct but little known species, but C. spinescens sensu Harvey (1855a, p. 560) is a synonym of A. hanovioides.

Silva et al. (1996, p. 378) point out that the original spelling of the species name, with a ‘v’ and not a ‘w’ should be followed.


*Figs 47D–G, 48A*

**Thallus** (Figs 47D, 48A) with prostrate axes bearing numerous erect lateral branches up to 4 mm long, with opposite, decussate, whorl-branchlets (pinnae) from each axial cell, curving upwards towards the branch apex. Attachment by rhizoids from the basal cells of pinnae with digitate haptera; epiphytic on geniculate coralline algae. **Structure.** Apical cells 4–5 μm in diameter and L/D 0.7–1.2, surrounded by young whorl-branchlets and enlarging to 60–90 μm (including a thick sheath) in diameter and L/D 0.7–2 in mature axial cells. Pinnae (Fig. 47E) 200–450 (~580) μm and 10–15 cells long, basal rachis cells 25–32 μm in diameter and L/D 1–1.5, tapering to terminal cells 6–9 μm in diameter and L/D 1–1.5, each of the lower 2 (1–3) cells with opposite pinnules and upper cells with alternate pinnules, pinnules 10–22 μm in diameter, cells L/D 1–1.5 (~2), tapering to their apices, usually with 1–3 simple branches in the plane of the pinnae; gland cells (Fig. 47E) occur on short 2–3-celled branches on the sides of pinnules. Lateral branches arise at irregular intervals on the short basal cells of pinnae. Cells uninucleate; rhodoplasts discoid to elongate, ribbon like in larger cells.

**Reproduction.** Carpogonial branches (Fig. 47F) occur in series of 4–8 on the basal cells of pinnae near branch apices which then cease elongation. Slight fusions only occur between the axial cell, supporting cell and other lower gonimoblast cells, and a terminal group (Figs 47G, 48A) 100–250 μm across of ovoid carposporangia 15–30 μm in diameter develops, followed by lateral groups. Spermatangia unknown. Tetrasporangia unknown in the type.

**Type** from Middle R., Kangaroo I., S. Aust., on *Corallina officinalis*, lower eulittoral; holotype in AD, A13031.

**Distribution:** Known from the type locality and Shark Bay, W. Aust. (Kendrick et al. 1988, p. 204). South Africa, doubtfully by Wollaston (1984, p. 284) and by Stegenga (1986, p. 28, pl. 4); Norris (1987, p. 19) and others.

**Selected specimens:** Only known from the type in southern Australia.

This little known species has particularly wide gelatinous sheaths around the cells, especially axial cells; the cell contents are only half the diameters given above. The South African specimens in AD (HOE) are more robust, with shorter whorl-branchlets and less prominent cell sheaths than the type (c.f. Stegenga 1986, pl. 4) and confirmation of their identity with *A. diminuatum* is still needed.


Callithamnion cruciatum sensu Harvey 1859b: 333; 1863, synop.: liii. Sonder 1881: 107 (NON C. Agardh 1827: 637.)

**FIGS 48B–D, 49**

_Thallus_ (Fig. 48B) red, delicate, with prostrate axes bearing erect laterals 5–25 mm high with dense apical tufts of decussate whorl-branchlets with mostly alternate distichous pinnules. Attachment by rhizoids (Fig. 49A) from the small basal cells of whorl-branchlets, developing a branched digitate hapteron on the host; epiphytic. **Structure.** Apical cells 5–10 μm in diameter and L/D 1–2, enlarging below to 40–65 μm in diameter and L/D 2–4 (-6), and to 90–180 μm in diameter and L/D (1.5–) 2–4 in lower erect and prostrate axes; whorl-branchlets formed in decussate pairs, (500–) 600–1200 (-1700) μm long, basal cells isodiametric, 15–35 μm in diameter, pinnules distichous and alternate [occasionally 1 (-3) opposite pairs basally], unbranched or with simple branches; cells of rachis above basal cells 20–35 μm in diameter and L/D (2-) 3–4, decreasing in the pinnules to 8–10 μm in diameter and L/D 3–8 several cells below the apices; gland cells (Fig. 49G) scattered, sparse, borne on short 2 (-3)-celled branches on the pinnules, 10–15 μm in diameter. Lateral branches (Fig. 49B) arise irregularly from the basal cells of whorl-branchlets. Cells uninucleate; rhodoplasts ovoid, elongate in larger cells.

**Reproduction.** Gametophytes dioecious. Procarps (Fig. 49C) successive below indeterminate apices, with the basal cells of whorl-branchlets acting as supporting cells and bearing 4-celled carposporial branches. Post-fertilization union with the auxiliary cell occurs via a connecting cell and the auxiliary cell divides to form a foot cell and upper cell which produces a terminal gonimolobe (Fig. 49D) 250–450 μm across of ovoid carposporangia 15–45 μm in diameter, occasionally with later gonimolobes laterally; the axial cell, supporting cell and foot cell usually fuse together, and the carposporophyte (Fig. 48B) is surrounded by an involucr of filaments. Spermatangia occur on special short branches (Figs 48C, 49E) on lower cells of the pinnules, in heads 25–35 μm in diameter and L/D 1.5–2.5, with a central axis of 5–10 cells bearing whorls of 4–6 cells with terminal spermatangia (Fig. 49F).

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**Fig. 47. A–C. Antithamnion pinnafolium.** A. Branch apex with developing whorl-branchlets. B. Pinna with branched basal pinnules and a gland cell on a reduced pinnule. C. Rhizoidal attachment organ. **D–G Antithamnion diminuatum** (AD, A13031). D. Habit. E. Pinna with branched pinnules and gland cells. F. Apex with carposporial branches borne on basal cells of pinnules. G. A young carposporophyte. (All as in Wollaston 1968, courtesy of Aust. J Bot.)
Tetrasporangia (Figs 45D, 49G) are usually borne on lower cells of the pinnules, ovoid, 35–75 μm in diameter, sessile, decussately or cruciately divided.

**Type** from King George Sound, W. Aust. (Harvey); lectotype in Herb. Harvey, TCD (Alg. Aust. Exsicc. 529 in lieu of Trav. Set 339, missing).

**Distribution:** Shark Bay, W. Aust. to Westernport Bay, Vic., and N Tasmania.


Wollaston (1968, p. 284) suspected the identity of *A. divergens* and *A. delicatulum*, and this was affirmed by Athanasiadis (1996, p. 155). *A. delicatulum* is based on Harvey’s Trav. Set No. 339 which is missing in TCD, but his Alg. Aust. Exsicc. 529 is a duplicate specimen. The species grows on a variety of hosts.

The record of *A. divergens* by Norris (1987, p. 27, figs 16–18) from South Africa is probably incorrect.

10. **Antithamnion uniramosum** Athanasiadis 1996: 157, fig. 74.

**FIG. 50**

*Thallus* (Fig. 50A) with prostrate and erect axes 2–7 mm long, more or less complanately branched with whorl-branchlets distichously or decussately arranged, with each axial cell producing a single or usually two opposite and equal whorl-branchlets each 500–1000 μm and 8–11 cells long and bearing short, opposite, 1–2 celled branches in 2 rows (Fig. 50C, D). Lateral axes arising from basal cells of whorl-branchlets, without an opposite branchlet. Attachment by rhizoids with terminal digitate pads, arising from basal cells of whorl-branchlets on prostrate axes; probably epiphytic. *Structure.* Apical cells 5–8 μm in diameter and L/D 0.8–1.2, enlarging to axial cells 20–80 μm in diameter and L/D 4–8. Whorl-branchlets (Fig. 50A, B) with lower and mid cells 20–25 μm in diameter and L/D 3–6, basal cell isodiametric and markedly shorter than upper cells, sub-terminal cells 8–12 μm in diameter and L/D 3–4, terminal cells with rounded ends; short lateral branches opposite on upper rachis cells, 10–15 μm long and 3–4 μm in diameter, often with terminal hairs; gland cells borne on the short lateral branches, lateral and touching both cells or occasionally terminal, ovoid, 15–20 μm in diameter. Lateral branches replacing a whorl-branchlet and without an opposite whorl-branchlet. Cells uninucleate; rhodoplasts discoid, becoming ribbon like in older cells.

*Reproduction.* Gametophytes unknown.

Tetrasporangia (Fig. 50B) borne on unicellular pedicels, on lower cells of pinnules or on short, gland cell bearing, branches, ovoid, 50–75 μm in diameter, cruciately or decussately divided.

**Type** from Arno Bay, S. Aust., drift (Kraft 4215, 12.xi.1971; holotype in GB, isotypes in MELU and AD, A67213).

**Distribution:** Only known from the type.

Some data for the type collection given by Athanasiadis (1996, p. 158) are incorrect (see above), and the specimen in AD has been presented by Kraft.
Fig. 49. Antithamnion delicatulum. A. Axial cells of prostrate axis with pinnae and attachment rhizoids from basal cells of whorl-branchlets. B. Young lateral branch on basal cell of a whorl-branchlet. C. Apex with a series of carpogonial branches borne on basal cells of whorl-branchlets. D. A carposporophyte with maturing gonimolobes. E. A spermatangial head. F. Spermatangial initials and spermatangia on axial cell (not shown) of a spermatangial head. G. Whorl-branchlet with tetrasporangia and gland cells. (All as in Wollaston 1968, courtesy of Aust. J. Bot.)

**FIG. 51**

*Thallus* (Fig. 51A) medium to dark red-brown, densely tufted, 5–25 mm high, with limited prostrate axes bearing much branched erect axes with opposite, decussate, laxly branched, whorl-branchlets. Attachment by rhizoids (Fig. 51B) with digitate multicellular haptera, arising from basal cells of whorl-branchlets; epiphytic. **Structure.** Apical cells 6–12 μm in diameter and L/D 1.5–2, within densely tufted apices, enlarging to mature axial cells 60–110 μm in diameter and L/D 2–3. Whorl-branchlets 700–1200 μm and 14–20 cells long, with opposite or unilateral, mostly erect, pinnules 200–500 μm long, pinnules simple or occasionally with a short gland cell bearing branch; rachis cells 16–22 μm in diameter and L/D 1.5–2, terminal cells conical with rounded ends; pinnule cells 18–26 μm in diameter and L/D 1.2–1.8 (-2); gland cells (Fig. 51C) borne on short 2–4-celled branches on the pinnules, alongside 2 or 3 pinnule cells, ovoid when mature, 18–25 (-30) μm in diameter. Lateral branches arising on basal cells of whorl-branchlets. Cells uninucleate; rhodoplasts discoid in smaller cells, ribbon like in older cells.

**Reproduction.** Gametophytes unknown in Australian collections. Tetrasporangia (Fig. 51D) pedicellate, ovoid, 55–80 μm in diameter, decussately divided; branching from the pedicel results in 2 (-3) adjacent tetrasporangia (Fig. 51E).

*Type* from Trieste, Italy; lectotype in Herb. Agardh, LD, 18774.

**Distribution:** Widespread in temperate Atlantic and European waters (see Athanasiadis 1996, p. 171).

In southern Australia, known only from Whyalla, S. Australia.

**Selected specimens:** Whyalla, S. Aust., in channel with tidal flow, 0.5 m deep (Harbison, 10.v.1994; 21.v.1994; 30.v.1994 and 24.viii.1994; AD, A63435, A63432, A63577 and A63581 resp.)

These collections of a single population agree well with descriptions of *A. cruciatum* from Europe, and the identification has been supported by Dr Christine Maggs. Their locality is near a major industrial port and it is highly likely that they are adventive.

Previous records (e.g. Harvey 1863, synop.: liii) of *A. cruciatum* probably all apply to *A. delicatulum.*

**Genus ACROTHAMNION** J. Agardh 1892: 23

*Thallus* one to a few cm high, with prostrate and erect indeterminate axes, ecorticate, bearing whorls of 4 pinnae (usually 2 larger and 2 smaller) each usually with a shorter basal cell and with opposite unbranched pinnules from each rachis cell; gland cells terminal on the rachis of the pinnules. Attachment of prostrate axes by rhizoids with terminal haptera; epiphytic. **Reproduction.** Gametophytes dioecious. Procarps in series of 4–8 on indeterminate axes, with 4-celled carpogonial branches on the basal (supporting) cells of the pinnae. Post-fertilization the supporting cell cuts off upwards an auxiliary cell and a terminal gonimolobe forms followed by lateral gonimoblasts, with slight fusion of the axial cell, residual supporting cell, and lower gonimoblast cells; the carposporophyte is partly enclosed by pinnae from lower axial cells. Spermatangia occur in branched clusters of cells on cells of the pinnules. **Tetrasporangia** occur on protrusions from the basal cells of major pinnae, cruciately divided.

**Type species:** *A. pulchellum* (Harvey) J. Agardh 1892: 25 [= *A. preissii* (Sonder) Wollaston 1968: 323].

A genus of 2 species (see Wollaston 1977b, p. 391), one from southern Australia. (Wollaston 1977b) and one from the West Indies, Solomon Is, and Japan (Itono 1977, p. 22).
Fig. 50. Antithamnion uniramum (A, AD, A67213; B–D, MELU, 4215). A. Thallus branching with terminal hairs. B. Branches with apical group, small lateral cells and tetrasporangia. C. Upper branches, with paired short branches on cells of whorl-branchlets. D. Whorl-branchlet cells with paired, short, unicellular branches.
Fig. 51. *Antithamnion cruciatum* (A, AD63581; B, C, AD, A63432; D, E, AD, A63577). A. Habit. B. Lower filament with attachment haptera and young erect branches. C. Gland cells alongside 2 or 3 pinnule cells. D. Branch with tetrasporangia. E. Pinnules with single or paired tetrasporangia.
Acrothamnion


Acrothamnion arcuatum Wollaston 1968: 326, fig. 23M–O.

FIGS 52A, B, 53A–J

Thallus (Figs 52A, 53A) rose red, with branched, prostrate and erect axes to 0.5–1.5 cm long, usually bearing whorls of 2 opposite major pinnae and (1–) 2 minor pinnae between them (Fig. 53B), sometimes pinnae equally developed (Fig. 53C). Attachment by rhizoids (Fig. 53E) with digitate haptera, arising from prostrate axial cells; epiphytic on various algae. Structure. Apical cells 6–8 μm in diameter and L/D 1–1.3, enlarging to 80–75 μm in diameter and L/D 1.5–3 (–5) in mature axial cells. Major pinnae usually 180–280 μm and 10–12 cells long, with short basal cells and rachis cells 20–28 μm in diameter and L/D 0.8–1.2, each bearing opposite, disjunctive, simple pinnules, 80–100 μm and 6–9 cells long, longest near the pinna base, cells 10–15 μm in diameter and L/D 0.8–1.2, tapering near their tips; minor pinnae smaller than major ones, with one usually lost producing a dorsiventral branch; gland cells (Figs 52B, 53D) terminal on the rachis of most pinnae, formed at maturity of the rachis, transversely oval and 16–22 μm in diameter. Lateral branches irregular, arising on the basal cells of pinnae. Cells uninucleate; rhodoplasts discoid, elongate or in chains in larger cells.

Reproduction. Gametophytes dioecious. Carpogonial branches (Fig. 53F, G) develop in series of 4–8 on the basal cells of pinnae, with 1 or 2 developing carpogonophores. Post-fertilization the supporting (basal) cell cuts off a rounded auxiliary cell with a terminal gonimoblast (Fig. 53H) 200–300 μm across of ovoid carpogonia 28–35 μm in diameter, usually with later lateral gonimoblasts, and with slight fusion of basal sterile cells. Pinnae on lower axial cells partly surround the carpogonophore. Spermatangia (Fig. 53 I) occur on branched clusters from short pinnules on lower rachis cells. Tetrasporangia (Fig. 52B, 53J) occur on elongate protrusions on the upper side of basal rachis cells of mainly major pinnae, sub-spherical, 40–50 μm in diameter, decussately divided.

Type from Rottnest I., W. Aust. (Preissi); holotype in MEL, 10260.


Wollaston (1977b, p. 391) considered her A. arcuatum (Wollaston 1968, p. 326) only an extreme form of A. pressii, with relatively evenly spaced pinnae of similar length. Wollaston (1968, p. 326) expressed doubt concerning the only non-Australian record (from Japan) of this species, but this is maintained by Yoshida et al. (1990).

**Genus MACROTHAMNION** Wollaston 1968: 328.

*Thallus* 1 to 30 cm high, axes irregularly branched and corticated below with loose rhizoidal filaments; holdfast rhizoidal, epilithic or epiphytic. Axial cells each with 3 whorl-branchlets (2 in *M. acanthophorum*), simple or bearing a few simple pinnules, with or without minute spinous processes on upper cells; gland cells on special short branches. Cells uninucleate.

**Reproduction.** Gametophytes dioecious. Carpogonial branches borne on basal (= supporting) cells of whorl-branchlets, usually in a succession at branch apices, post-fertilization with rounded gonimolobes of carposporangia, partly surrounded by whorl-branchlets from below. Spermatangia terminal in clusters borne on the special gland-cell branches.

Tetrasporangia also borne on the special gland-cell branches, decussately divided.

**Type species:** *M. pellucidum* (Harvey)Wollaston 1968: 329, fig. 25.

The genus contains 4 species, characterized by whorls of 3 (or 2) whorl-branchlets and both spermatangia and tetrasporangia borne on cells of the small special branches which bear the gland cells.

**KEY TO SPECIES OF MACROTHAMNION**

1. Whorl-branchlets in distichous pairs from each axial cell. ............. 4. *M. acanthophorum*
   1. Whorl-branchlets in whorls of 3 (rarely 2) from each axial cell ........................................ 2

2. *Thallus* to 30 cm high; bearing whorls of 3 unbranched whorl-branchlets from each axial cell; gland cells (1–14) on short, often much-branched special branches ............................................................. 1. *M. pellucidum*

3. *Thallus* usually 1–8 (-12) cm high. Axial cells bearing whorls of 3 whorl-branchlets, some of which are always secundly branched with 1–5 simple branches; gland cells 1 (-3) on simple 2–4-celled short special branches ....................................... 3

3. Thallus more or less robust, much branched, 1–4 (-12) cm high. Whorl-branchlets consistently in whorls of 3; gland cells on special short branches, sometimes extended to bear 2–3 gland cells ................................................................. 2. *M. secundum*

3. Thallus slender, sparsely branched, 3–8 cm high. Whorl-branchlets in whorls of 2 or 3; gland cells single on cells of short 2–4-celled branches ........................................ 3. *M. pectenellum*

   *Spyridia pellucida* Harvey 1844: 449.
   *Callithamnion pellucidum* (Harvey)Hooker & Harvey 1847: 412.
   *Callithamnion griffithsioides* Sonder 1855: 512 (NON Harvey 1860: pl. 160).
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Macrothamnion

FIGS 52C, 53K–S, 54A–D

Thallus (Figs 52C, 53K) medium to dark red-brown, erect, 10–30 cm high, much branched with several axes and long laterals, each axial cell with 3 whorl-branchlets (Fig. 53L), axes corticated by entwined rhizoids over basal parts. Holdfast rhizoidal, 2–10 mm across; epitheial. Structure. Apices densely branched, apical cells 8–10 μm in diameter and L/D 0.6–1, enlarging to 200–400 μm in diameter and L/D 1.5–2 (-3) in mid and lower axial cells. Whorl-branchlets 1–2.5 mm long, simple, basal cell 75–120 (-150) μm in diameter and L/D 0.8–1.2, cells above L/D 2–2.5, tapering to subterminal cells 25–35 μm in diameter and L/D 1–1.5, terminal cells macronate; some young whorl-branchlets have small, unilateral or opposite, cells (Fig. 53M) with extended curved walls (“hooked spines”) on their upper cells, these later lost; gland cells (Figs 53N, O, 54A) borne on special short branches on lower cells of whorl-branchlets, 1 to a few (but up to 14) gland cells on one branch cluster, 25–45 (-70) μm in diameter. Lateral branches arise on basal cells of whorl-branchlets at irregular intervals along the axes. Cells uninucleate when small; rhodoplasts elongate in small cells, becoming ribbon like in larger cells.

Reproduction. Gametophytes dioecious. Carposporangial branches (Fig. 53P) borne on basal (= supporting) cells of whorl-branchlets on 8–20 successive axial cells. Post-fertilization the auxiliary cell cuts off an upper gonimoblast cell which develops a terminal gonimolobe, and later lateral gonimolobes, 100–500 μm across of ovoid to angular carposporangia 20–25 (-30) μm across; fusions occur between the axial cell, residual supporting cell and the foot cell, and the carposporophyte (Figs 53Q, 54B) is surrounded by longer whorl-branchlets from below. Spermatangia occur terminally on the special tufted branches (Figs 53R, 54C) 70–120 μm across, which also each bear a single gland cell on their basal cells.

Tetrasporangia (Figs 53S, 54D) occur on the special, short, gland cell bearing, branches, sessile, ovoid, 45–55 μm in diameter, decussately or cruciately divided.

Type from Georgetown, Tasmania (Gunn); lectotype in Herb. Harvey, TCD (Gunn 1305).

Distribution: Lancelin, W. Aust., to Sorrento, Vic., and around Tasmania.


M. pellucidum is usually a deep water species on rough water coasts, but does occur on calmer coasts where there is strong current flow.


FIGS 52D, 54E–G, 56

Thallus (Figs 52D, 56A) medium to dark red-brown, erect, 1–4 (-12) cm high, much branched with several bushy axes, each axial cell with 3 whorl-branchlets, axes loosely corticated with rhizoids below. Holdfast rhizoidal, 2–10 mm across; epithelial or epiphytic. Structure. Apical cells 7–12 μm in diameter and L/D 1–1.5, enlarging to axial cells 130–400 μm in diameter and L/D 1 (-2)–4. Whorl-branchlets (Figs 54E, 56B) 0.8–1.5 mm long, usually successively branched with 1–5 simple pinnules, basal cells 40–100 μm in diameter and L/D 1–1.2, cells above L/D 2–3, tapering to subterminal cells 15–30 μm in diameter and L/D 1.3–2, terminal cells macronate. Corticating rhizoids 25–35 (-50) μm in diameter, cells L/D 4–6; gland cells (Fig. 56C) borne on special 2–3-celled short branches, single (or with 2–3), ovoid,
16–25 (-35) μm in diameter. Lateral branches arise irregularly 4–8 axial cells apart, on the basal cells of whorl-branchlets. Cells uninucleate; rhodoplasts discoid to elongate in smaller cells, ribbon like in larger cells.

**Reproduction.** Gametophytes dioecious. Carpogonial branches (Fig. 56D) borne on the basal (= supporting) cell of numerous (up to 18) whorl-branchlets near apices, with the auxiliary cell cutting off a gonimoblast cell which produces several gonimolobes; fusion occurs between the axial cell, residual supporting cell and the foot cell (Fig. 56E), and the carpogonophore (Fig. 56F) is largely covered by upcurved whorl-branchlets from below. Spermatangia occur on special short branches (Figs 54G, 56G) on the basal cell of gland-cell branches.

Tetrasporangia occur successively on the special branches (Figs 54G, 56H) bearing the gland cells, 1–3 per cell, sessile, ovoid, 50–90 μm in diameter, decussately divided.

**Type** from Vivonne Bay, Kangaroo I., S. Aust., lower eulittoral pools (Wollaston, 30.i.1956); holotype and isotypes in AD, A20161.

**Distribution:** Pearson Is to Port Phillip Heads, Victoria.


**M. secundum** is often a shallow water species on rough-water coasts, but occurs at depth in northern Spencer Gulf and Backstairs Passage, E of Penneshaw.

3. **Macrothamnion pectenellum** Wollaston 1968: 337, fig. 270–S.

**FIGS 52E, 55A**

*Thallus* (Fig. 52E) medium red-brown, erect, 3–8 cm high, with several sparsely branched axes, ecorticate or only lightly corticated near the base, each axial cell with (2-) 3 whorl-branchlets. Holdfast rhizoidal, 1–5 mm across; epilithic or on cockle shells. **Structure.** Apical cells 6–11 μm in diameter and L/D 0.8–1.2 (-2), enlarging shortly behind the apex and to 150–240 μm in diameter and L/D 1.5–3 in lower axial cells. Whorl-branchlets (Fig. 55A) 0.4–1 mm long, usually with 1–3 simple adaxial pinnules, basal cells 35–60 μm in diameter and L/D 0.8–1.2, L/D 2–3 above, tapering to subterminal cells 15–25 μm in diameter and L/D 1–1.5, terminal cells mucronate; upper cells often with short, lateral, curved spinous cells; gland cells borne on one or both cells of special, short, 2-celled branches on cells of whorl-branchlets, ovoid to subspherical, 16–25 (-50) μm in diameter. Corticating rhizoids arising from basal cells of whorl-branchlets, becoming entwined, (20-) 25–65 μm in diameter, cells L/D 4–7. Lateral branches arising from the basal cells of whorl-branchlets. Cells uninucleate in smaller cells; rhodoplasts discoid to elongate in small cells, ribbon like in larger cells.

**Reproduction.** Carpogonial branches borne on basal (= supporting) cells of whorl-branchlets, up to 12 at each branch apex. Post-fertilization successive rounded gonimolobes 150–350 μm across with ovoid to angular carpogonophores 25–40 μm across are produced, partly protected by whorl-branchlets from below. Spermatangia unknown.

Tetrasporangia (Fig. 55A) occur on the special short branches which often bear the gland cells, ovoid, 45–55 μm in diameter, decussately divided.

**Type** from South Arm, Hobart, Tas., drift on cockles (Wollaston, 28.ii.1964); holotype in AD, A28033.

**Distribution:** Known from the type, and Sorrento and Crawfish Rock, Westernport Bay, Victoria, and SE Tasmania.
Selected specimens: Sorrento, Vic., 11 m deep (Womersley, 7 iv 1959; AD, A22771). Crawfish Rock, Westernport Bay, Vic., 6–9 m deep (Watson, 15 ix 1968; AD, A32824) and 4 m deep (Watson, 29 v 1974; AD, A44046, and 17 st. 1974; AD, A46233). Arch Rock, Ninepin Point, Tas., 10–14 m deep (Kraft 9836a & Scott, 16 iii 1993: MEL and AD, A67797).

4. Macrotamnion acanthophorum (Kützing) Womersley, comb. nov.


Callithamnion acanthocarpum (Kützing) Sonder 1853: 673. (Specific name misspelt.)

FIGS 52F, 55B–D

Thallus (Fig. 52F) medium red-brown, 2–10 (–16) cm high, much branched with numerous axes from a matted base, ecoricate, each axial cell with 2 opposite, distichous, whorl-branchlets (Fig. 55B–D). Attachment by rhizoidal filaments with terminal haptera; epiphytic. Structure. Apical cells 10–15 μm in diameter and L/D 1–2, enlarging rapidly, then to 200–300 μm in diameter and L/D 1–1.5 in lower axial cells. Whorl-branchlets 400–900 μm long, mostly simple (some with 1–3 adaxial pinnules), basal cells 25–60 μm in diameter and L/D 0.7–1, mid cells L/D 1.5–2.5, tapering to subterminal cells 18–25 μm in diameter and L/D 1–1.5, terminal cells mucronate; gland cells borne on short, 2–3-celled branches (Fig. 55B–D) on cells of whorl-branchlets, subspherical, 20–25 μm in diameter. Lateral branches arising from the basal cells of whorl-branchlets. Cells uninucleate; rhodoplasts elongate, becoming ribbon like in larger cells.

Reproduction. Gametophytes unknown. (MEL, 15323 has carposporophytes but is inadequate.) Tetrasporangia occur on the special, short, gland cell-bearing branches (Fig. 55D) on cells of the whorl-branchlets, ovoid, 40–55 μm in diameter, decussately divided.

Type from Tasmania; in L, 938, 92... 345.

Distribution: Port Phillip Heads, Vic., and N Tasmania.

Selected specimens: Port Phillip Heads, Vic. (Wilson, 12 iv 1870; MEL, 15324, 19.1.1888; MEL 15326 and Jan. 1895; MEL, 15323, all as Wrangelia incurva, and 16–21 m and 17–21 m deep (on Caulerpa simpliciuscula), N of Quarantine Station (Kraft 10617, Saunders & Strachan, 5. iv 1995; MELU and AD, A66643, A67841), Georgetown, Tas. (Harvey, Alg. Aust. Exsicc. 546 I, in part).

This little known species is characterised by opposite, simple, whorl-branchlets, distichously arranged, and is provisionally placed in Macrotamnion due to the similarity in habit, form of the whorl-branchlets, and small branchlets bearing gland cells and also tetrasporangia.

Harvey’s Alg. Aust. Exsiccat. 546 I, from Georgetown, Tasmania, includes both M. acanthophorum (AD, A18191) and M. pellucidum (AD, A18192).

Kützing (1849, p. 647) recorded the type specimen as parasitic on Carpacanthus oligophyllus, which Womersley (1987, p. 436) regarded as a synonym of Sargassum tristichum. The nomen nudum Wrangelia incurva J. Agardh (see Wilson 1892, p. 170 and Gordon 1972, p. 39) was based on Wilson specimens (in MEL, e.g. 15324, 15326, 15327) from Port Phillip Heads, Vic. These are, at least mostly, M. acanthophorum; some are M. secundum.

Tribe GYMNOTHAMNIEAE Kajimura 1989: 129

by H.B.S. Womersley

Thallus small, ecoricate, with prostrate indeterminate branches attached by multicellular rhizoids and erect, pinnate, indeterminate, but limited, branches, with the erect branches and rhizoids arising from a common cell of the prostrate filaments. Apical cells of the erect branches dividing transversely, subapical cells initiating first one and soon two opposite
lateral branchlets, the lower cells of which form short, adaxial, filaments; gland cells absent. Cells uninucleate.

*Life history* triphasic with isomorphic gametophytes and tetrasporophytes.

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Reproduction. Gametophytes dioecious. Procarps borne on opposite branchlets which are shorter than the vegetative ones, with the fertile segment cutting off 1 or 2 periaxial cells, one (the supporting cell) bearing a 4-celled carpogonial branch plus a sterile cell which may produce a unicellular hair. Post-fertilization connection to the auxiliary cell occurs via a connecting cell and one to several gonimolobe initials are produced, with mature gonimolobes elongate, without any involucre. Spermatangia borne on short, opposite, branchlets, terminal on short cells.

Tetrasporangia terminal on the branchlets and their short adaxial branches, occasionally lateral on the cells, subovoid to ovoid, irregularly tetrahedrally divided.

Type (and only) genus: Gymnothamnion J. Agardh 1892: 27, pl. 1 figs 11–14.

Gymnothamnion when established was related to the Ptiloteae by J. Agardh, followed by Balakrishnan (1958) and Feldmann & Feldmann (1966). Moe & Silva (1979, p. 398) considered it was not a member of this tribe and Athanasiadis (1987, p. 68) assigned it to the Antithamnion. It was placed in its own tribe by Kajimura (1989).

Genus GYMNOTHAMNION J. Agardh 1892: 27

With the characters of the tribe

Type species: Gymnothamnion elegans (Schousboe)J. Agardh 1892: 28.

A genus with 2 species, the type and G. nigrescens from southern Australia.

KEY TO SPECIES OF GYMNOTHAMNION

1. Thallus 2–5 mm high, axes 10–15 mm in diameter, branchlets 5–9 mm in diameter

2. Thallus 2–3 cm high, axes 80–130 mm in diameter, branchlets 35–50 mm in diameter


**FIG. 57B–E**

Thallus (Fig. 57B) 2–5 mm high, with prostrate filaments bearing ecorticate plumose erect axes with opposite, distichous, simple or slightly branched branchlets (Fig. 57E) from each axial cell; erect axes mostly unbranched, occasionally with lateral branches developed from one of the paired branchlets. Attachment by multicellular rhizoids with branched ends, developed from cells (several cells apart) of the prostrate filaments, usually with an opposite erect branch. Structure. Apical cells (Fig. 57C) of axes 7–15 μm in diameter and L/D 1–1.5 (2.5), increasing to axial cells 10–15 μm in diameter and L/D 1.5–3 (Fig. 57D, E). Branchlets simple or with adaxial (and abaxial near the apices) branches, 60–180 (-240) μm and 3–9 (-12) cells long, cells 6–9 μm in diameter and L/D 1.5–2.5 (+3). Cells uninucleate; rhodoplasts elongate.

Reproduction. Gametophytes probably dioecious. Procarps (Fig. 56 L) developed mainly on shorter (3–6 short cells), opposite, upwardly curved, branchlets along the erect axes, separated by 2 pairs of sterile branchlets, sometimes near the end of full length branchlets. Fertile branchlets with the subterminal cell bearing a supporting cell with a 4-celled carpogonial branch and a sterile cell (occasionally with 2 or 3 successive procarps) with 1–2 hypogenous cells usually cutting off a lateral cell. Carposporophytes (unknown in this material) reported as pyramidal or elongate lobes. Spermatangia (unknown in Australian material) terminal or lateral on short branchlets.
Tetrasporangia (Fig. 56K) terminal on branchlets, ovoid, 20–25 μm in diameter, tetrahedrally divided.

**Type** from Tangier, Morocco; in Herb. Agardh, LD.

**Distribution:** Widespread (but inconspicuous) in warmer seas.

In southern Australia, known only from Point Lonsdale, Vic., on sponge under overhang, 0.3 m deep (Kraft 7810 & Millar, 25 iii. 1988; MELU and AD, A67814) and Bicheno, Tas., on tunicate, 17–19 m deep (Kraft 9362, 18 xii. 1992; MELU and AD, A67815). Also N.S.W. (Millar & Kraft 1993, p. 41).

The southern Australian specimens agree well in habit, structure and dimensions with descriptions of *G. elegans* by Feldmann & Feldmann (1966), Balakrishnan (1958) and Stegenga (1986, p. 84, pls 28, 29), but with minor differences. No secretary (gland) cells such as illustrated by (only?) Feldmann & Feldmann (fig. 1B) have been observed, and there appears to be a sterile cell on the supporting cell rather than a second periaxial cell, as described by Balakrishnan (1958, p. 139). However, the Bicheno material had not been fertilized and further observations are needed on the procarp structure.


**Fig. 57A**

Thallus (Fig. 57A) probably 2–3 cm high, dark red-brown, complanately branched with slightly incurved apices and axes bearing irregular laterals, all axial cells bearing opposite branchlets becoming 8–14 cells and 500–900 μm long, simple or with short adaxial branches from their 2–5 basal cells, the lowest ones branched. Attachment probably by rhizoids.

**Structure.** Apical cells 20–25 μm in diameter and L/D 2–3, dividing more or less transversely, increasing in axial cells to 80–130 μm in diameter and L/D 1–2, branchlets basally 35–50 μm in diameter, decreasing only slightly to apical cells 30–35 μm in diameter, cells basally L/D 1–1.5, mid cells L/D 1.5–2, apical cells L/D 1–1.5.

**Reproduction.** Unknown.

**Type** from Port Phillip Heads, Vic. (Wilson); holotype in Herb. Agardh, LD, 18128.

**Distribution:** Only known from the holotype specimen.

While the habit agrees with *Gymnothamnion*, new collections and reproductive plants are needed to establish the position of *G. nigrescens*. It has apparently never been found since the original collection.

**Tribe PTEROTHAMNIEAE** Athanasiadis 1996: 44

by H.B.S. Womersley & E.M. Wollaston

*Thallus* erect, 5–30 cm high, much branched with essentially complanate lateral branches, axial cells each with 2–4 whorl-branchlets which are of equal size or not (often as more-branched major ones and less-branched minor ones) and distichously, decussately, tristichously or irregularly branched; basal cells of whorl-branchlets laterally branched or not. Lateral branches arising from axial cells in place of a whorl-branchlet or from basal cells of whorl-branchlets. Lower axes corticate or not with loose rhizoids, arising from the basal cells of whorl-branchlets, and forming a basal rhizoidal holdfast. **Structure.** Apical cells usually small, young branches flexuous or straight. Whorl-branchlets with variously sized and shaped basal cells, upper branching usually relatively dense; gland cells usually present, or absent in some taxa. Cells uninucleate.
Life History triphasic with isomorphic gametophytes and tetralsporophytes.

Reproduction. Gametophytes dioecious. Carpogonial branches borne on the basal cells of rachides of whorl-branchlets, usually on several successive axial cells near apices, with post-fertilization fusions between the axial, residual supporting, and lower gonimoblast cells common. Carposporophytes with several lobes and surrounded by involucral whorl-branchlets from the axial cell below. Spermatangia terminal on special branch clusters on lower cells of the whorl-branchlets or their pinnules.

Tetrasporangia on cells of the whorl-branchlets or on special branches, sessile or pedicellate, decussately divided.

This tribe was established by Athanasiadis with Pterothamnion as the only genus. Ballia is here provisionally added to the tribe, since the two genera are similar in habit, branching, carpogonial branch position and enveloping whorl-branchlets, and in spermatangial arrangement and in tetrasporangia. There are, however, clear cut differences between them (see key).

KEY TO GENERA OF PTEROTHAMNIEAE

1. Axial apices straight to flexuous, axial cells with 2 or 4 opposite whorl-branchlets; gland cells common to rare, ovoid to conical at an angle to their bearing cell; tetrasporangia on cells of whorl-branchlets ........................................ PTEROTHAMNION
   1. Axial apices usually not flexuous, axial cells with 2 or 3 whorl-branchlets; gland cells absent; auxiliary cells developing a chain of 3 or 4 cells, the second fusing with the fertilized carpogonium; tetrasporangia on special branch systems on cells of the whorl-branchlet rachides ................................................................. BALLIA


Thallus usually 4–20 (-30) cm high, with erect, complanately branched, apices often flexuous with laterals usually every 2–8 axial cells, arising in place of whorl-branchlets and often overtopping the previous main axis; each axial cell with 2 or 4 whorl-branchlets; axes ecorticate or loosely to densely corticate with rhizoids on lower axes; holdfast of multicellular rhizoids; epilithic or epiphytic. Structure. Apices of small cells dividing transversely, enlarging below, each axial cell bearing first a single unilateral, then 2 opposite whorl-branchlets in the plane of the thallus, and between them usually 2 alternating, similar sized or shorter, whorl-branchlets; whorl-branchlets successively branched several times usually adaxially, usually bearing sessile gland cells variously orientated, and the basal or other cells with spinous processes in some species; corticating rhizoids arising from the basal cells of whorl-branchlets. Lateral branches arising from axial cells or the basal cells of whorl-branchlets. Cells uninucleate.

Reproduction. Gametophytes dioecious. Procarps usually borne along young axes in series of 2–5 (-20) on basal cells (which act as supporting cells) of successive whorl-branchlets; post-fertilization the auxiliary cell forms a foot cell and a gonimoblast initial, often with later fusion of this initial, the foot cell, residual supporting cell and the axial cell, with a single carposporophyte on each branch, consisting of several rounded gonimolobes surrounded only by whorl-branchlets from lower cells. Spermatangia are cut off from terminal initials on the whorl-branchlets.

Tetrasporangia are borne on cells of the whorl-branchlets, sessile or pedicellate, single or grouped, cruciately or decussately divided, sometimes appearing tetrahedral.

Type species: P. plumula (Ellis) Nägeli in Nägeli & Cramer 1855, p. 56.

Athanasiadis & Kraft (1994) considered that Platythamnion J. Agardh (1892, p. 22) and Glandothamnus Wollaston (1981, p. 113) should be regarded as synonyms of Pterothamnion, within which they include 27 species, with eight species on southern Australian coasts. However, further study is needed of the position of gland cells and possible recognition of more than one genus within the complex.
KEY TO SPECIES OF PTEROTHAMNION

1. Axes moderate to densely corticate with rhizoids ........................................................... 2
2. Major pinnae pectinate with adaxial simple pinnules; minor pinnae mostly without pinnules .......................................................................................... 1. *P. nodiferum*
3. Mature major and minor pinnae of similar size and development, with pairs of pinnules from central cells of the rachides, pinnules branched .......... 2. *P. squarrulosum*

3. Whorl-branchlets in each whorl in two opposite pairs, one (minor) pair markedly smaller than the other (major) pair ........................................................... 4
4. Major pinnae separated along the axes, pectinate with adaxial pinnules with short branches; terminal rachis cells often with slender, 3-4-armed, spinous processes ........................................................................................... 3. *P. cuspidatum*

5. Whorl-branchlets 300–400 μm long, pinnae with adaxial branches when young, becoming subdichotomously branched when mature; terminal rachis cells often with 3-4-armed, spinous processes ............................................................... 5. *P. aciculare*

6. Whorl-branchlets 500–1500 μm long, slightly to distinctly flexuous; spinous processes absent.......................................................... 6

7. Thallus complanately branched, pinnae adaxially branched, pinnules mostly simple; whorl-branchlets 200–650 μm long .......................................................... 7. *P. ramulentum*

8. Thallus complanately branched only near apices, irregular below, whorl-branchlets 600–1000 μm long, axes and whorl-branchlets long and slender, simple or with simple pinnules from 1–4 mid cells of rachis .......................................................... 8. *P. flexile*


*Callithamnion similis* Harvey 1862: pl. 207 (in part); 1863, synop.; liv [NON Hooker & Harvey in Hooker 1847, p. 489].

FIGS 58A, 59, 61A–K

*Thallus* (Fig. 58A) medium to dark red-brown, erect, 5–20 cm high, complanately branched (Fig. 61A) with alternate lateral branches usually 5–10 axial cells apart, rapidly overtopping the main apices; upper axes only slightly flexuous (Fig. 61B). Lower axes densely corticatized by curved rhizoids, forming an entwined matted base to the thallus. Holdfast discoid to conical, rhizoidal, 2–10 mm across; epilithic. *Structure*. Apical cells 7–9 μm in diameter and L/D 1–1.5, enlarging within a few cells to 100–150 μm in diameter and L/D 1.2–2.0 and to 300–450 μm in diameter in the lower thallus, cortical rhizoids 25–55 μm in diameter, arising from lower cells of pinnae (Fig. 61D). Axial cells each with 4 rigid pinnae (Fig. 59A), 2 larger ones 600–900 μm in diameter and 9–18 cells long, lying in the plane of the thallus and two smaller
unbranched pinnæ between them; larger pinnæ with simple pinnules (inner 1 or 2 sometimes branched) from most cells; rachides of pinnæ usually curved backwards, basal cells 45–75 μm in diameter and L/D 1–1.3, tapering to subapical cells 16–24 μm in diameter and L/D 1–1.5 with pinnules only slightly slenderer; apical cells mucronate and apical and subapical cells often with short lateral spines (Fig. 61E); gland cells (Figs 59A, 61C) sessile, usually on third to fifth cells of the rachis and also the corticating rhizoids, hemispherical to subspherical.

40–55 μm in diameter. Lateral branches arising from the basal cells of major pinnae. Cells uninucleate; rhodoplasts elongate in smaller cells, ribbon like in larger cells.

Reproduction. Gametophytes dioecious. Procarps formed on 3–6 (~20) successive pinnae (Fig. 61F) near apices, usually on major pinnae but sometimes on each pinna of a whorl, with the basal (supporting) cell bearing a 4-celled carpogonial branch (Fig. 61G). Post-fertilization a terminal gonimolobe develops and later lateral rounded gonimolobes (Fig. 61H), 100–270 μm across, of ovoid to angular carposporangia 20–25 μm across, partly surrounded by upcurved lower pinnae; only one carposporophyte (Fig. 59B) occurs per branch. Spermatangia (Figs 59C, 61I) occur terminally on special branches, usually densely branched, on lower cells of pinnae and pinnules, ovoid and 3–6 μm in diameter.

Tetrasporangia (Figs 59D, 61J, K) occur laterally on special branches on the inner cells of pinnules, terminal and lateral, ovoid, 37–45 μm in diameter, decussately divided.

Type from Port Fairy, Vic., lectotype in Herb. Agardh, LD, 18139 (Harvey, Alg. Aust. Essicc. 543).

Distribution: Robe, S. Aust., to Sealers Cove, Victoria.


Harvey (1855a, p. 561) recorded Callithamnion simile Hooker & Harvey (a Kerguelin I. species) from Rottnest I. and King George Sound, W. Aust., and later (1862, pl. 207) in his description and illustration, recorded it from Port Fairy and Sealers Cove, Victoria. Harvey’s Fremantle, W. Aust., plant (as in MEL, 10625) is Antithamnion armatum, whereas his Port Fairy, Vic., plant (MEL, 10268) is Pterothamnion nodiferum. Though superficially similar, the number of whorl-branchlets and the position and size of gland cells clearly distinguish the two species. There appear to be no records of the latter west of Robe, S. Aust., and P. nodiferum appears to be a deep water species on eastern South Australian and western Victorian coasts.


Wrangelia squarrulosa Harvey 1855c: 236.

Platythamnion squarrulosum (Harvey) Adams 1994: 246, pl. 90, upper right.

FIGS 58B, 60A–D

Thallus (Fig. 58B) medium to dark red-brown, erect, 5–20 cm high, complanately branched with alternate lateral branches usually 2–5 axial cells apart but also arising adventitiously; upper axes straight to slightly flexuous (Fig. 60A). Axes near the base of larger plants densely corticated by entwined rhizoids arising from the basal cells of whorl-branchlets. Holdfast rhizoidal, 1–2 mm across, epilithic or usually epiphytic on larger algae. Structure. Apical cells 6–8 μm in diameter and L/D 1.5–2, enlarging in the lower axis to 250–400 μm in diameter and L/D 1.5–2; basal cortical rhizoids 15–25 μm in diameter, cells L/D 5–8. Axial cells each with 4 whorl-branchlets, of similar development but the 2 minor ones slightly shorter (150–300 μm long) than the major ones (350–550 μm long) which lie in the plane of the thallus. Whorl-branchlets (Fig. 60A, D) adaxially branched but becoming subdichotomous; basal cells (30–) 45–90 μm in diameter and L/D 1.5–2, tapering to subterminal cells 8–12 μm in diameter and L/D 1–1.5, with mucronate terminal cells; gland cells (Fig. 60A) profuse, often in series on cells of whorl-branchlets or on the corticating rhizoids, ovoid, oblique, 10–25 μm in diameter. Lateral branches arising from axial cells or by further growth of whorl-branchlets. Cells uninucleate; rhodoplasts discoid to elongate in small cells, in chains or ribbon like in larger cells.

Reproduction. Gametophytes dioecious. Carposporophyte branches are borne on the basal (supporting) cells of whorl-branchlets, singly or up to 3 on successive branchlets. Post-fertilization the auxiliary cells divide to form a foot cell and upper gonimoblast initial which cuts off 2–7 successive globular gonimolobes (Fig. 60B) 150–225 μm across of angular carposporangia 10–15 μm across; cells basal to the carposporophyte form a fusion cell, and
lower whorl-branchlets laxly surround the carpogonia. Spermatangial clusters (Fig. 60C) occur on cells of the pinnules, with ovoid spermatangia 2–2.5 μm in diameter. Tetrasporangia (Fig. 60D) occur laterally or terminally on special branches on the whorl-branchlets, ovoid, 20–30 μm in diameter, cruciately or decussately divided.

**Type** from Preservation Harbour, South I., New Zealand (Lyall, Jan. 1851); lectotype in Herb. Hooker, BM.

**Distribution:** Southern New Zealand.

In southern Australia, known from Cape Northumberland, S. Aust., and Warrnambool, Victoria.

**Selected specimens:** 1.3 km off Cape Northumberland, S. Aust., 15 m deep (Shepherd, 26.x.1977; AD, A48820). Warrnambool, Vic., drift (Kraft & Herring, 6.xi.1989; MEL, 39989, AD. A66647 and A61244).


**FIGS 60E–G, 61L–N**

**Thallus** (Fig. 60E) red, erect, 1–2 cm high, complanately branched with lateral branches 7–10 axial cells apart, upper axes flexuous (Fig. 60E), ecorticate throughout, basally attached by rhizoids from axial cells; epizoic or epiphytic. **Structure.** Apical cells 6–11 μm in diameter and L/D 1–1.6, enlarging to 60–140 μm in diameter and L/D 1–2 in lower axes. Axial cells each with 4 whorl-branchlets, 2 opposite major ones (Fig. 60E) 200–250 μm long in the plane of the thallus, and 2 smaller alternating minor ones 50–130 μm long; major pinnae with simple or branched pinnules directed upwards, tapering to an acute terminal cell, basal cells of rachides 20–35 μm in diameter and L/D 1–1.5, tapering to subterminal cells 4–8 μm in diameter and L/D 1–2, apical cells mucronate; minor pinnae simple or branched, often with 3–4 slender, spinous, branches (Fig. 61L); gland cells (Fig. 60F) lateral on mid cells of rachides or pinnules, ovoid, 12–18 μm in diameter. Lateral branches arising in place of a major pinna. Cells (smaller) uninucleate, rhodoplasts discoid in small cells, becoming ribbon like in larger cells.

**Reproduction.** Gametophytes dioecious. Procarps not observed. Carpogonia terminal in branched clusters (Figs 60F, 61M) on cells of pinnules. Tetrasporangia (Figs 60G, 61N) occur on cells of pinnules or their branches, sessile or terminal, subspherical, 20–30 μm in diameter, decussately divided.

**Type** from Port Kembla, N.S.W., 20 m deep (Watson, 16.ix.1976); holotype in AD, A47994.

**Distribution:** Port Kembla, N.S.W., and Portland and Gabo I., Victoria.

**Selected specimens:** Portland, Vic., 7–9 m deep (Kraft 8266a, 27.iv.1990; MELU and AD, A61243). Gabo I., Vic., on *Carpoglossum*, 28 m deep (Shepherd, 19.ix.1973; AD, A43550).


**Platythamnion francisciulm** Wollaston 1978: 6, figs 10–14, 18, 19.

**FIGS 61O–Q, 62A, B**

**Thallus** (Fig. 62A) erect, 1–8 cm high, complanately branched with alternate, flexuous, lateral branches (Fig. 61P) mostly every 5–6 axial cells, overtopping previous apices, ecorticate throughout. Attachment by short lateral branches affixed by rhizoids; epiphytic (e.g. on *Ballia mariana*) or epilithic. **Structure.** Apical cells 5–7 μm in diameter and L/D 1–1.4, enlarging to 120–230 μm in diameter and L/D 1.5–2.5 in mid thallus and 1–2 in lower axial cells. Axial cells each with 4 whorl-branchlets, first developed unilaterally in curved apices, when mature with 2 opposite major ones 300–700 μm long (often one larger than the other), adaxially branched (Fig. 62B) often with pairs of pinnules (Fig. 61O) (to 90–270 μm long) from the
inner rachis cells and single pinnules from the outer cells, larger pinnules sub-branched; minor pinnae 150–250 μm long, simple or with simple pinnules; basal cells of pinnae 20–50 μm in diameter and L/D 1–1.5, tapering to subapical cells 4–8 μm in diameter and L/D 2.5–3.5, apical cells mucronate; gland cells on rachis and pinnule cells, lateral, ovoid to hemispherical, 12–17 μm in diameter. Lateral branches arising from axial cells. Cells uninucleate; rhodoplasts elongate, ribbon like and longitudinal in larger cells.

Reproduction. Gametophytes unknown.

Tetrasporangia (Fig. 61Q, 62B) borne on short branches from cells of pinnules, terminal or lateral, ovoid, 20–50 μm in diameter, cruciately or decussately divided.

**Type** from St Francis I., Isles of St Francis, S. Aust., 55 m deep (Shepherd, 9.1.1971); holotype in AD, A38087.

**Distribution:** Known from the type specimen, and from Blanche Harbor, S. Aust., and Tinderbox, Tasmania.


*P. franciscianum* is distinguished by the overlapping major pinnae and the frequent pairs of adaxial pinnules on the whorl-branchlets. Athanasiadis (1996, p. 73) suggests it may be a synonym of *P. antarcticum* (Kylin) Moe & Silva (1980, p. 12, figs 1–9). The two species are clearly closely related, but *P. franciscianum* is maintained here until further studies are possible based on sexual material.


**FIGS 62C, 64A–C**

Thallus (Fig. 62C) erect, 0.5–2 cm high, more or less complanately branched usually 3–4 axial cells apart, apices only slightly flexuous, with 4 whorl-branchlets of equal size, ecoricote. Holdfast rhizoidal; epilithic. **Structure.** Apices (Fig. 64A) of short cells 6–8 μm in diameter, enlarging below to axial cells 200–400 μm in diameter and L/D (1.5–) 2–3. Whorl-branchlets formed unilaterally (Fig. 64A) at branch tips, becoming 200–400 μm long, usually densely adaxially branched with branched pinnules 90–200 μm long, often in pairs from lower and central rachis cells; terminal rachis cells occasionally modified to form acute, slender, spines (Fig. 64B) with 2–4 arms, 2–4 cells long and 6–9 μm in diameter, probably caducous; basal cells of whorl-branchlets 35–45 μm in diameter and L/D 1.5–2.5, tapering to subterminal cells 10–12 μm in diameter and L/D 1.2–1.6, terminal cells mucronate. Lateral branches replacing a whorl-branchlet or arising on the basal cell of whorl-branchlets; gland cells occur on rachis or pinnule cells, 14–18 μm across, obliquely orientated. Cells uninucleate; rhodoplasts discoid, in chains or ribbon like in larger cells.

Reproduction. Gametophytes unknown.

Tetrasporangia (Fig. 64C) occur on lower cells of pinnules of whorl-branchlets, sessile, subspherical, 20–35 μm in diameter, decussately divided.

**Type** from Taroona, Tas., 2–3 m deep on rock (Shepherd, 19.iii.1975; holotype in AD, A46154).

**Distribution:** Only known from the type collection.

*P. aciculare* was recorded with some doubt from Natal, South Africa, by Wollaston (1984, p. 286). Its presence in South Africa needs confirmation from further collections.


Pterothamnion

PTEROTHAMNIEAE

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FIGS 58D, 63A, B, 64D–J

Thallus (Fig. 58D) red-brown, erect, 4–10 cm high, complanately branched with alternate lateral branches usually every 2–3 axial cells, ecorticate throughout. Attachment by rhizoids (Fig. 64F) from basal axial cells; epiphytic. Structure. Apical cells 6–8 μm in diameter and L/D 1–1.5, with straight to slightly flexuous apices first developing whorl-branchlets unilaterally, enlarging to 150–300 μm in diameter and L/D 1.5–3 in lower axial cells. Axial cells each with 4 whorl-branchlets (Fig. 63A, B) of similar size, 450–750 μm long, each at first adaxially branched but becoming subdichotomous (Fig. 64D); basal cells of whorl-branchlets 20–40 μm in diameter and L/D 1.5–3, tapering to 7–12 μm in diameter and L/D 1.5–2.5 in subapical cells, terminal cells mucronate; gland cells (Fig. 64D, E) prominent, abundant (often on 2–4 successive cells), sessile, ovoid becoming oblique, 18–22 μm in diameter. Lateral branches arising from axial cells or on the basal or next cell of whorl-branchlets. Cells uninucleate; rhodoplasts discoid to elongate in smaller cells, becoming ribbon like and reticulate in larger cells.

Reproduction. Gametophytes dioecious. Carpogonial branches (Fig. 64G) borne on the basal (supporting) cell of whorl-branchlets, often in a short series. Post-fertilization the carpogonium and auxiliary cell connect by a tubular process and the auxiliary cell cuts off a rounded gonimoblast initial (Fig. 64H) and successive gonimolobes (Figs 63A, 64 I) from elongate basal cells, developing into rounded groups 200–400 μm across of ovate to angular, carposporangia 10–18 μm in diameter. Spermatangial clusters (Figs 63B, 64I) occur on inner and central cells of whorl-branchlets, with terminal and lateral spermatangia. Tetrasporangia unknown.

Type from Satellite I, D’Entrecasteaux Ch., Tas., 0–2 m deep, probably epiphytic (Shepherd, 17.11.1972); holotype in AD, A41641.

Distribution: Known from the type and Satellite I., Tas., 10 m deep (Shepherd, 18.11.1972; AD, A41699) and from Arch Rock, Nirepin Point, Tas., on Zonaria turneriana, 6–12 m deep (Kraft 9837 & Scott, 16.1.1994; AD, A66645).


Glandothamnus ramulentus Wollaston 1981: 114, figs 12–18, 41.


Antithamnion plumula (Ellis)Thuret sensu Lucas 1929a: 25. May 1946: 123.

FIGS 58C, 63C–E, 65

Thallus (Fig. 58C) medium red-brown, erect, 2–5 cm high, complanately branched and flexuous, with alternate lateral branches usually every 5–6 axial cells, ecorticate throughout. Holdfast small, rhizoidal; epilithic. Structure. Apical cells 6–9 μm in diameter and L/D 1–2, axial cells enlarging to 150–450 μm in diameter and L/D 1–2 (-3) in lower axes, each with (2–) 4 whorl-branchlets of similar development (transverse ones slightly shorter) initiated unilaterally (Fig. 65A) at branch apices, occasionally branch apices develop into attachment rhizoids (Fig. 65B). Whorl-branchlets (Fig. 63D, E) 250–600 (-850) μm long, adaxially branched (occasionally opposite) from lower and mid cells of the curved rachides, with simple or branched pinnules 300–600 μm long; basal cells of rachis 30–45 μm in diameter and L/D 1.5–2 (mid cells L/D 2–3), tapering to subterminal cells 8–12 μm in diameter and L/D 1–2, terminal cells mucronate; gland cells (Figs 63D, 65B) prominent on cells of the whorl-branchlets, ovoid, oblique, 12–20 μm in diameter. Lateral branches arising from axial cells or the basal cells of whorl-branchlets. Cells uninucleate; rhodoplasts elongate in small cells, becoming ribbon like in larger cells.

Reproduction. Gametophytes probably dioecious. Carpogonial branches (Fig. 65C) borne on basal (= supporting) cells of whorl-branchlets, with 1 to several at branch tips. Auxiliary cell cutting off a gonimoblast cell (Fig. 65D) which forms a terminal and later lateral gonimolobes (Figs 63C, 65E) 150–300 μm across of ovoid to angular carposporangia 8–20 μm across, without involucral whorl-branchlets from lower axial cells. Spermatangia (Fig. 63D) in branched clusters on cells of pinnules.
Tetrasporangia (Figs 62E, 64F) occur on special branches on inner to mid cells of whorl-branchlet rachides, usually on short 1–3-celled stalks, terminal or lateral, ovoid 20–35 μm in diameter, decussately divided.

Type from Georgetown, Tas. (Harvey, Alg. Aust. Exsicc. 541 I); holotype in MEL, 516229.
Distribution: Investigator Strait, S. Aust. to N.S.W. (May 1946, p. 123) and the N coast of Tasmania and D’Entrecasteaux Channel.

Selected specimens: Investigator Strait, S. Aust., 41 m deep (Watson, 14.i.1971; AD, A38159), 31 and 33 m deep (Watson, 24.i.1971; AD, A40998 and A41084). Oedipus Point, West L., S. Aust., 21–26 m deep (Shepherd, 8.x.1966; AD, A30874). Port Phillip Heads, Vic. (Wilson, 17.i.1893; MEL, 10281 and 6.n.1893; MEL, 10258). Bombay Rock, Tamar Est., Tas. (Ferron, 24 ii.1948; AD, A46358)?

P. ramulosum (as Antithamnion plumula) was recorded by May (1946, p. 123) as prevalent on the N.S.W. coast from Batemans Bay to Jervis Bay, in 20–50 fathoms. It appears to be confined to deep water. May and also Athanasiadis (1996, p. 72) have also recorded it from D’Entrecasteaux Ch., Tasmania.


FIGS 58E, 62D, 66A–D

Thallus (Figs 58E, 61D) rose-red, 4–8 cm high, slender, much branched with upper parts complanately branched with laterals 5–8 axial cells apart, flexuous near apices, ecorticate throughout, basally attached by rhizoids; on shells or hard substrates. Structure. Apical cells 6–9 μm in diameter and L/D 1–1.5 in curved apices with unilateral development (Fig. 66A) of whorl-branchlets, enlarging to 50–100 μm in diameter and L/D 3–4 in mid parts, and to 200–400 μm in diameter and L/D 1.5–2 in lower axes, with (2 or) 4 whorl-branchlets of similar size. Whorl-branchlets 0.5–1.5 mm long, axially branched above, oppositely branched below, branches long and slender, unbranched or occasionally with terminal rhizoids (Fig. 66B); basal cells 35–55 μm in diameter and L/D 2–3, tapering gradually to mid and upper cells 15–20 μm in diameter and L/D (2 or) 3–4, apical cells terminally rounded; gland cells (Fig. 66B, C) prominent, sessile on mid cells of the whorl-branchlets, ovoid and oblique, 18–25 μm in diameter. Lateral branches arise from axial cells or the basal cells of whorl-branchlets (Fig. 66C). Cells uninucleate; rhodoplasts elongate in smaller cells, ribbon like in larger cells.

Reproduction. Gametophytes unknown. Tetrasporangia (Fig. 66D) borne on inner cells of whorl-branchlets, sessile or usually stalked, subshperical, 20–30 μm in diameter, daccusately divided.

Type from 20 km WSW of Outer Harbor, S. Aust., 22–25 m deep on shells (McFarlane, 11 ix.1975); holotype in AD, A46637.

Distribution: Known from the type and Fitzgerald Bay (Point Lowly), Spencer Gulf, S. Aust., 14 m deep on artificial reef (Branden, 13 ix.1987; AD, A59341).

Genus BALLIA Harvey 1840: 191, pl. ix.

Thallus erect, several to many cm high, much branched more or less complanately, lower axes corticated with rhizoids; holdfast rhizoidal, epilithic. Axial cells relatively large, with small or large (depending on the species) apical cells, with prominent umbonate pit-connections; each axial cell with two or three whorl-branchlets, usually one major and 2 minor and often pinnate in form, sometimes the pinnules themselves pinnate; basal cells of whorl-branchlets similar in size to upper cells and bearing pinnules; gland cells absent. Lateral branches developing in place of whorl-branchlets. Cells uninucleate.

Reproduction. Gametophytes (unknown in type species) dioecious. In B. mariana and B. ballioides, carpogonial branches borne on the basal (= supporting) cells of successive major whorl-branchlets, with the auxiliary cell forming 3–4-celled branches and the second cell fusing with the fertilized carpogonium; one or more gonimolobes develop and the carposporophyte is enveloped by 2 branched involucral branches from the basal (supporting) cell and one from the whorl-branchlet. Spermatangia terminal on special branches on cells of the pinnules.

Tetrasporangia terminal on special branch systems on the basal cells of pinnules, daccusately divided.
Ballia

PTEROTHAMNIEAE

Type species: B. brunonia Harvey 1840: 191 [= B. callitricha (C. Agardh) Kützing].

A genus of 6 species, 4 from Australia and two [B. sertularioides (Suhr) Papenfuss and B. beckeri Schmitz] from South Africa. Two previous Australian species are now referred to Camontagnea, C. oxyclada and C. hirsuta (see Womersley 1994, pp. 73-76).

KEY TO SPECIES OF BALUA

1. Whorl-branchlets in opposite pairs (in 3s in the tristichous form of B. callitricha) from each axial cell and usually about equal in length ............................................................ 2

2. Pinnules branched with opposite pairs of simple branches. Short branches, arising from basal cells of pinnas, always branched ........................................ 1. B. callitricha

3. Pinnules, and short branches arising from basal cells of pinnas, always simple and unbranched .............................................................. 2. B. pennoides

3. Pinnules of pinna-like whorl-branchlets in whorls of 3 from each cell of the rachis and arranged in longitudinal rows (2 above and 1 below); pinnules usually alternately branched .............................................................. 3. B. mariana

4. Pinnules of pinna-like whorl-branchlets distichous in opposite pairs from each cell of the rachis; each pinnule bearing pairs of simple, opposite branches .............. 4. B. hallioides


FIGS 66E–I, 67

Thallus (Fig. 67A) medium to dark red-brown, erect, 10–20 (-36) cm high, alternately distichously and complanately branched (Fig. 67B) with prominent main axes and laterals, densely corticated below with entwined rhizoids. Holdfast rhizoidal, conical, 2–15 mm across with 1 to several axes; epilithic. Structure. Apical cells (Figs 66E, 67C) prominent, 130–180 µm in diameter and L/D 1–2, enlarging gradually to 200–300 µm in diameter and L/D 2–4 in lower axial cells, cells with upper concave and lower convex ends (Fig. 66H), pit-connections prominent and umbonate. Corticating rhizoids produced from basal cells of whorl-branchlets, forming a closely adherent layer, cells long and 25–40 µm in diameter, with curved, simple, branches arising from their cells. Whorl-branchlets (pinnas) in opposite pairs (Fig. 66F) (rarely in 3s) 5–10 mm long, closely branched with opposite, distichous, first simple but soon also pinnate, pinnules 200–500 µm long; basal cells of rachis of pinnas 60–90 µm in diameter and L/D 1–1.5, tapering gradually to subapical cells 12–15 µm in diameter and L/D 1.5–2, with rachides often continuing growth to form an extended filament (Fig. 66F, G) without pinnules. Whorl-branchlets and pinnules with the basal cell elongate (Fig. 67D) along the pinnule rachis cell, supra-basal cells 15–20 µm in diameter and L/D 1–1.5, tapering gradually, branches thereof 3–6 cells long, cells of similar dimensions, end cell pointed. Lateral branches occur in the position of whorl-branchlets, at irregular intervals and often in pairs. Cells uninucleate; rhodoplasts discoid in smaller cells, in chains in larger cells.
Reproduction. Gametophytes unknown.
Tetrasporangia (Fig. 66 I) borne on special branch systems on the basal cells of pinnae, terminal, ovoid to subspherical, 40–55 μm in diameter, decussately divided.

Type from the Falkland Is (Gaudichaud); holotype in Herb. Agardh, I.D, 19357.

Distribution: Cooler and subantarctic waters of the Southern Hemisphere; in southern Australia, from Nuyts Reef, S. Aust., to Green Cape, N.S.W., and around Tasmania, with one record from Geographe Bay, W. Aust. (MEL, 8515).

Fig. 67. Ballia callitricha (AD, A46374). A. Habit. B. Branch with apical cell and lateral pinnate pinnae. C. Apical part of axis with young pinnae. D. Older axial cells with bases of pinnae and filaments from transversely elongate basal cells.

Ballia callitricha is one of the commonest species of Rhodophyta on southern Australia coasts, usually in relatively deep water or under an algal canopy.


FIGS 66J, K, 68

Thallus (Fig. 68A) dark red-brown, erect, 10–25 cm high, much branched with long laterals, complanately branched above, densely corticated on central and lower axes which become denuded. Holdfast rhizoidal, conical to rounded, 0.5–2 cm across; epilithic. Structure. Apical cells prominent, 90–120 μm in diameter and L/D 1–2.5, enlarging gradually to 150–200 μm in diameter and L/D 1.5–2.5 in lower axes, cells with relatively transverse upper and lower end walls, pit-connections prominent and umbonate, each cell with two opposite whorl-branchlets. Corticating rhizoids produced from basal cells of whorl-branchlets (Fig. 66K), cells long and 20–30 μm in diameter, forming a compact, adherent, cortical layer on lower axes; basal cells and rhizoid cells also producing an outer cortex of short, curved, simple branches (Fig. 68B, D). Whorl-branchlets (Fig. 68B, C) 2–6 mm long, pinnate with closely adjacent, simple, pinnules (Fig. 66J), basal cells of rachis elongate along the axial cell, suprabasal cells 50–70 μm in diameter and L/D 1–1.5, tapering to apical cells 18–22 μm in diameter, mucronate and L/D 1.5–3; basal cells of pinnules broad based, upper cells 25–35 μm in diameter and L/D 1–1.8, tapering above to mucronate terminal cells. Lateral branches originating on axial cells at irregular intervals. Cells unicellular; rhodoplasts discoid in smaller cells, in chains in larger cells. Reproduction. Unknown.

Type from Robe, S. Aust., drift (Wollaston, 14.xi.1955); holotype and isotypes in AD, A19999.

Distribution: Robe to Port MacDonnell, S. Aust., and probably around Tasmania.


B. pennoides is closely related to B. callitricha, differing in having simple pinnules in contrast to the pinnate pinnules in the latter. It is far less common than B. callitricha but probably more widespread than records indicate.

Fig. 68. *Ballia pennoides* (A, AD, A19999; B–D, AD, A67164). A. Habit. B. Branch with pinnae and short curved filaments along axis. C. Part of a pinna with simple pinnules. D. Short curved filaments from basal cells of pinnae.
**Ballia**

**PTEROThAMNIEAE**

**FIGS 69A–C, 70A–I**

*Thallus* (Fig. 69A) medium to dark red-brown to grey-brown, erect, 5–20 cm high, more or less complanately branched above, densely rhizoidally corticated below, with each axial cell bearing a whorl of 3 whorl-branchlets (Fig. 69B, 70A), one longer major pinna opposite a pair of shorter minor pinnae. Holdfast of entwined rhizoids, 2–15 mm across with several axes; epilithic. Structure. Apical cells 25–40 μm in diameter and L/D 0.8–1.2, enlarging rapidly and to 180–250 μm in diameter and L/D (0.8–1.5)–2 in lower axial cells; corticating rhizoids (Fig. 70C) 40–50 μm in diameter, cells long. Whorl-branchlets upwardly curved, the major ones 1–1.7 mm long, more or less distichous on the axes and overlapped by minor pinnae on the lower axial cell, with each rachis cell bearing a whorl of 3 pinules in longitudinal rows, the upper pinules with alternate or opposite branches; minor pinnae (Fig. 70B) branched similarly to major pinnae, with 2 or 3 rows of branches on the pinules; basal cells of rachis 4–70 μm in diameter and L/D 0.6–1. upper cells L/D 1.5–2.5, tapering to subterminal cells of pinules 8–15 μm in diameter and L/D 1–1.2, terminal cells rounded; cells of pinule branches 10–13 μm in diameter and L/D 0.8–1.3. Lateral branches develop in place of major pinnae. Cells uninucleate; rhodoplasts discoid, in chains in larger cells.

Reproduction. Gametophytes dioecious. Carpogonial branches (Fig. 70E) borne on the basal (= supporting) cells of successive major pinnae (Fig. 69D). Post-fertilization an auxiliary cell branch is formed and fusion occurs between the carpogonium and the second cell of this branch, and the fourth cell of the branch (Fig. 70F) produces successive gonimolobes 300–500 μm across of ovoid carposporangia 10–15 μm across. The supporting cell also produces 2 involucral branches and these, together with the major pinna which produced the carpogonial branch, form an involucre around the carposporophyte (Fig. 70G). Spermatangia (Figs 69C, 70H) are cut off from initials in small groups on cells of the rachis or pinules.

Tetrasporangia (Fig. 70I) are terminal on special short branches on the basal cells of the rachides, ovoid, 25–35 μm in diameter, decussately divided.

Type from Port Fairy, Vic. (Harvey); lectotype in Herb. Harvey, TCD.

Distribution: St Francis I., S. Aust., to San Remo, Vic., and around Tasmania.


*Cali*thamnion ballioides* Sonder 1853: 674.


**FIGS 69D–F, 70J–N**

*Thallus* (Fig. 69D) dark red-brown, erect, 10–18 cm high, more or less complanately and alternately branched above, densely rhizoidally corticated below, with each axial cell bearing a whorl of 3 whorl-branchlets (Fig. 69E, 70K), 1 major opposite 2 minor. Holdfast rhizoidal, conical, 1–4 mm across. Structure. Apical cells 8–10 μm in diameter and L/D 0.8–1.2 (Fig. 70I), enlarging rapidly to 200–350 μm in diameter and L/D (1–) 1.5–2 in lower axial cells; corticating rhizoids 20–35 μm in diameter, cells long. Major whorl-branchlets (Fig. 69E, F) 1.5–3 mm long, distichously branched with 8–16 opposite pairs of pinules which are pinnate with close set opposite branches and 200–400 μm long; basal cells of whorl-branchlets 100–150 μm in diameter and L/D 0.7–1, suprabasal cells L/D 2–3, tapering to subterminal cells.
10–15 μm in diameter and L/D 0.8–1, terminal cells pointed; pinnule basal cells 20–28 μm in diameter and L/D 0.8–1.2, tapering to 8–12 μm in diameter and L/D 0.8–1, apical cells pointed. Minor whorl-branchlets 500–800 (1–1000) μm long, rachis upwardly curved, bearing pairs of pinnules which are simple or branched. Lateral branches arise in place of major whorl-branches. Cells uninucleate; rhodoplasts discoid.

Reproduction. Gametophytes dioecious. Procarp and carposporophyte development very similar to that in B. mariana. Carpogonial branches (Fig. 70L) borne on the basal cells of successive, alternating, major whorl-branchlets, with 2 involucral branches from the supporting cell and the whorl-branchlet surrounding the carposporophyte (Fig. 70M), with gonimolobes 180–250 μm across and carposporangia 16–20 μm across. Spermatangia borne terminally on special branch systems on cells of the minor whorl-branchlets and branches of the pinnules.

Tetrasporangia (Fig. 70N) occur terminally on branches from the basal cells of major whorl-branchlets, ovoid, 30–50 μm in diameter, decussately divided.

Type from Guichen Bay, S. Aust. (Mueller); holotype in MEL, 8545.

Distribution: St Francis 1., S. Aust., to Port Phillip, Vic., and E Tasmania.


Tribe HETEROTHAMNIEAE Wollaston 1968: 407
by H.B.S. Womersley & E.M. Wollaston

Thallus erect, without or with slight prostrate filaments, erect axes ecorticate, bearing whorls of 2–6 whorl-branchlets from each axial cell, often fewer per whorl on lower axial cells, whorl-branchlets usually branched; attachment by rhizoids; usually epiphytic; gland cells usually present on whorl-branchlet cells, touching the bearing cell and often the next outer cell. Cells mostly uninucleate.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes dioecious or monoecious. Procarps on normal or reduced whorl-branchlets (often 2-celled) on 1–3 (4) axial cells near branch apices, with the basal cell acting as the supporting cell and with 4-celled carpogonial branches; the auxiliary cell cuts off a gonimoblast cell which produces a terminal and then lateral, rounded, gonimolobes, the carposporophyte without a distinct involucre but often partly surrounded by branchlets or branches from lower cells. Spermatangia cut off from terminal cells of whorl-branchlets or on special clusters borne on lower cells of whorl-branchlets. Tetrasporangia sessile or on special branches on cells of the whorl-branchlets, tetrahedrally or decussately divided.

The Heterothamnieae, based on Heterothamnion J. Agardh and as recognised here, differs from the Anthothamnieae in having gland cells on normal whorl-branchlets and not on reduced 2–4-celled branches on the whorl-branchlets. Athanasiadis (1996) separated from the Heterothamnieae the genera Antithamnionella, Trithamnion and Acrothamniopsis, which he placed in the Dohrnielleae, but without giving
a key to the tribes. The Dohrniiellae originally included *Dohrnella* and *Callithamnion*, which have alternate branching with a single branchlet per axial cell and tetrasporangia borne on a single pedicel cell directly on the axes. It appears that genera with whorled branchlets and tetrasporangia on normal whorl-branchlet cells are best kept separate, and they are here retained in the Heterothamniaceae. The Perithamniaceae of Athanasiadis is also not recognised here, since the differences in spermatangial arrangement appear inadequate for tribal separation, and tetrasporangia are essentially similarly situated to other genera. *Amenothamnion* and *Leptoklonion* appear best placed in the Heterothamniaceae rather than the Ceramieae with its closely appressed cells derived from periaxial cells.

Relationships between the various genera of the Heterothamniaceae need further assessment. The tribe is one of the most complex of the Ceramieae, and comprehensive material is need for determination of most species and studies of their variation.

**KEY TO GENERA OF HETEROTHAMNIACEAE**

1. Thalli erect from clumped endophytic basal rhizoids as continuations of axes, epiphytic on *Cystophora* spp. (or *Platythallia*) .............................................................. HETEROTHAMNION

2. Axial cells with whorls of (2-) 3 (-4) whorl-branchlets (5-6 in *Antithamnionella multiramosa*), not branched from their basal cells (except *Scageliopsis* and *A. glandifera*) ............................................................................................................ 3

3. Whorl-branchlets variable in number, 2-4 (-6) per whorl ...... ANTITHAMNIONELLA

4. Whorl-branchlets mostly 3 per whorl .............................................................. 4

5. Whorl-branchlets short (less than 150 μm long), simple or usually with a few branches, whorls distinctly separated on axes ................................................................................. 6

6. Thallus branching essentially subdichotomous, originating close to the apices ............................................................................................................ AMENOTHAMNION

7. Axes with 2 opposite major whorl-branchlets and usually 2 minor whorl-branchlets on each side; rhizoids formed from successive cells of minor whorl-branchlets, with clumped digitate haptera .................................................................................................................... ACROTHAMNIOPISS 8

8. Tetrasporangia borne on special branched filaments of short cells on the lower cells of whorl-branchlets .............................................................. ELISIELLA

9. Spermatangia terminal on further divisions of terminal cells of whorl-branchlets .............................................................. PERITHAMNION
9. Spermatangia borne on branched clusters adaxial on lower cells of whorl-branchlets

Genus HETEROTHAMNION J. Agardh 1892: 25

_Thalloid with erect axes in dense tufts attached to the host by penetrating rhizoids; epiphytic on Cystophora spp. or Platythalia. Each axial cell with (2-) 4 whorl-branchlets (with basal cells slightly longer than next outer cells) which are simple or only slightly branched from basal or upper cells, decreasing in length, branching and number of whorl-branchlets towards the base of the thallus; gland cells on the third to fifth cells of rachides of whorl-branchlets, cut off from terminal or lower cells, touching the bearing cell and sometimes the next cell. Lateral branches develop from the basal cells of whorl-branchlets. Cells uninucleate.

_Reproduction._ Gametophytes dioecious. Procarps on the second or third axial cells below apices, consisting of a supporting cell with a sterile cell and a 4-celled carpogonial branch (possibly derived from a 2-celled whorl-branchlet). Carposporophytes with several rounded gonimolobes loosely surrounded by whorl-branchlets from below, each lobe with a basal elongate sterile cell. Spermatangia terminal on branched clusters of cells on the whorl-branchlets.

Tetrasporangia produced on the upper side of whorl-branchlet cells, with or without a basal pedicle, tetrahedrally divided.

_Type species:_ H. _muelleri_ (Sonder) J. Agardh 1892: 25.

A genus of 4 species, distinguished by the habit of epiphytic tufts of erect filaments, the basal axial cells tapering to endophytic rhizoids, whorls of four whorl-branchlets which are simple or only slightly branched, with gland cells on the rachides, gonimolobes with elongate sterile cells at their base, and tetrasporangia borne on several cells of the rachides.

KEY TO SPECIES OF HETEROTHAMNION

1. Thalloid tufts occurring on the margins of receptacles of Platythalia angustifolia; axial cells usually with 2 whorl-branchlets at right angles ................................. 4. _H. platythaliae_

   1. Thalloid tufts arising from within the cortex of Cystophora spp.; axial cells with usually 4 similar whorl-branchlets ................................................................. 2

   2. Epiphytic on Cystophora siliquosa; whorl-branchlets (3-) 4-6 cells long .................................................................................................. 3. _H. episiliquosum_

   2. Epiphytic on Cystophora platylobium; whorl-branchlets (5-) 8-12 cells long . 3

3. Whorl-branchlets usually unbranched, mostly 8-12 cells long; tetrasporangia pedicellate ........................................................................................................ 1. _H. muelleri_

3. Whorl-branchlets usually branched. 5-10 cells long; tetrasporangia sessile . 2. _H. sessile_


_FIGS 71, 74A–H_ .

_Thalloid_ (Fig. 71A) in small, dense, tufts 3-5 mm high, with several clumped axes from the base (Fig. 74A) of penetrating rhizoids, each axial cell bearing (2-) 4 whorl-branchlets (Figs 71B, 74C) at right angles to the axis, usually unbranched and upwardly curved. Attachment by basal rhizoids (with branching from just under the host surface) penetrating the host; epiphytic on Cystophora platylobium. _Structure._ Apical cells 6-8 μm in diameter and L/D 1-1.5, enlarging rapidly (Fig. 74B) to axial cells 70-100 μm in diameter and L/D 2-
3, tapering towards the base. Whorl-branchlets developing close to axial apices, 200–320 μm and 8–12 cells long but the lowest 100–150 μm and 4–6 cells long, usually simple (Fig. 71B, E) but occasionally with 1–3 short, simple branches 1–5 cells long on their upper side; basal cells slightly longer than next upper cell, 20–36 μm in diameter and L/D 1.5–2, tapering evenly to terminal cells 12–20 μm in diameter and L/D 1–1.5; gland cells on central to upper cells of whorl-branchlets, cut off from terminal (and subterminal?) cells, scattered, sessile,

Fig. 71. Heterothamnion muelleri (AD, A24470). A. Tufts on Cystophora platylobium. B. Branches with whorl-branchlets bearing gland cells and tetrasporangia. C. Branches with carposporophytes. D. Spermatangial clusters borne adaxially on cells of whorl-branchlets. E. Whorl-branchlets with tetrasporangia.
Heterothamnion

ovoid, 12–25 μm in diameter, touching only the bearing cell. Lateral branches replacing a whorl-branchlet. Cells uninucleate; rhodoplasts discoid, some becoming elongate.

Reproduction. Gametophytes dioecious. Usually a single procarp is borne on the second or third axial cell at branch apices, the bearing cell being smaller than the cell below; whorl-branchlets are absent from fertile axial cells. Carpogonial branches (Fig. 74D) occur on a supporting cell with a small sterile cell, probably analogous to a 2-celled whorl-branchlet. Post-fertilization, fusion between the carpogonium and auxiliary cell (Fig. 74D) occurs via a tube-like connecting cell and following division the upper central cell (Fig. 74E) develops a terminal gonimolobe and 2 rounded lateral gonimolobes (Figs 71C, 74F) 80–150 μm across of ovoid carpogonia 12–18 μm in diameter, loosely surrounded by whorl-branchlets from below. Spermatangia (Figs 71D, 74G) occur terminally on special branch clusters on several successive cells of whorl-branchlets.

Tetrasporangia (Figs 71E, 74H) occur on pedicels (becoming branched) on the upper side of several successive cells of whorl-branchlets, subspherical, 30–40 μm in diameter, tetrahedrally divided.

Type from Wilsons Promontory, Victoria (Mueller, 1853); holotype in MEL 10249.

Distribution: Nora Creina, S. Aust., to Wilsons Prom., Victoria; epiphytic on Cystophora platylobium.


Thallus (Fig. 72A) in small tufts 2–5 mm high, with several clumped axes from the base, each axial cell bearing 4 whorl-branchlets (1–3 on lower axial cells), curved slightly upwards and branched (Fig. 72A, 74R). Attachment by basal rhizoids penetrating the host, with new axes arising from upper cells of the rhizoids; epiphytic on Cystophora platylobium. Structure. Apical cells 4–6 μm in diameter and L/D 1–1.5, enlarging rapidly to axial cells 80–100 μm in diameter and L/D 1.5–2.5, tapering and with shorter cells towards the base. Whorl-branchlets (Fig. 72A) developing close to and surrounding the apices, 200–320 μm and 5–10 cells long with 3–6 alternate branches (from the basal or mid cells) each 1–5 cells long, on the central axes, 100–200 μm and 4–6 cells long, simple or once branched, on lower axes; basal cells slightly longer than next upper cell, 25–37 μm in diameter and L/D 1.5–2, tapering to terminal cells 10–12 μm in diameter and L/D 1–1.5, with rounded ends; gland cells occur on the lower to upper cells of whorl-branchlets, sessile, ovoid, 16–20 μm in diameter, touching only the bearing cell. Lateral branches arise on the basal cell of whorl-branchlets (Fig. 74S), frequent and 1–4 axial cells apart on the upper thallus. Cells uninucleate; rhodoplasts discoid to elongate.

Reproduction. Gametophytes dioecious. Carpogonial branches occur on the basal cells of short, 2-celled branches on axial cells close to apices. Post-fertilization development as in H. muelleri, involving a tubular connecting cell and the auxiliary cell dividing to a foot cell and upper cell which produces a terminal and 1–2 lateral, rounded, gonimolobes 80–120 μm across with chains of carpogonial branches 8–10 μm in diameter; whorl-branchlets and lateral branches from cells below loosely surround the carpogonium (Fig. 72B). Spermatangia are borne on branched clusters of cells (Fig. 72C), adaxially on successive lower cells of whorl-branchlets.

Tetrasporangia (Figs 72D, 74T) occur on successive lower cells of whorl-branchlets, sessile, subspherical, 25–35 μm in diameter, tetrahedrally divided.

Type from Victor Harbor, S. Aust., on Cystophora platylobium, drift (Wollaston, 2.x.1963); holotype in AD, A29304.
Fig. 72. *Heterothamnion sessile* (AD, A29304). A. Branches of a male thallus. B. Branches with young and mature carposporophytes. C. Branches with spermatangial clusters on whorl-branchlets. D. Branch with whorl-branchlets bearing tetrasporangia.
Distribution: Known only from the type and Seal Bay, Kangaroo I., S. Australia.

Selected specimen: Seal Bay, Kangaroo I., S. Aust., on Cystophora platylobium, drift (Womersley, 29.x.1966; AD, A31059).

*H. sessile*, which occurs on the same host as *H. muelleri*, differs from the latter in having more branched whorl-branchlets and sessile tetrasporangia.


**FIGS 73, 74 I–Q**

*Thallus* (Fig. 73A, 74 I) densely tufted, 2–5 mm high, with several to many axes from the base, each axial cell bearing 4 whorl-branchlets. Attachment by clumps of slender basal rhizoids (Fig. 74J), from which further axes arise, penetrating the host; epiphytic on *Cystophora siliquosa*. Structure. Apical cells 5–6 μm in diameter and L/D 1–1.5, closely surrounded by young whorl-branchlets, enlarging rapidly to axial cells 70–100 μm in diameter and L/D (1) 1.5–2, tapering and shorter towards the base. Whorl-branchlets rigid (Fig. 73B, 74K), 90–160 μm and (3–) 4–6 cells long, upwardly curved when young, horizontal or downwardly curved when older, often with 1–2 (1–5) simple branches from the basal or mid cells; basal cells slightly longer than next outer cell, 25–35 μm in diameter and L/D 1–1.5, tapering to terminal cells 18–22 μm in diameter and L/D 1–1.2; gland cells (Figs. 74L, M) lateral, usually on terminal or subterminal cells of the whorl-branchlets, touching the bearing cell and often partly the next cell, ovoid, 20–25 μm in diameter, sometimes with a smaller lateral gland cell. Lateral branches arising on the basal cells of whorl-branchlets. Cells uninucleate; rhodoplasts discoid to elongate.

Reproduction. Gametophytes dioecious. Procarps (Fig. 74N) occur in whorls of 1–4 on the third axial cell at branch apices, each carposporangial branch on a supporting cell which bears a small sterile cell. Post fertilization fusion occurs between the axial cell, foot cell and central cell and a terminal gonimolobe (Figs 73C, 74 O), followed by several lateral gonimolobes, develops, with ovoid carposporangia 18–22 μm in diameter, not protected by lower whorl-branchlets. Spermatangia (Fig. 74P) occur terminally on densely branched clusters on rachis cells of whorl-branchlets.

Tetrasporangia (Figs 73D, 74Q) are borne on cells of short branches on whorl-branchlets, ovoid to subospherical, 25–35 μm in diameter, tetrahedrally divided.

Type from Robe, S. Aust., on *Cystophora siliquosa*, drift (Womersley, 29.viii.1949); holotype and isotypes in AD, A10935.

Distribution: D’Estrees Bay, Kangaroo I., S. Aust., to Cape Shank, Victoria.


**FIG. 75**

*Thallus* (Fig. 75A) in dense spreading tufts 3–5 mm high, with numerous erect axes, each axial cell bearing (1–) 2 whorl-branchlets. Attachment by rhizoids (Fig. 75B) from erect axes, penetrating the host edges, probably at conceptacles; epiphytic on *Platythalia angustifolia*. Structure. Apical cells 12–16 μm in diameter and L/D 1–1.5, enlarging rapidly to axial cells 50–80 μm in diameter and L/D 1.5–2.7, tapering and with shorter cells near the base. Whorl-branchlets (Fig. 75C) one or two per axial cell, if two situated usually at right angles and alternating on successive cells, with one of the 2 often more branched than the other and with
2–4 branches from the basal or upper cells; whorl-branchlets 200–500 μm and 6–10 cells long, basal cells slightly longer than next outer cell, 25–40 μm in diameter and L/D 1.2–1.6 (--2), tapering to terminal cells 12–22 μm in diameter and L/D 1–1.5, ends rounded; gland cells apparently absent. Lateral branches borne on the basal cell of whorl-branchlets. Cells probably uninucleate; rhodoplasts discoid.

Fig. 73. Heterothamnion episiliquosum (AD, A10935). A. Tufts on Cystophora siliquosa. B. Branches with short whorl-branchlets. C. Branches with near-apical carposporophytes. D. Branch with whorl-branchlets bearing tetrasporangia on short branches.
Reproduction. Gametophytes probably monoecious. Carpogonial branches borne on the basal cells of reduced 2-celled whorl-branchlets which may continue growth. Carposporophytes (Fig. 75C) terminal, surrounded by 4 whorl-branchlets, with rounded gonimolobes 100–200 μm across of ovoid carposporangia 20–25 μm in diameter. Spermatangia on small branched clusters on the adaxial side of lower cells of whorl-branchlets shortly below the carposporophytes.

Tetrasporangia (Fig. 75D) borne on lower cells of whorl-branchlets, sessile, subspherical, 30–40 μm in diameter, tetrahedrally divided.

Type from Sarge Bay, Cape Leeuwin, W. Aust., on Platytalia angustifolia, drift (Woelkerling, 16.xi.1968; AD, A34205—“Marine Algae of southern Australia” No. 387). Holotype in GB, isotypes distributed from AD.

Fig. 75. Heterothamnion platythaliae (AD, A34205). A. Tufts on Platytalia angustifolia. B. Rhizoidal base of a tuft, penetrating the edge of the host. C. Branches with whorl-branchlets and young carposporophytes. D. Axes with whorl-branchlets bearing tetrasporangia.
**Antithamnionella**

*Distribution:* Only known from the type collection.

*H. platythaliae* is based on AD material and is only known from the type. It is very doubtful if this species is correctly placed in *Heterothamnion*, since it differs significantly from the other species in number (1 or 2) and arrangement of whorl-branchlets.

**Genus ANTITHAMNIONELLA** Lyle 1922: 347

*Thallus* usually with prostrate axes attached by haptera, and erect lateral axes with long (sometimes short) series of small subapical cells and whorls of 2-4 (-6) simple or branched whorl-branchlets from each axial cell, often more branched near thallus base, with the basal cells usually not branched (except in *Aa glandifera*) and smaller or similar in size to the next outer cell; gland cells usually present, sessile, usually single on second to fifth cell of whorl-branchlets, numerous in some species, touching only the bearing cell or sometimes also the next outer cell. Lateral branches produced in place of a whorl-branchlet or developing on the basal cell of a whorl-branchlet. Cells uninucleate.

*Reproduction.* Gametophytes dioecious or monoecious. Procarps 1–3 near branch apices, borne on normal or reduced whorl-branches with the basal cell acting as the supporting cell of a 4-celled carpogonial branch and usually bearing only one further cell; the fertile axial cell usually lacks other whorl-branchlets. Carposporophyte usually terminal, with axial growth continued by laterals from below, and surrounded by lateral branches or whorl-branchlets from below. Spermatangia cut off from initials formed laterally on short axes borne adaxially on rachis cells of whorl-branchlets.

Tetrasporangia sessile on lower cells of whorl-branchlets, subspherical to ovoid, tetrahedrally or subdecussately divided.

*Type species:* *A. sarniensis* Lyle 1922: 348, figs 1–4.

Wollaston (1968, p. 339) recognised *Antithamnionella* as a distinct genus on vegetative features (such as inconsistency in number and branching of whorl-branchlets, and position of gland-cells on normal whorl-branchlets) as well as tetrahedrally divided tetrasporangia. Athanasiadis (1996, p. 101) also recognised it as a distinct genus and suggests it contains some 19 species. However, he considered the genus is not monophyletic and found no characters that could be considered distinctive for the genus. Clearly *Antithamnionella* is one of the least well defined genera of the tribe and much further study is needed.

**KEY TO SPECIES OF ANTITHAMNIONELLA**

1. Whorl-branchlets in close whorls of 5–6 .......................................................... 4. *Aa multiramosa*
2. Whorl-branchlets in separated whorls of 2-4 (-5) ............................................ 2

2. Whorl-branchlets in whorls of (2-) 3–4, with their basal cells distinctly shorter than the next cell(s). Carposporophyte producing up to 7 ovoid to elongate groups of carposporangia ......................................................... 1. *Aa ternifolia*
3. Whorl-branchlets in whorls of 1–2 (-3), basal cells as long as the next cell. Carposporophyte seldom producing more than 3 rounded groups of carposporangia .......................................................... 3

3. All whorl-branchlets usually unbranched; gland cells sessile on upper side of 2nd or 3rd cell of whorl-branchlet, more abundant in upper parts of plant...... 2. *Aa spirographidis*
4. Whorl-branchlets becoming branched with (2-) 3–5 alternate laterals; gland cells numerous (up to 20) on whorl-branchlets, most abundant in lower parts of plants .......................................................... 3. *Aa glandifera*

Callithamnion ternifolium Hooker & Harvey 1845: 272.


**FIGS 76, 77A, B, 78A–I**

*Thallus* (Fig. 76A, B) medium to dark red-brown, tufted (often dense), with prostrate axes bearing erect axes (Fig. 78A) 4–40 mm high, each axial cell with (2-) 3–4 whorl-branchlets (Figs 76C, E, 78B). Lateral branches mostly every 3–4 axial cells, replacing whorl-branchlets or arising from lower cells of whorl-branchlets (Fig. 78D). Attachment of prostrate axes by single (-3) rhizoids from basal cells of whorl-branchlets, each with terminal digitate haptera (Fig. 78D); epiphytic on various algae, or on solid substrates. **Structure.** Apical cells 5–6 μm in diameter and L/D 1.5–2, initiating whorl-branchlets 3–7 cells from branch apices; axial cells increasing gradually to 30–75 μm in diameter and L/D 3–5 (–8). Whorl-branchlets overlapping near apices (Fig. 76C, E), separated below, 200–300 μm and 10–15 cells long, simple or with 1 to a few simple branches (Fig. 78C) which are often unilaterally arranged; cells of whorl-branchlets basally unbranched. 12–18 μm in diameter and L/D 1.4–1.8, decreasing gradually to tapering terminal cells 6–9 μm in diameter and L/D 1.5–2.5, with rounded ends; basal cell usually distinctly shorter than next cells (Fig. 77B); gland cells (Fig. 78B) on lower to mid (commonly third or fourth) cells of whorl-branchlets, cut off from subterminal cells, touching only the bearing cell, ovoid, 8–11 μm in diameter. Cells uninucleate; rhodoplasts elongate in smaller cells, becoming ribbon like in axial cells.

**Reproduction.** Gametophytes usually monoecious. Carpogonial branches (Fig. 78E) borne on the basal cells of short, 2-celled whorl-branchlets several cells below apices, with usually only one at each branch apex: no other whorl-branchlets occur on the fertile axial cell, and the terminal cell of the fertile branchlet is lost during carposporophyte development. Post-fertilization, fusion occurs between the carpogonium and auxiliary cell via a connecting cell, and a terminal gonimolobe develops from the central cell following division of the auxiliary cell, with the axial cell, residual supporting cell and foot cell fusing (Fig. 78F). A terminal and up to 6 lateral, ovoid to elongate, gonimolobes 90–120 μm across develop (Figs 76D, E, 78G), with ovoid carposporangia 10–20 μm in diameter; no involucral branchlets develop (Fig. 76D). Spermatangia (Figs 77A, 78H) commonly occur on carposporophytic plants, with short adaxial clusters on cells of the rachides, the spermatangia cut off terminally.

Tetrasporangia (Figs 76C, 77B, 78 I) occur on the upper side of basal and often the second cells of several successive whorl-branchlets on upper branches, sessile, ovoid, 25–35 μm in diameter, subdecussately divided.

**Type** from St Martin's Cove, Cape Horn, Chile.

**Distribution:** South Africa, South America, New Zealand, Macquarie I, Europe.

In southern Australia, from Shark Bay, W. Aust. (Kendrick et al. 1990, p. 51) and from Port Stanvac, S. Aust., to Westernport Bay, Vic., and N and E Tasmania. N.S.W (Millar & Kraft 1993, p. 36).


Athanasiadis (1996, p. 128) has referred *A. tasmanica* to the older and widely distributed species *A. ternifolia*. It is probably widespread in calm situations on SE Australian coasts.


**FIGS 77C–E, 78J–S**

*Thallus* (Fig. 77C) medium red-brown, with prostrate axes bearing free, flexuous, branches 4–10 mm long from usually every fourth cell, each axial cell with (1-) 2 (-3) mostly simple
whorl-branchlets (Fig. 78J, K), distichously to irregularly arranged. Attachment by rhizoids (Fig. 78M, O) from the basal or occasionally second cell of whorl-branchlets, with branched hapteroid ends; epiphytic. *Structure.* Apical cells 6–8 μm in diameter and L/D 1.5–2, with straight rows of isodiametric cells near apices (Fig. 78L), enlarging gradually to axial cells 40–100 μm in diameter and L/D (1-) 3–8. Whorls separated (Fig. 78K), branchlets 130–380

μm and 10–15 cells long, basal cells 8–14 μm in diameter and L/D 1.5–2, tapering to terminal cells 5–8 μm in diameter and L/D 1.5–2.5, with rounded ends and tapering only slightly; basal cells usually as long as next cells; gland cells (Fig. 78N) occur usually on second or third cells of whorl-branchlets of the upper thallus, touching only the bearing cell, 10–14 μm in diameter, ovoid. Cells uninucleate; rhodoplasts discoid in small cells, becoming ribbon like in larger axial cells.

**Reproduction.** Gametophytes probably monoecious. Carpogonial branches (Fig. 78P) occur on the basal cells of 2-celled whorl-branchlets, usually singly near branch apices, with thallus growth continuing from a lateral below the fertile apex. Following fusion between the fertilized carpogonium and auxiliary cell via a connecting cell, a terminal gonimolobe (Fig. 78Q) develops from the central cell and later 2–3 lateral gonimolobes, as rounded groups 70–140 μm across of carposporangia 10–15 μm in diameter; no involucral branches occur (Fig. 77D). Spermatangial clusters (Fig. 78R) occur adaxially on cells of the whorl-branchlets, with 2–4 lateral spermatangia from initials. Tetrasporangia (Figs 77E, 78S) occur singly on the basal (and occasionally second) cells of whorl-branchlets, sessile, ovoid, 25–35 μm in diameter, subdecussately divided.

**Type** from Trieste, Italy (Schiffner, 12. viii. 1914); holotype in BERL, 16841; isotype in BM.

**Distribution:** Widespread on European coasts, the N Pacific, and Australia. In southern Australia known from Port Adelaide and Kingscote, Kangaroo I., S. Aust., and Point Wilson, Port Phillip, Victoria. Sydney, N.S.W.


**Antithamnionella spirographidis** is found in harbours in southern Australia and is probably an adventive species.


**FIGS 79, 81A-J**

Thallus (Figs 79A, 81A) medium red-brown, largely erect, 1–2.5 cm high, with lateral branches from every third axial cell above but often up to 6 cells apart below, arising on basal cells of whorl-branchlets (Fig. 81D). Axial cells with 1–3 (usually 2) whorl-branchlets (Figs 79E, 81B). Attachment by several-celled rhizoids from the basal cells of whorl-branchlets in the lower thallus, with terminal branched haptera (Fig. 81E); probably epiphytic. Structure. Apical cells 5–6 μm in diameter and L/D 2–4 in the mid thallus, then to 70–180 μm in diameter and L/D 1–3 in the lower thallus, with the lower end broader than the upper. Whorl-branchlets usually separated, unbranched near the apices but with (2–) 3–5 alternate branches below (Figs 79B, C, 81B), 200–350 μm and 10–14 cells long; basal rachis cells branched or not, as long as next cells, 12–20 μm in diameter and L/D 1.5–2 (2.5), tapering gradually to terminal cells 5–7 μm in diameter and L/D 2–4, with rounded ends; gland cells prolific on lower whorl-branchlets (Figs 79B, C, 81F), sparser above, on cells of the rachis or its branches, cut off from subterminal cells and touching only the bearing cell, ovoid, 6–8 μm in diameter. Cells uninucleate; rhodoplasts discoid to elongate in small cells, ribbon like in larger axial cells.

**Reproduction.** Gametophytes probably dioecious. Carpogonial branches (Fig. 81G, H) occur on 2-celled whorl-branchlets close to branch apices, singly or on 2 successive axial cells, with the terminal cell appearing as a small sterile cell on the supporting cell. Post-fertilization a terminal gonimolobe develops (Fig. 81I) followed by 2 (or more) lateral, rounded to elongate, gonimolobes (Figs 79D, 81J); no involucral branches occur. Spermatangia on small adaxial clusters on lower whorl-branchlet cells (Fig. 79E).
Fig. 79. Antithamniionella glandifera (A, D, E, AD, A59025; B, C, AD, A26660). A. Thallus with branched whorl-branchlets and gland cells. B, C. Axial cells with branched whorl-branchlets and numerous gland cells. D. Branch with a carposporophyte. E. Branch with minute spermatangial clusters (arrows).
Tetrasporangia unknown.

_Type_ from 5–8 km off Outer Harbor, S. Aust., 16 m deep (Loan, 9.viii.1963); holotype in AD, A26660.

_Distribution_: Known from the type, Port Stanvac, S. Aust., and Beauty Point, Tamar Estuary, Tasmania.

_Selected specimens_: Port Stanvac, S. Aust., on jetty pylons, 3–12 m deep (Clarke, 23.ii.1977; AD, A59025). Beauty Point, River Tamar, Tas., upper sublittoral on an old barge (Wollaston & Mitchell, 5.iii.1964; AD, A28019).

4. _Antithamnionella multiramosa_ Athanasiadis 1996: 110, fig. 48.

**FIG. 80**

_Thallus_ (Fig. 80A) 1–2 (-3) mm high, forming small tufts on the hosts, with prostrate filaments bearing erect, simple or slightly branched, ecorticate axes, each axial cell bearing (5-) 6 (Fig. 80G) equally developed whorl-branchlets. Attachment by haptera on whorl-branchlets on prostrate filaments; epiphytic on the surface of _Corallina officinalis_ and _Halipiton roseum_. _Structure_. Apical cells 4–5 μm in diameter and L/D 0.8–1.2, with 3–6 small cells in a straight apex (Fig. 80B), then enlarging to mature axial cells 30–65 μm in diameter and L/D 1.5–2 (-2.5), with very thick walls. Prostrate axial cells (Fig. 80A, C) 40–55 μm in diameter and L/D 1.5–2, with the lower whorl-branchlets developing digitate haptera. Whorl-branchlets (Fig. 80A) in regular, evenly spaced whorls of 5 or 6, dense and overlapping near branch apices and separated below, complanate and usually slightly upwardly curved and facing the axis, 80–150 μm and (2-) 4–7 cells long (shorter on lower axes), basal cell unbranched (Fig. 80G), subdichotomous to alternately branched 1–3 times above with simple terminal rows of 2–4 cells; basal cells similar in size to mid cells, 20–30 μm in diameter and L/D 1–1.2, tapering over outer cells to apical cells 8–12 μm in diameter and L/D 1–1.5, with rounded ends; gland cells (Fig. 80G, E) frequent to profuse, 1–4 per whorl-branchlet on mid to upper branchlet cells, cut off from terminal or subterminal cells, touching the bearing cell and the end usually abutting the next cell above, ovoid, 15–20 μm in diameter. Lateral branches arising from the basal cell of a whorl-branchlet. Cells uninucleate; rhodoplasts discoid in small cells, becoming ribbon like in axial cells.

_Reproduction_. Gametophytes dioecious. Carpogonial branches borne on the basal cell of whorl-branchlets. Carposporophytes (Fig. 80D) terminal on lateral axes, with 1 (-2) rounded gonimolobes 180–240 μm across of ovoid carposporangia 15–20 μm across; lower whorl-branchlets or lateral branches from them extend further to form an involucre around the carposporophyte. Spermatangial clusters (Fig. 80E) branched, occurring on the upper side of basal and mid cells of whorl-branchlets. Tetrasporangia (Fig. 80F, G) occur on basal and mid cells of whorl branchlets, situated adaxially above the branchlet, sessile, subspherical, 30–40 μm in diameter, decussately or tetrahedrally divided.

_Type_ from Restless Point, West I., S. Aust., on _Corallina officinalis_, low eulittoral (Shepherd, 13.iii.1970); type collection in AD, A56301; holotype in GB.

_Distribution_: Greenly Beach, Eyre Pen., to West I., and Cape Willoughby, Kangaroo I., S. Australia.


_Antithamnionella multiramosa_ was placed in _Antithamnionella_ by Athanasiadis but his reasons were not given; presumably they include the unbranched basal cells
Scageliopsis HETEROTHAMNIEAE

of whorl-branchlets, similar in size to the next cells, gland cells on normal whorl-branchlets, spermatangia on much branched clusters on whorl-branchlet cells, and subspherical tetrasporangia sessile on lower and mid cells of the whorl-branchlets. It is doubtful if *A. multiramosa*, with its regular whorls of 5 or 6 whorl-branchlets, much branched spermatangial clusters, and short series of subapical cells, is correctly placed here.

*A. multiramosa* is superficially similar to *Perithamnion muelleri* but differs in having distinct adaxial spermatangial clusters whereas the latter has spermatangia developed by continued divisions of terminal whorl-branchlet cells; the basal cells of whorl-branchlets are also branched in *P. muelleri* but unbranched in *A. multiramosa*.


*Thallus* erect from a prostrate base, 2–10 mm high, axes irregularly radially branched, axial cells bearing 3 (rarely 2 or 4) similar whorl-branchlets more or less horizontally and subdichotomously branched, 4–7 cells long, terminal cells with rounded ends; gland cells sessile, ovoid, touching only the bearing cell. Lateral branches arising from the basal cell of whorl-branchlets. Cells uninucleate.

Reproduction. Gametophytes dioecious. Carpogonial branches borne on the basal (=supporting) cell of whorl-branchlets, usually only one per branch apex which continues development after initiation of a procarp. Carposporophytes with rounded gonimolobes, protected by enlarged whorl-branchlets and branches from lower axial cells. Spermatangial clusters on cells of whorl-branchlets, branched, with terminal spermatangia.

Tetrasporangia sessile on cells of whorl-branchlets, decussately or cruciately divided.

**Type species.** *S. patens* Wollaston 1981: 110, figs 1–11.

Scageliopsis is characterised by whorls of 3 whorl-branchlets which become subdichotomously branched, by fusion of cells below the carposporophyte, by continued development of both axes and whorl-branchlets after procarp formation, and by ovoid gland cells touching only the bearing cell.

*S. patens* is the only species in the genus.


**FIGS 81K–P, 82**

*Thallus* (Fig. 82A, D) erect, 2–10 mm high, axes sparsely laterally and radially branched, each axial cell with 3 similar-sized whorl-branchlets. Lower prostrate axial cells attached by rhizoids; usually epiphytic or epizoic. Structure. Apical cells 5–8 μm in diameter and L/D 1.2–2, with a chain of 4–12 small cells (Fig. 81K), then enlarging to 12–15 μm in diameter and to 30–45 (–55) μm in diameter and L/D (1.5–) 2–5 (–8) in mid and lower axial cells, with thick walls. Each axial cell with a whorl (Fig. 82B, D, E) of 3 (rarely 2 or 4) similar whorl-branchlets, 90–140 μm and 4–7 cells long, perpendicular to slightly upwardly curved to the axes, branched 1–3 times from the basal cell and soon appearing subdichotomously more or less in a horizontal plane to the axes; basal cells of whorl-branchlets usually slightly larger than next outer cell, 8–12 μm in diameter and L/D 2–3, tapering evenly to terminal cells 5–7 μm in diameter and L/D 2–3, with rounded ends and often bearing a long hair; gland cells (Fig. 81K, P) cut off from terminal or lower cells of whorl-branchlets, usually touching only the bearing cell, ovoid, 8–12 μm in diameter. Lateral branches arise from the basal cells of whorl-branchlets (Fig. 81K). Cells uninucleate; rhodoplasts discoid to elongate in small cells, ribbon like in larger cells.

Reproduction. Gametophytes dioecious. Carpogonial branches (Fig. 81L) borne, usually only one per branch, on the basal (=supporting) cell of whorl-branchlets; post fertilization a connecting cell transfers the diploid nucleus to the auxiliary cell, which cuts off an upper gonimoblast initial (Fig. 81M) and later successive gonimolobes 100–250 μm across of ovoid...
carposporangia 15–25 μm across; fusion of the lower cells occurs (Fig. 81M, N). The axis continues growth (Fig. 82B) and the carposporophyte is partly surrounded by enlarged whorl-branchlets or lateral branches from below. Spermatangial clusters (Fig. 81O, 82C) occur on the upper side of whorl-branchlet cells, as branched systems with terminal spermatangia.

Fig. 82. Scageliopsis parens (A, C–E, AD, A50237; B, AD, A49122). A. Branches with carposporophytes. B. Branch with continuing axis and lateral carposporophyte. C. Axis with whorl-branchlets bearing spermatangial clusters. D. Branches with tetrasporangia. E. Axes with whorl-branchlets bearing tetrasporangia.
Tetrasporangia (Figs 81P, 82D, E) are borne on inner and central cells of whorl-branchlets, situated adaxially, sessile, ovoid, 20–35 μm in diameter, decussately or cruciately divided.

**Type** from Port Stanvac, S. Aust., on bryozoans on jetty pylons, 3–12 m deep (Clarke & Engler, 14.iv.1979); holotype in AD, A50327.

**Distribution:** Only known from Semaphore to Port Noarlunga, S. Aust., but probably more widely distributed.

**Selected specimens:** Semaphore, S. Aust. (coll. unknown, 7.i.1977; AD, A50320), Port Stanvac, S. Aust., on jetty pylons, 3 m deep (R. Lewis, 24.ii.1972; AD, A41320), and 3–12 m deep (Clarke, 23.ii.1977; AD, A47974). Port Noarlunga, S. Aust., 2–5 m deep (Hagstrom & Owen, 19.vi.1970; AD, A35972) and 6 m deep (Ricci, 18.iv.1993; AD, A61937).

**Genus TRITHAMNION** Wollaston 1968: 388

**Thallus** with prostrate and erect axes or entirely erect axes, attached by branched rhizoids; usually epiphytic. Axial cells each bearing 3 (occasionally 2 or 4) whorl-branchlets with one longer branchlet between two shorter branchlets, branchlet rachis cells with pairs of short branches, often with a pair of small terminal cells; basal cell of whorl-branchlet usually unbranched; gland cells sessile on subterminal to lower cells of the branches of the whorl-branchlets, cut off from subterminal cells. Lateral branches replacing, or extending from, the longer whorl-branchlets. Cells usually uninucleate.

**Reproduction.** Carpogonial branches on the basal cell of short, 2-celled branchlets on axial cells near branch apices, with the terminal cell appearing as a sterile cell on the supporting cell; carpogonophores with 4–6 rounded gonimolobes, surrounded by curved whorl-branchlets or lateral branches from below. Spermatangia unknown.

Tetrasporangia borne on cells of whorl-branchlets, sessile, ovoid to subspherical, tetrahedrally to sub-decussately divided.

**Type species:** *T. gracilissimum* Wollaston 1968: 389, fig. 38 I–P.

A genus of 4 species from southern Australia, and one [*T. tenellum* (Harvey) Wollaston 1968, p. 389] known only from Rottnest I., W. Australia; the latter, however, may be identical with *T. aculeatum*.

**KEY TO SPECIES OF TRITHAMNION**

1. Thallus erect, clumped, attached by a rhizoidal holdfast from lower cells of erect axes; epiphytic on *Caulerpa* spp. and firm-surfaced algae .............................................. 4. *T. vulgare*
   2. *T. gracilissimum*
   1. Thallus with prostrate axes bearing erect branches; epiphytic on various algae, or other substrates .......................................................... 2
   2. Long whorl-branchlets 100–250 μm long, branchlets separate; axial cells 25–55 μm in diameter and L/D 4–6 ...................................... 1. *T. gracilissimum*
   2. Long whorl-branchlets usually above 250 μm long, branchlets overlapping; axial cells 70–160 μm in diameter and L/D 1.5–4 ................................. 3
   3. All whorl-branchlets overlapping, short whorl-branchlets 130–180 μm long; gland cells touching only the bearing cell .................................. 3. *T. eubryantii*

**Trithamnion**

**HETEROTHAMNIEAE**

**FIGS 83A, B, 84A–G**

**Thallus** (Figs 83A, 84A) with prostrate axes and erect branches to 5 mm high, each axial cell bearing (2-)3 (–4) whorl-branchlets with a longer central branchlet or indeterminate branch between a pair of short branchlets (Fig. 84A, B). Attachment by rhizoids (Fig. 84D) of elongate cells with terminal branched haptera, arising from the basal cells of whorl-branchlets on prostrate axes; epiphytic. **Structure.** Apical cells 5–7 μm in diameter and LID 1–1.2, enlarging after 6–8 cells to axial cells 25–55 μm in diameter and LID 4–6, with the whorl-branchlets separated. Long whorl-branchlets (Figs 83A, 84A, B) 100–250 μm and 6–10 cells long but extending to indefinite branches, with each rachis cell bearing 2–3 short branches (1–)2–3 (–5) cells long, sometimes further branched and often with 2 (–3) small stalk cells with or without hairs; rachis cells 10–15 μm in diameter and LID 4–6, basal cell shorter and usually unbranched, tapering to terminal cells 4–6 μm long and LID 1.5–2; gland cells (Fig. 84B) occur on branches of long whorl-branchlets or on short whorl-branchlets, usually on and touching only the subterminal cell below the terminal pair of small cells, ovoid, 8–12 μm in diameter. Lateral branches extending from long whorl-branchlets or arising on the basal cell of whorl-branchlets (Fig. 83D). Cells uninucleate; rhodoplasts discoid, elongate or in longitudinal chains in larger cells. **Reproduction.** Carpogonial branches (Fig. 84E) occur on the basal cell of a short-branchlet, the terminal cell forming a sterile cell on the supporting cell; apical axial growth ceases on development of the procarp. The auxiliary cell is cut off from the supporting cell and after fusion with the carpogonium forms a lower foot cell and upper central cell, which develops a terminal gonimolobe and 4–6 lateral rounded gonimo)obes (Figs 83B, 84F) 50–80 μm across of ovoid carposporangia 18–22 μm in diameter, surrounded by 2–4 long whorl-branchlets (Figs 83A, 84A) from the axial cell below. Spermatangia unknown. Tetrasporangia (Fig. 84G) are borne on the basal cells of short whorl-branchlets, sessile, ovoid, 35–40 μm in diameter, tetrahedrally to subdecussately divided.

**Type** from Saunders Beach, Kangaroo I., S. Aust., on Chondria, drift (Womersley, 25.viii.1963); holotype in AD, A29511.

**Distribution:** Houtman Abrolhos, W. Aust., to Rocky Cape, Tas. (at scattered localities).


2. **Trithamnion aculeatum** (Harvey) Womersley & Wollaston, **comb. nov.**


**FIGS 83C, D, 84H–N**

**Thallus** (Figs 83C, 84H) with prostrate and erect axes 1–2.5 cm high, each axial cell bearing (2-)3 (–5) whorl-branchlets, often unilaterally placed (Fig. 84I) with 1 long branchlet and 2 or 3 equal short branchlets, occasionally with other combinations; the lowest whorl on a lateral branch often consists of 4 short branchlets only. Attachment by rhizoids of elongate cells (Fig. 84K) borne on basal cells of whorl-branchlets on prostrate axes, with digitate haptera; epiphytic. **Structure.** Apical cells 5–7 μm in diameter and LID 1–1.2, with chains of 6–12 small cells, enlarging to axial cells 70–160 μm in diameter and LID 1.5–2.5 (–3), with the long whorl-branchlets upwardly curved and slightly overlapping (Fig. 84H). Long whorl-branchlets (Fig. 84I) 400–700 μm and 8–11 cells long, with opposite or slightly more abaxial branches, sometimes further branched; short whorl-branchlets (Fig. 84J) 40–100 μm and 3–6 cells long, branched one to several times; basal rachis cells usually unbranched (unless the long branchlet is developing further), 10–16 μm in diameter and LID (1.5–) 2–3, tapering to single or paired terminal cells 4–8 μm in diameter and LID 1–2,
often with a hair; gland cells (Fig. 84 I) occur on the basal or second cells of short whorl-branchlets or on laterals of long whorl-branchlets, cut off when the bearing cell is subterminal and touching both it and abutting the next outer cell of a dichotomy with 1–3 cells above the gland cells. Ovoid, 10–15 μm in diameter. Lateral branches arising on basal cells of whorl-branchlets. Cells uninucleate; rhodoplasts discoid to elongate in smaller cells, becoming ribbon like in larger cells.

Reproduction. Carpogonial branches (Fig. 84L) occur on the basal cell of 2-celled whorl-branchlets near branch apices, with the terminal cell remaining as a small sterile cell on the supporting cell. Post-fertilization (Fig. 84M) 4–6 rounded gonimolobes (Fig. 83D) 90–180 μm across develop, with ovoid carposporangia 16–22 μm in diameter; 2–4 long whorl-branchlets from the lower axial cell envelop the carposporophyte. Spermatangia unknown [possible dense, much branched tufts on a mixed phase plant (with tetrasporangia)] – AD, A44324.

Tetrasporangia (Fig. 84N) occur on lower cells of rachides or on branches of both long and short whorl-branchlets, ovoid, sessile, 20–30 μm in diameter, tetrahedrally to subdecussately divided.


It is possible that Callithamnion spinescens Kützing (1843, p. 373), Lucas (1909, p. 49) and Sonder (1881, p. 10) from W. Aust. (Preiss) is an older name for this species, but the type (in L, 938, 303...221) is a poor specimen and for the present the name is regarded as a "nomen dubium". Also C. tenellum from Rottnest I., W. Aust., may not be distinct from T. aculeatum.


FIG. 85

Thallus (Fig. 85A) red-brown, 5–12 mm high, with slight prostrate parts bearing erect branches, each axial cell with (2–) 3 whorl-branchlets (Fig. 85B), one distinctly larger than the other 2 and often developing into a longer lateral branch. Attachment by slender rhizoids (Fig. 85C) produced from the basal cells of whorl-branchlets; on solid substrates (jetty piles and rope). Structure. Apices relatively straight, overtopped by whorl-branchlets from below, with several small cells then enlarging gradually. Apical cells 5–8 μm in diameter and L/D 1.5–2, enlarging to mid axial cells 20–30 μm in diameter and L/D 3–4 (–5), then to 70–120 μm in diameter and L/D 2–4 in the lower erect thallus and prostrate axes. Whorl-branchlets slender, with usually 2 shorter ones 130–180 μm long, simple or usually with 1 or 2 short branches, and 1 longer branchlet 200–450 μm long with several branches; the latter often extends further as a lateral branch; basal cells unbranched, 11–18 μm in diameter and L/D 1.5–2, of similar size to next cells, tapering gradually to single or twinned apical cells 6–10 μm in diameter and L/D 1.2–1.8, with rounded ends; gland cells (Fig. 85D) usually touching only the bearing cell and shorter than it, cut off from terminal and subterminal whorl-branchlet cells, ovoid when mature, 8–16 μm in diameter. Lateral branches arising on the basal cells of whorl-branchlets (Fig. 85D). Cells usually binucleate (1–3); rhodoplasts discoid in small cells, becoming ribbon like in axial cells.

Reproduction. Carpogonial branches borne on 2-celled whorl-branchlets close to axial apices; post-fertilization, partial fusions of procarpic cells occur and a terminal then lateral rounded gonimolobes 150–200 μm across develop with ovoid carposporangia 10–15 μm in diameter. The carposporophyte (Fig. 85E) is terminal on lateral branches, surrounded by usually 4 lateral branches from the lower 1 (or 2) cells. Spermatangia unknown.

Tetrasporangia (Fig. 85A, B) occur adaxially on the basal and next cell of whorl-branchlets, sessile, ovoid, 30–35 μm in diameter, tetrahedrally, subdecussately or cruciately divided.
Fig. 85. *Trithamnion eubryyanii* (AD, A35977). A. Habit of thallus with tetrasporangia. B. Axes with whorl-branchlets bearing tetrasporangia. C. Base of axis with attachment rhizoids from basal cells of whorl-branchlets. D. Lateral branch borne on basal cell of a whorl-branchlet. E. Branch with a terminal carposporophyte.
**HETEROTHAMNIEAE**

Amoenothamnion

*Type* from Port Noarlunga, S. Aust., on rock near jetty, 5 m deep (*Hergstrom & Owen*, 19.vii.1970); collection in AD, A35977, holotype in GB.


*T. eubryanii* appears to occur in relatively sheltered waters, but further study is needed of a larger range of specimens.


**FIGS 83E–G, 84 O–S**

*Thallus* (Figs 83E, 84 O) erect, 2–4 (-7) mm high, with clumps of erect axes, each axial cell with 3 upwardly curved whorl-branchlets (Fig. 83F) unilaterally placed (within 180°) and rotated on successive axial cells, the central whorl-branchlet slightly longer than the other two. Attachment by branched, clumped, rhizoids forming a distinct holdfast (Fig. 83G) 50–200 μm across, arising from the basal cells of erect axes (Fig. 84R); epiphytic on *Caulerpa* spp. and other firm-surfaced algae. *Structure.* Apical cells 4–6 μm in diameter and L/D 1–2, within clusters of lateral whorl-branchlets of small branched cells, then enlarging rapidly to axial cells 30–100 μm in diameter and L/D 1–2.5, with thick walls and the contents slightly greater in diameter at their upper end. Longer whorl-branchlets 200–320 μm and 6–8 cells long, longest centrally on the axes, each rachis cell with usually more or less opposite branches 1–3 cells long (Fig. 84P), usually terminating in a pair of small terminal cells often with hairs (Fig. 84Q); shorter whorl-branchlets 100–250 μm long, with fewer pairs of branches; rachis cells basally unbranched and usually shorter than outer cells, 30–40 μm in diameter and L/D 1.5–2, tapering to terminal and lateral cells 7–10 μm in diameter and L/D 1–1.5; gland cells usually frequent and prominent (Fig. 84Q), borne on basal to mid cells of whorl-branchlets, touching the bearing cell and abutting one of the pair of terminal cells, ovoid, 15–22 μm in diameter. Lateral branches replacing longer whorl-branchlets. Cells uninucleate; rhodoplasts discoid in smaller cells, elongate to ribbon like in larger cells.

*Reproduction.* Gametophytes unknown. Tetrarosporangia borne (Fig. 84S) on special short branches on the basal cells of whorl-branchlets, sessile, subspherical to slightly ovoid, 15–25 μm in diameter, tetrahedrally divided.

*Type* from D’Estrees Bay, Kangaroo I., S. Aust., on *Caulerpa papillosa* (*Womersley*, 24.viii.1950); holotype and isotypes in AD, A15421.

**Distribution:** Pearson I., S. Aust., to Lawrence Rock, Vic., and E Tasmania.


*T. vulgare* is characterised by the habit and branching, cell sizes, and especially by the holdfast of clumped, elongate, rhizoids from the basal cells of erect axes.

**Genus AMOENOTHAMNION** Wollaston 1968: 376

*Thallus* erect, with subdichotomous axes bearing separated whorls of 3–5 relatively short whorl-branchlets from the upper ends of axial cells; whorl-branchlets usually branched from...
their basal cells, often with terminal hairs; gland cells absent or lateral on outer cells. Attachment by rhizoids from basal cells, but without penetration of host; epiphytic (or free floating). Lateral branches arising close to apices, from subapical cells and axes becoming subdichotomous. Cells uninucleate.

**Reproduction.** Gametophytes dioecious. Procarps borne on the basal cells of 1–3 reduced whorl-branchlets near branch apices, with the basal cell acting as the supporting cell for the 4-celled carpogonial branch. Post-fertilization a terminal and 2–3 lateral gonimolobes are produced, with only loose involucral branches from below. Spermatangia occur on special short branches on basal cells of whorl-branchlets.

Tetrasporangia occur on lower cells of whorl-branchlets, sessile, obliquely tetrahedrally divided.

**Type species:** *Amoenothamnion planktonicum* Wollaston 1968: 377, fig. 35D–Q, pl. 10.

Wollaston (1968) included 3 newly described species in *Amoenothamnion*, one of which (*Am. elongatum* = *L. fastigiatum* (Harvey) Womersley, comb. nov.) has been separated by Athanasiadis (1996, p. 183) in a separate genus *Leptoklonion*. A further species, *A. lycopodioides* Stegenga (1986, p. 10) has been described from South Africa. *Leptoklonion* was separated by Athanasiadis (1996, p. 183) on the basis of 2-celled whorl-branchlets bearing procarps, development of secondary axes in place of whorl-branchlets, and development of tetrasporangia on protrusions of the basal cells of whorl-branchlets. However, 2-celled fertile whorl-branchlets comprise only a slight reduction of the short whorl-branchlets in *Am. planktonicum*, the lateral (secondary) axes in *Am. planktonicum* arise from apical cells above the whorl-branchlets or (in female plants) from the basal cells of whorl-branchlets, and degree of protrusion of the cell bearing the tetrasporangium is variable (Wollaston 1968, figs 36F–H). Further study is necessary of these differences.

**KEY TO SPECIES OF AMOENOTHAMNION**

1. Axial cells 120–180 (–220) μm in diameter and L/D 1–2 (–2.5); whorl-branchlets 60–90 μm long, with large, rounded, basal cells bearing usually 3 branches, 4–7 cells long, terminal cells acute; gland cells absent ............................................ 1. *Am. planktonicum*

2. Axial cells 60–100 μm in diameter and L/D 1–2 (–2.5); whorl-branchlets (90–) 100–150 μm long, with rounded to elongate basal cells bearing 2–4 branches, terminal cells acute; gland cells usually present but sparse ...................................................... 2. *Am. minimum*


**PLATE 1** fig. 1; Figs 86, 87A–I

*Thallus* (Pl. 1 fig. 1; Fig. 86A, B) medium red, erect, 0.5–1.5 cm high or in balls 0.5–1 cm across, with subdichotomous axes bearing whorls of 4 (–5) small whorl-branchlets (Fig. 87A) per axial cell. Attachment by branched rhizoids (Figs 86D, 87E) from basal axial cells or from the basal cells of the lowest whorl-branchlets, forming a rhizoidal holdfast; planktonic (free floating) form (Fig. 86B) without attachment; epiphytic, epiphytic or free floating. **Structure.** Apical cells (Fig. 87B, C) tapering, 5–8 μm in basal diameter and L/D 1–1.5, enlarging rapidly (within 4–6 cells) to axial cells 30–50 μm in diameter, then to 120–180 (–220) μm in diameter and L/D 1–2 (–2.5), branched every 2–4 cells (Fig. 87A). Whorl-branchlets unbranched (Fig. 87I) or with 1–3 short branches from the basal cells (Fig. 87D), occasionally digitately branched, 60–90 μm and 4–7 cells long, basal cell largest (20–40 μm in diameter and L/D 0.5–1), then tapering markedly, terminal cell acute, (4–) 6–10 μm in basal diameter and L/D 1–1.5; hairs frequent on any cells of whorl-branchlets; gland cells absent. Lateral branches from just subapical cells, the axes becoming subdichotomous (Fig. 87B), or (especially in female plants) from the basal cells of whorl-branchlets below the
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Amoenothamnion

procars. Cells uninucleate; rhodoplasts discoid to elongate in smaller cells, becoming ribbon like in axial cells.

Reproduction. Gametophytes dioecious. Carpogonial branches (Fig. 87F) borne on the basal (= supporting) cell of whorl-branchlets 3–5 cells long, close to apices of axes. Post-

fertilization the supporting cell enlarges upwards and cuts off the auxiliary cell, which after fusion with the carpogonium divides to form a foot cell and a central cell which produces a terminal and then lateral gonimolobes (Fig. 87G) 200–300 μm across with ovoid carposporangia 20–35 μm in diameter; the axial cell, residual supporting cell and foot cell fuse, with a broader connection to the central cell (Fig. 87G). Lateral branches from the axial cell below loosely surround the carposporophyte. Spermatangia (Fig. 87H) occur on short special adaxial branches on the basal and lower cells of whorl-branchlets, each branch with 2 or 3 tri- or quadrichotomies.

Tetrasporangia (Fig. 87 I) occur on basal cells of whorl-branchlets usually singly, sessile, subspherical to slightly ovoid, 40–50 μm in diameter, decussately to tetrahedrally divided.

**Type** from Bridgewater Bay, Vic. (Beauglehole, 21.11.1961); holotype in AD, A29292.


*Amoenoathamnion planktonium* occurs on a variety of larger algae and seagrasses, with scattered records along the whole southern Australian coast. The free-floating tetrasporangial form is of frequent occurrence in Bridgewater Bay, Victoria, where it was first observed in 1959 (Womersley & Norris 1959) and has been observed by Mr Bill Steele, a previous proprietor of the Bridgewater Bay Kiosk, on numerous occasions mainly during summer months. This form is also known from Port Fairy and Cape Nelson Bay, Victoria.


**FIGS 87J–P, 88A, B**

**Thallus** (Figs 87J, 88A) medium red, erect, 5–15 mm high, with several subdichotomous axes (Fig. 87J, L), each axial cell with 4 (-5) small, equal or unequal, whorl-branchlets. Attachment by multicellular rhizoids (Fig. 87M) from basal axial cells, becoming digitately branched on contact with host, epiphytic. **Structure.** Apical cells 6–8 μm in diameter and L/D 1–1.2, enlarging rapidly (Fig. 87L) to axial cells 60–100 μm in diameter and L/D 1–2 (-2.5), shorter near the base. Whorl-branchlets (90-) 100–150 μm and 4–5 cells long, branched from the basal cell (Fig. 87K) 3–4 times with 2–4 cells at each branching; basal cells markedly longer than next cell, 20–30 μm in diameter and L/D 1.5–2, with thick walls, tapering to terminal mucronate cells 7–11 μm in basal diameter and L/D 1–1.3 (including mucro), often also with small lateral (basal hair?) cells; gland cells absent or sparse (Fig. 87K), on terminal or subterminal cells of whorl-branchlets, ovoid, 6–8 μm in diameter. Lateral branches arise on axial cells close to apices. Cells uninucleate; rhodoplasts discoïd to elongate in smaller cells, becoming ribbon like in larger cells.

**Reproduction.** Gametophytes probably dioecious. Carpogonial branches (Fig. 87N) borne on the basal (=supporting) cells of young whorl-branchlets, with apical growth of the axis then ceasing. Post-fertilization the supporting cell cuts off upwardly an auxiliary cell (Fig. 87 O), with the upper central cell producing a terminal and then 3–5 lateral gonimoblasts (Fig. 87P) 90–120 μm across with ovoid carposporangia 20–30 μm in diameter; fusion of cells below the carposporophyte occurs, and branches from the axial cell below surround the terminal carposporophyte (Fig. 88A). Spermatangial (Athanasiadis 1996, p. 182) clusters borne on basal and lower cells of whorl-branchlets.

Tetrasporangia (Fig. 88B) occur on the inner cells of whorl-branchlets, adaxially situated, sessile, subspherical, 30–45 μm in diameter, tetrahedrally divided.

**Type** from Stanley Beach, (2 km E of Pennington Bay), Kangaroo I., S. Aust., on Wrangelia abietina, drift (Wollaston, 7.ii.1956); holotype in AD, A20058.

**Distribution:** Elliston, S. Aust., to Walkerville, Victoria.

Genus LEPTOKLONION Athanasiadis 1996: 183

Thallus erect, distantly branched with short laterals above, main axes becoming subdichotomous, axial cells bearing distally 4 (-5) short whorl-branchlets -5 cells long, subequal or with 1 slightly larger; branching lateral, independent of or from the basal cell of whorl-branchlets; gland cells present. Attachment by rhizoids from basal axial cells; epiphytic. Cells uninucleate.

Reproduction. Gametophytes dioecious. Carpogonial branches borne on the basal cell of 2-celled whorl-branchlets near apices; post-fertilization the carposporeophyte forms 1-3 gonimolobes with the basal cells fusing, and the fertile axis does not develop further leaving the carposporeophyte terminally situated and loosely surrounded by 3-4 branches developed from the lower axial cell. Spermatangia on cell clusters borne on the cells of whorl-branchlets.

Tetrasporangia occur on whorl-branchlet cells, sessile, ovoid, decussately divided.

Type species: L. elongatum (Wollaston)Athanasiadis (1996: 183) [=L. fastigiatum (Harvey)Womersley, comb. nov.]


Most whorl-branchlets are only 2- (occasionally 3-) celled near apices where carpogonial branches arise, and those bearing carpogonial branches cannot be considered to be reduced. Lateral branches develop mostly independently of the whorl-branchlets but some probably from basal cells of whorl-branchlets. Separation from Amoellothamnion needs to be further assessed and is probably doubtfully justified.

Leptoklonion fastigiatum (Harvey)Womersley, comb. nov.


Amoellothamnion elongatum Wollaston 1968: 380, fig. 36A-Q.

Leptoklonion elongatum (Wollaston)Athanasiadis 1996: 184, fig. 92.

FIG. 88C-G

Thallus (Fig. 88C) medium red, erect, 1-4 cm high, delicate with long axes bearing laterals at intervals of 5-8 cells, often becoming subdichotomous with an additional shorter lateral branch at the branchings, axial cells (Fig. 88D) with 4 (-5) short whorl-branchlets. Attachment by slender rhizoids from basal, more or less erect, axial cells; epiphytic. Structure. Apical cells (Fig. 88E) 6-8 μm in diameter and L/D 1-2, with a short, straight to slightly curved, chain of 5-8 (-14) such cells (Fig. 88F), then enlarging rapidly to axial cells 50-200 μm in diameter and L/D 1-2 (-2.6). Whorl-branchlets (Fig. 88D) 30-40 (-70) μm and 2-4 cells long, simple or branched 2-3 times, branching from the basal cell; basal cells 10-13 μm in diameter and L/D 1-1.5, tapering to terminal cells 4-6 μm in diameter and L/D 2-3, often with a hair; gland cells (Fig. 88E, F) prominent and frequent, on terminal (or subterminal) cells of (usually) each branch of a whorl-branchlet and touching only the bearing cell, ovoid to hemispherical, 10-15 μm in diameter. Lateral branches arising from basal cell of whorl-branchlets. Cells uninucleate; rhodoplasts elongate in small cells, ribbon like in larger cells.

Reproduction. Gametophytes dioecious. Carpogonial branches borne on basal (=supporting) cells of 2-celled whorl-branchlets, often with a gland cell on the terminal cell; the branch apex ceases development as the procarp develops. Post-fertilization the auxiliary cell develops a foot cell and a central cell which produces a terminal and usually 2 lateral
gonimolobes 50–100 µm across, with ovoid carposporangia 15–20 µm in diameter; fusions occur between the axial cell, residual supporting cell and foot cell; branches from below loosely surround the carposporophyte. Spermatangial clusters (Fig. 88G) dense, borne on cells of the whorl-branchlets. Tetrasporangia occur on basal cells of whorl-branchlets, often on projections from the initial cell, sessile, subspherical to slightly ovoid, 40–70 µm in diameter, subdecussately divided.

Type from Georgetown, Tas., on Zostera (Gunn); holotype in Herb. Harvey, TCD.

Distribution: The southern Gulf region and Kangaroo I., S. Australia.


L. fastigiatum is an older name for L. elongatum (Wollaston) Athanasiadis. It appears to be a deep water species, known from depths of 10 to 41 m in the Troubridge I. – Tapley Shoal region of Gulf St Vincent, South Australia.

Genus ACROTHAMNIOPSIS Athanasiadis & Kraft in Athanasiadis 1996: 92

Thallus largely prostrate with more or less erect laterals, basically complanately branched, each axial cell with 2 pinnate major whorl-branchlets and (1-2) minor whorl-branchlets on both dorsal and ventral surfaces. Attachment by a series of rhizoids with clumped haptera, from successive cells of minor whorl-branchlets; epiphytic on crustose coralline algae. Structure. Apical cells enlarging relatively rapidly to mature axial cells, with lateral branches developed alternately usually 2 axial cells apart. Major whorl-branchlets over 200 µm long, pinnately branched with pinnules also becoming pinnate; minor whorl-branchlets shorter and less developed; rachides with a shorter basal cell; gland cells frequent, on lower pinnule cells, touching the bearing cell and abutting the next cell. Cells uninucleate.

Reproduction. Gametophytes dioecious. Carposgonial branches borne on the basal cell of major whorl-branchlets; carposporophytes terminal, with 1–3 gonimolobes, partly surrounded by whorl-branchlets from below. Spermatangia on branched filaments on pinnule cells. Tetrasporangia occur on rachis and lower pinnule cells, sessile or pedicellate, ovoid, tetrahedrally or subdecussately divided.

Type species: A. eliseae Athanasiadis & Kraft in Athanasiadis 1996: 92.

Acrothamniopsis is a distinctive monospecific genus, characterised by its habit, arrangement of major and minor whorl-branchlets, and the unusual arrangement of rhizoids, emitted from a series of cells and with clumped hapteroid ends but the shafts of the rhizoids free from each other.


FIG. 89

Thallus (Fig. 89A) medium red, largely prostrate with unattached, more or less erect, lateral branches 2–10 mm long, complanately branched apart from crowding of major whorl-branchlets and the minor whorl-branchlets, each axial cell with 2 opposite major whorl-branchlets (Fig. 89A) and often (not always) with 2 or 4 minor whorl-branchlets, (1–2) on each side of the axial cells between the major whorl-branchlets. Attachment by a series of rhizoids with digitate multicellular clumped haptera (Fig. 89C), arising from successive cells of modified rachis cells of minor whorl-branchlets; epiphytic on crustose coralline algae in the upper sublittoral. Structure. Apical cells 6–9 µm in diameter and L/D 1–1.5, increasing
Acrothamniopsis eliseae (A, C, E, AD, A29503; B, MELU, 9438; D, MELU and A66662).  
A. Prostrate and semi-erect laterals, with pinnate whorl-branchlets on axial cells.  
B. Axis with opposite major whorl-branchlets with gland cells.  
C. Prostrate axis with whorl-branchlets and rhizoids with clumped haptera on minor whorl-branchlets.  
D. Carposporophyte with two gonimolobes.  
E. Whorl-branchlets with tetrasporangia.
Eliella

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evenly over 6–10 cells to axial cells becoming 25–45 (-65) μm in diameter and L/D 3–5, with thick walls. Major whorl-branchlets 200–320 μm and 12–15 rachis cells long, pinnate with opposite pinnules (Fig. 89A, B) themselves becoming pinnate; the lower pinnules 90–120 μm and 8–10 cells long. Minor whorl-branchlets usually evenly spaced between the major branchlets, simple or becoming irregularly pinnate, 90–200 μm long. Lower cells of rachides of major whorl-branchlets 30–40 μm in diameter and L/D 1–1.5 (the basal cell shorter), tapering gradually to terminal cells 6–8 μm in diameter and L/D 1–1.2; pinnule cells isodiametric, 10–12 μm in diameter, tapering to 6–8 μm in diameter; terminal cells with rounded ends; gland cells (Fig. 89B) frequent, cut off from terminal and lower cells, usually situated adaxially on the second to fourth cell of pinnules just below branching, touching the bearing cell and abutting the next upper cell. Ovoid, 12–15 μm in diameter. Lateral branches replace (or develop from) major whorl-branchlets, usually alternately and 2 axial cells apart. Cells uninucleate; rhodoplasts discoid in small cells, elongate in larger cells.

Reproduction. Gametophytes dioecious. Carpogonial branches borne on basal cells of 1–3 major whorl-branchlets near apical axes; post-fertilization 1–3 rounded gonimolobes (Fig. 89D) develop, 150–300 μm across, with ovoid carposporangia 20–25 μm in diameter, the carposporophyte remaining terminal on a branch, partly surrounded by whorl-branchlets from below. Spermatangia are terminal on branched filaments arising adaxially on pinnule cells.

Tetrasporangia (Fig. 89E) occur on rachis and lower pinnule cells, sessile or shortly pedicellate, ovoid, 20–30 μm in diameter, tetrahedrally to subdecussately divided.

Type from Point Lonsdale, Vic., on crustose coralline algae, 2.5–4 m deep (Kraft, 1.i.1992); holotype in MELU.

Distribution: Cape Northumberland, S. Aust., to Point Lonsdale, Vic., and SE Tasmania.

Selected specimens: Cape Northumberland, S. Aust., 2–3 m deep (Kraft, 1.i.1992); A5509, Point Lonsdale, Vic., on crustose coralline algae, 2–4 m deep off Lighthouse reef (Kraft, 28.v.1993; AD, A66660-A66662). Point Puer, Port Arthur, Tas., on a crustose coralline alga (Cribb, 31.iii.1950; AD, A29503).

A. eliseae appears to be a sublittoral species occurring on crustose Corallinaceae, distinguished by the presence of major and minor whorl-branchlets and the distinctive arrangement of rhizoids.

Genus ELISIELLA Womersley, gen. nov.

Thallus with or without prostrate axes, with numerous lateral erect branches, radially or distichously branched, axial cells each with 4 or 5 similar or dissimilar whorl-branchlets usually over 200 mm long, closely arranged along the axes. Attachment by rhizoids from basal axial cells (just penetrating the host cortex) or from prostrate filaments. Lateral branches arising on the basal cells of whorl-branchlets. Structure. Subapical cells in short series of small cells then enlarging rapidly. Whorl-branchlets branched from their basal cells, with several successive di- or trichotomies, terminal cells mucronate or with rounded ends; gland cells on outer cells of whorl-branchlets. Cells uninucleate.

Reproduction. Gametophytes dioecious. Carpogonial branches borne on adjacent whorls close to apices, on normal or reduced whorl-branchlets; carposporophytes with 1–3 gonimolobes, surrounded by whorl-branchlets from below. Spermatangia borne on branched clusters developed adaxially on lower cells of whorl-branchlets. Tetrasporangia occur terminally on cells of special branch clusters borne adaxially on lower cells of whorl-branchlets, subspherical, tetrahedrally divided.

Thallus cum multis ramis erectis et lateribus, radiatim aut distiche ramosis, omnes cellulæ axiales cum 4 vel 5 ramulis verticillatis. Affixus per rhizoidia e cellulis axialibus basi aut e filimentis prostratis. Rami laterales in cellulis basaliis ramulorum verticillatorum.
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Elisiella

Structura. Cellulæ subapicales in serie brevi cellularum parvorum, deinde celeriter accrescentes, Ramuli verticillati e cellulis basalisbus orientes, cum aliquot successivis di aut trichotomatibus, cellulæ terminales mucronatae vel in extremis rotundatae; cellulæ glandulosae in cellulis exterioribus ramulorum verticillorum. Cellulæ uninucleatae.


Type species: E. arbuscula (J. Agardh)Womersley, comb. nov.

The two species here placed in a separate genus, Elisiella, were placed by Wollaston (1968) in Perithamnion, and transferred to Tetrathamnion by Athanasiadis (1996). They differ from both these genera in having tetrasporangia borne on branched filaments of small cells developed adaxially on lower whorl-branchlet cells, in contrast to sessile tetrasporangia in both the above genera. They also differ from Perithamnion in having spermatangia borne on adaxial clusters on lower whorl-branchlet cells.

The genus Elisiella is named after Dr Elise Wollaston, for her significant contributions to studies on tribes of the Ceramiaceae.

KEY TO SPECIES OF ELISIELLA

1. Axial cells with 4 whorl-branchlets, the two lateral ones often developing longer branches. Terminal whorl-branchlet cells rounded. 1. E. arbuscula

1. Axial cells with 4 or 5 whorl-branchlets, usually uneven in length. Terminal whorl-branchlet cells mucronate. 2. E. dispar

1. Elisiella arbuscula (J. Agardh)Womersley, comb. nov.

Tetrathamnion arbuscula (J. Agardh)Athanasiadis 1996: 190, fig. 99 (in part, not figs 100–102).
Perithamnion ceramioides sensu Wollaston 1968: 369, fig. 35A–C.
Perithamnion densum Wollaston 1968, 370, fig. 34A–G.
Tetrathamnion densum (Wollaston)Athanasiadis 1996: 193, fig. 103.

FIGS 90, 91, 93A–G

Thallus (Figs 90A, 93A) 2–6 cm high, somewhat complanately branched with several erect main axes bearing lateral branches more or less distichously (Fig. 90B) from lower and central parts of the thallus, few from upper parts, each axial cell with 4 similar whorl-branchlets (Fig. 90C–E) with the lateral branchlets often slightly more developed; lateral branches arising from basal cell of whorl-branchlets (Fig. 93B), especially from opposite lateral whorl-branchlets. Attachment by rhizoids from basal cells of axes, just penetrating the host cortex; epiphytic, usually on Cystophora spp. Structure. Apical cells 4–6 µm in diameter and L/D 1–1.5, enlarging rapidly to thick walled axial cells 80–130 µm in diameter and L/D 2–4 (7) in mid axes and 150–350 µm in diameter and L/D (1–) 1.5–2 in lower axes. Whorl-branchlets (Fig. 90D, E) coarse, more or less complanately branched and slightly upwardly curved, usually closely adjacent, (180-) 200–350 µm long, branched from the basal cell with several successive subdi (or tri-)chotomies and sometimes a terminal chain of 2–3 cells, often with a unicellular terminal hair; basal cells of whorl-branchlets 40–60 (-90) µm in diameter and L/D 1–2, tapering to rounded terminal cells 8–12 µm in diameter and L/D 1–1.5 (2); gland cells (Fig. 93C) prominent on terminal and subterminal cells of whorl-branchlets, hemispherical to ovoid, touching only the bearing cell or abutting the next upper cell, (12-) 15–25 µm in diameter. Cells uninucleate; rhodoplasts discoid in small cells, becoming ribbon like in axial cells.
Fig. 96. Elisiella arbuscula (A, AD, A32942; B–E, AD, A67296). A. Habit, on Cystophora siliquosa. B. Frond with distichous branches from opposite whorl-branchlets. C. Branch with whorl-branchlets, carposporophyte on lower right. D. Whorl-branchlets (slightly flattened). E. Cross section of a branch with 4 whorl-branchlets bearing tetrasporangia.
Reproduction. Gametophytes monoecious. Carpogonial branches (Fig. 93D) borne near apicies on short lateral indeterminate branches, on the basal cells of whorl-branchlets. Post-fertilization a terminal rounded gonimolobe 90-170 μm across with ovoid carposporangia 15–20 μm across develops, often with 1–2 lateral gonimolobes; basal procarp cells usually fuse. The carposporophytes (Figs 91A, 93E) terminate short lateral branches along the axes, without involucral branchlets apart from whorl-branchlets from below. Spermatangia (Figs 91B, C, 93F) are borne terminally on much branched clusters situated adaxially on lower cells of whorl-branchlets.

Tetrasporangia when first formed appear sessile but when profuse they occur on branched clusters of ovoid cells (Figs 91D, E, 93G), lying abaxially above the whorl-branchlet, subspherical, 25–50 μm in diameter, tetrahedrally divided.

_Type_ from Port Phillip Heads, Vic. (Wilson, 26.x.1889); holotype in Herb. Agardh, LD, 18202.

_Distribution:_ Cape Leeuwin, W. Aust., to Port Phillip Heads, Victoria.


_Eliisella arbuscula_ is superficially similar to _Perithamnion ceramioides_ but differs in the absence of subdichotomous apical branching and in having coarser and larger axial cells, whorl-branchlets, and the cells thereof. Male thalli also show distinct adaxial clusters of spermatangia, as in _Tetrathamnion_, in contrast, usually occurs subtidally in calmer conditions.

_P. densum_ Wollaston appears to be only a densely branched form of _E. arbuscula_.

_E. arbuscula_ is a common species on rough-water coasts along most of southern Australia (perhaps especially on Kangaroo I.), usually epiphytic on _Cystophora_ at or just below low tide level. _Tetrathamnion linearatum_, in contrast, usually occurs subtidally in calmer conditions (see under this species).

2. _Eliisella dispar_ (Harvey) Womersley, _comb. nov._


_Perithamnion dispar_ (Harvey) Wollaston 1968: 373, fig. 34H–P.

_Tetrathamnion dispar_ (Harvey) Athanasiadis 1996: 194, fig. 104.

_FIGS 92, 93H–N_

_Thallassa_ (Figs 92A, 93H) with a prostrate base bearing free main axes 2–8 cm long, these with shorter more or less alternately distichous laterals (Fig. 92B) and further irregular laterals, some developing into long axes, each axial cell with (4-)5 whorl-branchlets (Fig. 92B, C), closely arranged along axes. Attachment by multicellular rhizoids (Figs 92C, 93I) with digitate ends, from prostrate filaments (Fig. 92D) 100–200 μm in diameter and L/D 1.5–2; epiphytic on various larger algae, especially on _Perithalia_. _Structure_. Apical cells 6–8 μm in diameter and L/D 1–1.2, enlarging within a few cells to axial cells 60–100 μm in diameter and L/D 1.2–1.5; and in main axes 300–500 (600) μm in diameter and L/D 1–1.4. Each whorl of whorl-branchlets (Fig. 92C) with 3 longer ones, 220–380 μm long and two shorter ones 60–90 μm long, one of the longer ones usually forming an alternate lateral branch more or less distichously arranged and 600–800 μm long; in the lower thallus any of the whorl-branchlets may form a lateral branch, and short lateral branches bear only 4 equally spaced whorl-branchlets 200–260 μm long; whorl-branchlets are usually shorter and less branched towards the base of axes. Whorl-branchlets (Fig. 93J) consist of several successive subdichotomies, with basal cells 45–80 μm in diameter and L/D 1.5–2, tapering only over the last 2–3 cells to subterminal cells 8–12 μm in diameter and L/D 0.8–1, with the terminal cell mucronate (Fig. 93K); gland cells (Fig.
93K) prominent, borne on outer cells of whorl-branchlets, touching the bearing cell and abutting the next outer cell, more or less ovoid but adjoining walls sharply angled, 12–20 µm in diameter. Cells uninucleate; rhodoplasts discoid to elongate, becoming ribbon-like in larger cells.

Reproduction. Gametophytes dioecious. Carpogonial branches (Fig. 93L) borne on basal cells of short branchlets near apices, with a small sterile cell. Carposporophytes (Figs 92E, 93M) borne near apices of lateral branches, never on the main axes, with a terminal and several lateral gonimolobes 100–180 µm across of carposporangia 16–25 µm in diameter. Spermatangia on branched clusters borne on lower cells of whorl-branchlets (Athanasiadis 1996, fig. 104F, G).

Tetrasporangia (Figs 92F, 93N) occur terminally on special short branchlets on basal (or second) cells of whorl-branchlets, subspherical, 40–55 µm in diameter, tetrahedrally divided.

Type from the E coast of Tasmania (Gunn); lectotype in Herb. Harvey, TCD, on Mychodea disticha, isotype in BM.

Distribution: Vivonne Bay, Kangaroo I., S. Aust., to Point Lonsdale, Vic., and E Tasmania.


Genus PERITHAMNION J. Agardh 1892: 25

Thallus erect, often basally clumped, attached by basal rhizoids to the host, occasionally with secondary prostrate axes, axial cells with 4 or 5 whorl-branchlets usually equal in size and over 150 µm long, successively branched di- (or tri-)chotomously with terminal chains of 2–3 small cells and prominent gland cells on outer cells. Lateral branches arising on subapical cells and becoming subdichotomous, also with shorter lateral branches arising from the basal cells of whorl-branchlets. Cells uninucleate or multinucleate.

Reproduction. Gametophytes dioecious or monoecious. Procarps borne in closely adjacent whorls of (1-) 2–3 close to apices of short lateral branches, with the carpogonial branches on normal whorl-branchlets. Post-fertilization the auxiliary cell fuses with the carpogonium via a connecting cell and divides, the upper central cell developing a terminal and lateral gonimolobes, not or partly protected by lower branchlets; carposporophytes lateral on continuing axes. Spermatangia terminal on further divisions of the terminal cells of the whorl-branchlets.

Tetrasporangia sessile, adaxial on the basal (or second) cells of whorl-branchlets, tetrahedrally or decussately divided.

Type species: P. ceramioides J. Agardh 1892: 30, pl. 1 figs 1, 2.

Perithamnion is distinguished by subdichotomous branching from close to the apex, so that this branching occurs just above the whorl of whorl-branchlets, with shorter lateral branches arising from the basal cells of whorl-branchlets. The occurrence of spermatangia terminally on further divisions of terminal whorl-branch cells is also characteristic.

A genus of 2 species, the type and P. muelleri (Harvey)Womersley, on southern Australian coasts. Athanasiadis (1996, pp. 175, 189) considered that J. Agardh's second species of Perithamnion, P. arbuscula is generically distinct from P. ceramioides and identical with the type species of Tetrathamnion Wollaston. However, it is now separated (see above) in a separate
Perithamnion HETEROTHAMNIEAE

genus, Elisiella, since the tetrasporangia are not sessile but are borne on branched, adaxial filaments of ovoid cells.

KEY TO SPECIES OF PERITHAMNION

1. Thallus 2-6 cm high, axial cells each with 4 whorl-branchlets, lower axial cells 150-250 μm in diameter ......................................................... 1. P. ceramioides

2. Thallus 2-10 (-15) cm high, axial cells each with 5 whorl-branchlets; lower axial cells 350-500 μm in diameter ....................................................... 2. P. muelleri

1. Perithamnion ceramioides J. Agardh 1892: 30, pl. 1 figs 1, 2. Athanasiadis 1996: 176, figs 85, 86.

Thallus (Fig. 94A) 2-6 cm high, much branched with several erect subdichotomous axes bearing lateral branches from lower and central parts of the thallus, few from upper parts, each axial cell with 4 similar whorl-branchlets (Fig. 94A, E); main lateral branches arising apically (Fig. 94B) and becoming subdi- (or tri-) dichotomous, with the upper axial cells pith-connected above the whorl of 4 whorl-branchlets, with laterals also from basal cells of whorl-branchlets to form shorter lateral branches. Attachment by rhizoids from basal cells of axes; epiphytic on other taxa than Cystophora.

Structure. Apical cells 4-6 μm in diameter and LID 1-1.5, enlarging rapidly to thick walled axial cells 30-60 μm in diameter and L/D 1.4-2.2 in mid axes and 150-250 μm in diameter and L/D 0.6-1 in lower axes,. Whorl-branchlets more or less complanately branched and slightly upwardly curved, usually closely adjacent, 50-110 μm long, branched from the basal cell with several successive subdichotomies and sometimes a terminal chain of 2-3 cells; basal cells of whorl-branchlets (10-) 14-20 (-25) μm in diameter and L/D 1.2-1.7 (-2), tapering to terminal cells 5-9 μm in diameter and L/D 1-1.5 (-2); gland cells prominent on the terminal and subterminal cells of whorl-branchlets, hemispherical to ovoid, touching only the bearing cell or abutting the next upper cell, 6-10 μm in diameter. Cells uninucleate; rhodoplasts discoid in small cells, becoming ribbon like in axial cells.

Reproduction. Gametophytes dioecious (or monoecious?). Carpogonial branches borne near the apices of short lateral branches, on the basal cells of short whorl-branchlets. Postfertilization a terminal rounded gonimolobe (Fig. 94A, C) 90-140 μm across develops, with ovoid carposporangia 15-20 μm across, often with 1-2 lateral gonimolobes; basal procarp cells usually fuse. The carposporophytes occur laterally along the axes, usually without involucral branchlets. Spermatangia (Fig. 94D) cut off terminally from terminal cells of whorl-branchlets, sparse, ovoid, 2-3 μm in diameter.

Tetrasporangia (Fig. 94E) occur on mid cells of whorl-branchlets, lying above the whorl-branchlet, sessile, subspherical, 25-40 μm in diameter, tetrahedrally divided.

Type from Spring Creek, Port Phillip Heads, Vic. (Wilson); holotype in Herb. Agardh, LD, 18201. Spring Creek enters the sea at Torquay, some 40 km W of Port Phillip Heads.


P. ceramioides is superficially similar to Elisiella arbuscula but the latter differs in dimensions, in lack of near apical subdichotomous branching, and it occurs mainly on species of Cystophora, whereas P. ceramioides is known on other taxa than Cystophora.

Athanasiadis (1996, p. 175, fig. 86A) considered the spermatangia to be terminal on extended divisions of whorl-branchlet terminal cells. While his fig. 86A is unconvincing, since the supposed spermatangia are 5-5.5 μm in diameter (corresponding to smaller terminal...
Fig. 94. *Perithamnion ceramioides* (AD, A53610). A. Branches with whorl-branchlets and carposporophytes. B. Axial apex with subdichotomous branching. C. Young carposporophyte. D. Whorl-branchlets with spermatangia. E. Branches with whorl-branchlets bearing tetrasporangia.
cells of the vegetative short-branchlets), similar but smaller terminal spermatangia have been observed in AD, A53610 (Fig. 94D). However, further studies on male thalli of *P. ceramioides* are needed, since such terminal spermatangia are very few in number.

2. **Perithamnion muelleri** (Harvey) Womersley, *comb. nov.*


**FIG. 95**

Thallus (Fig. 95A) medium red-brown, 2–10 (-15) cm high, ecorticate, much branched irregularly radially with long laterals from lower axes, often with laters 4–5 cells apart on upper branches, axial cells with 5 whorl-branchlets (Fig. 95B) in distinct whorls. Attachment by branches with recurved ends or by rhizoids; epithyptic or epilithic. **Structure.** Apical cells 6–8 μm in diameter and L/D 1–2, partly surrounded by young whorl-branchlets, enlarging to axial cells in mid thallus 120–240 μm in diameter and L/D 1–2, and in lower axes cells 350–500 μm in diameter and L/D 1–2.5: axial cells conspicuous throughout thallus, with gaps between whorl-branchlets 40–90 μm broad in lesser branches, increasing to 400–500 μm broad in lower axes (2–3 times the length of the whorls of whorl-branchlets). Whorl-branchlets normally 5 per axial cell, evenly spaced, becoming 200–300 μm long with 5–7 successive di- to quadrichotomous branches from the basal cells, basal cells 20–30 μm in diameter and L/D 1–1.5, decreasing to terminal cells 6–8 μm in diameter and L/D 1.5–2, often with long multicellular hairs; gland cells usually prolific, on mid to outer cells of the whorl-branchlets, arising on terminal cells and touching only the bearing cell, sessile, subepithelial to ovoid, 10–15 μm in diameter. Lateral branches arising from basal cells of whorl-branchlets. Cells multinucleate; rhodoplasts discoïd, forming a reticulum or ribbon like in larger cells.

**Reproduction.** Gametophytes dioecious. Carpogonial branches on the basal (= supporting) cell of whorl-branchlets, single per whorl and on 1–3 successive whorls. Post fertilization the supporting cell cuts off a larger, lateral, auxiliary cell which develops a terminal and lateral gonimolobes (Fig. 95B) 160–220 μm across of ovoid carposporangia 20–30 μm in diameter. The axial cell, residual supporting cell, auxiliary cell and lower gonimoblast cells fuse somewhat, with broader pit-connections. No involucral filaments develop and the carposporophytes remain more or less terminal on branches. Spermatangia (Fig. 95 C, D) cut off from initials on terminal cells of whorl-branchlets. Tetrasporangia (Fig. 95E) borne on mid cells of whorl-branchlets, situated above the whorl-branchlets, sessile, subepithelial; 35–55 μm in diameter, decussately divided.

**Type** from Phillip I., Western Port, Vic. (= *Mueller*); lectotype (female) in Herb. Harvey, TCD; isolectotype (female) in MEL, 8435. The specimen designated as "TYPE" by HBSW in 1952 appears sterile, and it would be better to select an alternative female specimen as lectotype.

**Distribution:** Eyre, W. Aust., to Waratah Bay, Victoria.


*P. muelleri* occurs mainly in deep water in moderately sheltered situations. It is a larger species than *P. ceramioides* and agrees in structure and reproduction, notably in having spermatangia cut off terminally from end cells of the whorl-branchlets. However, lateral
Fig. 95. *Perithamnion muelleri* (A, AD, A37691; B, D, AD, A33607; C, AD, A41224; E, AD, A37691). A. Habit. B. Branches with whorl-branchlets and a carposporophyte. C. Branches with whorl-branchlets bearing terminal spermatangia. D. Whorl-branchlets with terminal spermatangia. E. Branch with whorl-branchlets bearing tetrasporangia.
branches appear to arise mainly on the basal cells of whorl-branchlets, so that the lateral is one of 5 in each whorl, pit-connected at the same level as the other 4.

**Genus TETRATHAMNION** Wollaston 1968: 360

*Thallus* erect, irregularly branched, with rhizoids from the basal axial cells attaching to and just penetrating the host, each axial cell with 4 similar whorl-branchlets over 200 \( \mu m \) long and successively branched 4–6 times; gland cells on outer cells of whorl-branchlets. Lateral branches arising on the basal cells of whorl-branchlets. Cells uninucleate.

**Reproduction.** Gametophytes dioecious. Procarps (2 or 3) borne on axial cells close to apices, with a supporting cell bearing a sterile cell and a 4-celled carpogonial branch. Carposporophyte with a terminal and several lateral lobes of carposporangia, not or slightly protected by lower whorl-branchlets; carposporophytes terminal, surrounded by 2–4 extended branches from the lower axial cell. Spermatangia on small, partly adaxial, clusters on whorl-branchlet cells.

Tetrasporangia sessile on basal to mid cells of whorl-branchlets, tetrahedrally divided.

**Type species:** *T. lineatum* Wollaston 1968: 361, fig. 33A–P.

A genus of a single southern Australian species distinguished by the erect, tufted habit with lower cells of axes attached by just-penetrating rhizoids, axial cells with 4 whorl-branchlets which are successively branched 4–6 times, lateral branches arising on basal cells of whorl-branchlets and hence in a whorl of 4, gland cells subterminal on whorl-branchlets, and sessile tetrasporangia on mid to outer cells of whorl-branchlets, and especially by adaxial spermatangial clusters on whorl-branchlet cells. The latter feature separates it from species of *Perithamnion*.

Wollaston (1968, p. 360) considered *Tetraphymnion* to be intermediate between *Heterothamnion* and *Perithamnion*. Athanasiadis (1996, p. 189) considered the type species to be the same as *Perithamnion (=Elisiella) arbuscula* J. Agardh, but the latter is considered distinct from *P. ceramioides* and also *T. lineatum*. Illustrations of Athanasiadis (1996) of the type of *P. arbuscula* (Fig. 99) are distinct from his illustrations (Figs 100–102) of plants placed by Wollaston (1968, p. 361), and here, under *T. lineatum*, and study of large numbers of these two species supports their separation.

*E. arbuscula* has coarser whorl-branchlets and larger gland cells than *T. lineatum* and the latter has sessile tetrasporangia instead of those on branched adaxial filaments as in *Elisiella*. Athanasiadis (1996, p. 190) also suggested that *T. pyramidatum* and *T. ramosum* are forms of *T. lineatum*, and this is accepted here.

**Tetraphymnion lineatum** Wollaston 1968: 361, fig. 33A–P.

* T. pyramidatum* Wollaston 1968: 364, fig. 33Q–X.

* T. ramosum* Wollaston 1968: 366, fig. 32P–U.

**FIGS 93 O–U, 96, 97**

*Thallus* (Figs 93 O–U, 96A) 5–50 mm high, often pyramidal in form with erect axes sparsely and distantly branched, each axial cell with 4 more or less horizontal whorl-branchlets (Figs 93P, 96B). Attachment by slender, just-penetrating branched rhizoids (Fig. 93Q) from lower cells of erect axes; epiphytic, mainly on brown algae. Structure. Apical cells 6–8 \( \mu m \) in diameter and L/D 1–1.5, enlarging rapidly to axial cells 70–200 \( \mu m \) in diameter and L/D 3–4, narrower and shorter towards the base. Whorl-branchlets usually separated alo 12 the axes, 200–350 \( \mu m \) long with 4–6 successive pseudodichotomies and terminal or upper short chains 2–3 (4) isodiametric cells long often with a terminal hair; basal cells of whorl-branchlets 20–30 \( \mu m \) in diameter and L/D 2–3, decreasing to 8–12 \( \mu m \) in diameter and L/D 1–1.5 in terminal cells; gland cells (Fig. 93P) usually on subterminal cells of whorl-branchlets, ovoid, 10–16 \( \mu m \) in diameter, touching the bearing and the next upper cell. Lateral branches arising on basal cells of whorl-branchlets, resulting in 3 whorl-branchlets and 1 lateral in a whorl. Cells uninucleate; rhodoplasts discoid to elongate, ribbon like in larger cells.
Fig. 96. *Tetrathamnion lineatum* (A-C, E, AD, A32942; B, AD, A27686). A. Habit, on *Cystophora siliquosa*. B. Branches of the type specimen, with cystocarps. C. Axis and whorl-branchlets, with gland cells. D. Young carposporophyte, with old carpogonial branch on left. E. Terminal carposporophyte with subtending branches from lower axial cell.
Fig. 97. Tetrahamnion lineatum (A, AD, A32942; B-D, AD, A64598). A. Axis and whorl-branchlets with spermatangial clusters. B. Adaxial spermatangial clusters on whorl-branchlets. C. Whorl-branchlets with tetrasporangia. D. Tetrahedrally divided tetrasporangia on whorl-branchlets.
Reproduction. Gametophytes dioecious. Procarps (Fig. 93R) usually in whorls of 3 just subapically, with a supporting cell bearing a small sterile cell and a 4-celled carpogonial branch, with only one carposporophyte (Fig. 96D, E) developing per whorl; auxiliary cell producing a terminal gonimolobe and 2 lateral, rounded, gonimolobes 100–150 μm across of ovoid carposporangia 30–40 μm in diameter. Carposporophytes (Figs 93S, 96E) terminal, without involucral branches apart from 2–4 extended lateral branches from below. Spermatangial clusters (Fig. 97A, B) formed on small cell branches on upper whorl-branchlet cells, slightly adaxial.

Tetrasporangia (Figs 93T, 97C, D) occur singly on lower cells of whorl-branchlets, sessile, subspherical, 30–50 μm in diameter, tetrahedrally divided.

**Type** from White Beach, Wedge Bay, Tas., on *Sargassum verruculosum*, upper sublittoral on reef (Wollaston & Mitchell, 29.xii.1964); holotype in AD, A27686.

**Distribution**: Tiparra reef, S. Aust., to Green Cape, N.S.W., and SE Tasmania.


*T. lineatum* is less densely branched, with longer branches, than *T. pyramidatum* and *T. ramosum*, but it is likely (as Athanasiadis 1996, p. 190 suggests) that these two species are only forms of *T. lineatum*. This species occurs on a variety of hosts, but not on *Cystophora siliquosa* which is the most common host of *Elisiella arbuscula*. It occurs under a variety of water movement, with the type and other laxly branched, sheltered water specimens being of the *T. lineatum* form whereas under stronger water movement specimens are more densely branched as in *T. pyramidatum* and *T. ramosum*.

**Tribe SPERMOTHAMNIEAE Schmitz 1889: 449**

by H.B.S. Womersley

**Thallus** with erect, slightly to moderately and irregularly branched filaments arising from prostrate filaments attached by haptera; cortication absent; gland cells absent. Cells multinucleate.

**Life history** triphasic with isomorphic gametophytes and tetrasporophytes.

**Reproduction.** Gametophytes monoecious or dioecious. Procarps on the subapical cell of the female axis, enclosed in a gelatinous sheath together with associated sterile cells (one or two sterile periauxial cells, the apical cell and the sterile cell on the supporting cell) which remain undivided after fertilization in most genera (no inner involucre), but may divide to form small groups (*Interthamnion*) or a pericarp of erect filaments (*Lejolisia*). Auxiliary cells one or two per procarp, fusion cell present or absent, carposporangia terminal. An outer involucre of filaments on the hyponogenous or subhyponigenous cells present or absent. Spermatangia formed on compact heads.

Meiosporangia sessile or pedicellate on the erect filaments, tetrahedrally or polyhedrally divided (monosporangia absent).
The tribe Spermothamnieae includes some 9 genera. As well as the seven genera which occur on southern Australian coasts (see also Gordon 1972), *Ptilothamnionopsis* Dixon (1971, p. 61) occurs in California, and *Gordoniella* Itono (1977, p. 53) in Japan. Other genera previously placed in this tribe, but which produce 1–3-celled propagules, are now referred to the Monosporae (Huisman & Gordon-Mills 1994).

This account is based very largely on that of Gordon 1972.

The following key is based entirely on female reproductive structures; many species can be identified only with doubt if only male or tetrasporangial thalli are present. Further studies of members of the tribe from other countries is necessary to support or modify the generic concepts developed by Gordon (1972) and others.

**KEY TO GENERA OF SPERMOTHAMNIEAE**

1. Carposporophyte with erect inner involucral filaments developing from sterile cells of the procarp; outer involucral filaments absent .............................................................. 2

1. Carposporophyte without inner involucral filaments from sterile cells of the procarp (except *Interthamnion*, with slight post-fertilization subdivision), but with or without outer involucral filaments arising from the hypogenous or subhypogenous cells ............. 3

2. Inner involucral filaments forming a pericarp of associated filaments within a gelatinous sheath, with an apical ostiole ................................................................. **LEIOLISIA**

2. Inner involucral filaments loosely arranged, not forming a pericarp within a gelatinous sheath .............................................................. **RHIPIDOThAMNION**

3. Carposporophyte without inner or outer involucral filaments .................................................. 4

3. Carposporophyte with (*Interthamnion*) or without inner involucral filaments, with 2–4 free outer involucral filaments from the hypogenous or subhypogenous cells ................. 5

4. Carposporophyte developing from 2 auxiliary cells per procarp; fusion cell prominent, T-shaped, involving the hypogenous cell .................. **TIIFFANIELLA**

4. Carposporophyte developing from a single auxiliary cell; fusion cell absent ........................................................................................................... **LOMATHAMNION**

5. Carposporophyte developing from a single auxiliary cell; hypogenous cell much longer (L/D 2–4) than subapical cell, producing 2 opposite outer involucral filaments ........................................................................ **PTILOThAMNION**

5. Carposporophyte developing from 2 auxiliary cells; hypogenous cell only slightly longer (L/D 1–2) than subapical cell, with or without outer involucral filaments ..................... 6

6. Sterile procarp cells producing post-fertilization three small groups of 3–5 cells; fusion cell absent; hypogenous cell producing four branched outer involucral filaments ............................................................. **INTERTHAMNION**

6. Sterile procarp cells not dividing; fusion cell prominent, incorporating the hypogenous cell; outer involucral filaments produced only from the subhypogenous cell ........................................................................... **SPERMOTHAMNION**

**Genus LEIOLISIA** Barnet 1859: 80

*Thallus* tufted and spreading, with prostrate filaments attached by digitate haptera, and erect, irregularly branched, uniseriate filaments 2–15 mm high; epiphytic. Cells multinucleate.

*Reproduction.* Gametophytes dioecious. Procarps subapical on laterals of erect filaments, with 3 periaxial cells, 2 sterile and one (the supporting cell) bearing a sterile apical cell and a lateral carpogonial branch; the auxiliary cell divides post-fertilization to produce a terminal gonimoblast initial and 2 lateral non-functional cells, the initial producing chains of short gonimoblast cells (which later fuse) and terminal carposporangia. The sterile cells of the
procarp divide post-fertilization to form 4 inner involucral filaments which branch and surround the carposporophyte, forming a pericarp of erect, discrete, filaments enclosed in a firm gelatinous sheath with an apical ostiole; outer involucral filaments absent. Spermatangial heads are subspherical to elongate, borne on erect filaments, each head with a short row of axial cells each bearing 2 or 3 periaxial cells each cutting off 2 or 3 terminal spermatangia, and often further spermatangial initials.

Tetrasporangia borne terminally on short pedicels occurring laterally on the erect axes, tetrateradially divided.

Type species: *L. mediterranea* Bornet 1859: 91, pls 1, 2.

A genus of some six species, some of which are not known from cystocarpic plants and hence uncertain (see Gordon 1972, p. 143 and Itono 1977, p. 56). The genus is characterised by the carposporophyte being surrounded with a cellular pericarp enclosed in a firm gelatinous sheath.


**FIG. 98**

Thallus (Fig. 98A) medium red to dark red-brown, 2–15 mm high, forming dense and extensive tufts on various hosts. Attachment by haptera; epiphytic on *Amphibolis, Codium galeatum, Lenormandia* and other algae. Structure. Prostrate and erect filaments irregularly branched, the erect filaments sometimes unilaterally and tapering only slightly. Cell size variable on different hosts, prostrate axes 70–110 μm in diameter and L/D 1.5–3, erect axes (25–) 65–80 (105) μm in diameter with cells L/D 2–5, extended hair-like ends 18–20 μm in diameter and L/D up to 15. Cells multinucleate; rhodoplasts discoidal to elongate.

Reproduction. Gametophytes dioecious; mixed phase plants occur rarely. Female axes (Fig. 98B) terminal, the last 3 cells short and the fourth (subhypogenous cell) 2–4 times as long as the hypogenous cell; subapical cell bearing 2 sterile periaxial cells and the supporting cell with a terminal sterile cell and lateral carpogonial branch. Fertilized carpogonium producing connecting cells and the auxiliary cell dividing to form gonimoblast filaments of small cells which fuse as radiating arms (Fig. 99D) but cut off terminal ovoid carposporangia 40–50 μm in diameter. The apical cell, sterile periaxial cells and sterile cell on the supporting cell divide to produce four erect, slightly branched, filaments, forming an urceolate and ostiolate pericarp (Fig. 98C) 150–200 μm in diameter, enclosed in a firm gelatinous sheath. Spermatangial heads (Fig. 98E, F) are slightly ovoid, 40–45 μm in diameter, terminal on short lateral branchlets of erect filaments.

Tetrasporangia (Fig. 98G) are terminal on 1–3 short pedicel cells, lateral on erect filaments, 70–80 μm in diameter, tetrateradially divided.

Type from “Novam Hollandiam austr.”; in Herb. Agardh, LD, 35288.

**Distribution:** Houtman Abrolhos (Huisman 1997) and Flat Rocks, S of Geraldton, W. Aust., to Twofold Bay, N.S.W. (Millar & Kraft 1993, p. 41).

L. aegagropila is a considerably larger species than the type species from the Mediterranean, and plants on different hosts may differ considerably in cell size.

**Genus RHIPIDOThAMNION** Huisman 1985: 55

Thallus with prostrate filaments bearing erect, uni- and secund branches. Prostrate filaments attached by digitate haptera; cortication absent; cells multinucleate.

**Reproduction.** Gametophytes dioecious. Female axes terminal, displaced laterally, with 2 small cells and a larger hypogenous cell. Sub-apical cell bearing two sterile periaxial cells and a supporting cell with a sterile cell and a lateral carpogonial branch. Post-fertilization cell occurs between the carpogonium and auxiliary cell, and a fusion cell develops with gonimolobes bearing terminal carposporangia. Sterile cells of the procarp produce 4-branched, inner involucral filaments which loosely surround the gonimoblast. No outer involucres develop. Spermatangial heads ovoid, sessile, adaxial on each cell of curved branches, with 4–7 axial cells each cutting off 2–3 periaxial cells which, directly or via further initials, each produce 2–4 spermatangia.

Tetrasporangia borne adaxially on cells of curved branches, 1–3 per cell, sessile, tetrahedrally divided.

**Type (and only) species: R. secundum** Huisman 1985: 56, figs 2–15.

Rhipidothamnion is distinguished by formation only of inner involucral branchlets from sterile cells of the procarp, with no outer involucral branchlets, and differs from the only other genus with these features (Lejolisia) in that the branchlets are loosely arranged and not in the form of a pericarp within a gelatinous sheath.


**FIG. 99**

Thallus (Fig. 99A) medium red-brown, 0.5–7 cm high, much branched with strongly developed unilateral and secund branching, upper branches often curved, erect filaments arising from prostrate filaments. Attachment by digitate haptera from prostrate filaments; epizooic on bryozoans or mussels, epiphytic on algae, or epilithic. Structure. Prostrate filaments 65–90 (–120) μm in diameter with cells L/D 1.5–3, erect filaments tapering from 110–150 μm in diameter with cells L/D 2.5–7 near their base to 20–40 μm in diameter with cells L/D 3–5 several cells below the apices. Cortication absent. Cells multinucleate; rhodoplasts discoid.

**Reproduction.** Gametophytes dioecious. Female axes (Fig. 99B) apical on erect filaments, with 3 small cells, the subapical cell producing two sterile periaxial cells and the supporting cell bearing a sterile cell and a lateral carpogonial branch. Post-fertilization the carpogonial branch cells fuse and the auxiliary cell connects with the carpogonium via a connecting cell, producing up to four gonimolobes from a lobed fusion cell, with terminal ovoid carposporangia 30–45 μm in diameter; sterile cells of the procarp divide to form 4 inner involucral branchlets up to 5 cells long, which loosely surround the carposporophyte (Fig. 99C), 300–400 μm across; outer involucres absent. Spermatangial heads occur adaxially on each cell of curved branchlets, sessile, ovoid, 50–60 μm in diameter, producing surface spermatangia 5–6 μm in diameter.

Tetrasporangia (Fig. 99D, E) borne adaxially on cells of curved branches, up to 3 on each cell, ovoid, sessile, 40–60 μm in diameter, tetrahedrally divided.

**Type from Keyhole, One Tree I., Qld, 20 m deep (Huisman & Millar, 17.xi.1982); holotype in MELU, 24258.
Fig. 99. _Rhipidothamnion secundum_ (A, AD, A58707; B, C, MELU, 42534; D, E, AD, A58703). A. Habit. B. Procarp system (carpogonial branch on right). C. Carposporophyte with carposporangia and involucral branches. D. Branch with secund laterals and tetrasporangia. E. Tetrasporangia on cells of pinnules.
SPERMOTHAMNIEAE

**Tiffaniella**

*Distribution:* One Tree I., Qld, to Jervis Bay, N.S.W.; Gellibrand Light, Port Phillip, Victoria.

*Selected specimens:* Gellibrand Light, Port Phillip, Vic., 5–6 m deep on mussels (Kraft, Lewis & O'Brien, 12.ix.1975; AD, A5870). Other collections by Kraft and colleagues from this locality during most months of 1976, in AD, A58701–A15708.

*R. secundum* is distinctive morphologically and most widely distributed on the eastern Australian coast; the Port Phillip occurrence may be as an adventive, but it was present throughout 1976. The Port Phillip specimens (2–7 cm high) are considerably larger than the type and N.S.W. specimens (2–6 mm high) but agree well structurally.

**Genus TIFFANIELLA** Doty & Menez 1960: 135

*Thallus* tufted and expanding, with prostrate filaments attached by saccate or digitate haptera, and erect, irregularly branched, uniseriate filaments 5–20 (–50) mm high; epiphytic (usually) on *Codium*. Cells multinucleate.

*Reproduction.* Gametophytes dioecious or monoecious. Procarps subapical on laterals of erect filaments, the upper 3 or 4 cells shorter, with 3 periaxial cells, one sterile, one fertile producing only an auxiliary cell, and the other (the supporting cell) producing a sterile apical cell and a lateral carpogonial branch; fusion cell with 2 arms, involving both auxiliary cells and the hypogenous cell, with short gonimoblast filaments producing clavate to pyriform carposporangia; inner and outer involucral filaments absent, the carposporophyte naked. Spermatangial heads elongate, sessile or pedicellate on erect filaments, with axial cells cutting off radially initials which produce spermatangia.

Sporangia terminal on short pedicels, usually clustered on upper part of erect filaments, tetrahedrally or polyhedrally divided.


A genus of eight species (Gordon 1972, p. 125), one on southern Australian coasts. Most species occur on *Codium*, and are attached by saccate rhizoids. The southern Australian species was considered by Gordon (1972, p. 124) to be the same as the Mauritius *T. cymodoceae*, though differing in host and digitate rather than saccate haptera. *T. cymodoceae* differs from the other described species in having tetrasporangia instead of polysporangia. Huisman (1985, p. 63) further discusses the characteristics of *Tiffaniella*.


**FIG. 100**

*Thallus* (Fig. 100A) medium to dark red-brown, forming spreading tufts on the hosts, 3—7 mm high, with prostrate filaments bearing subdichotomous erect filaments. Attachment of prostrate filaments by digitate haptera; epiphytic on *Codium galeatum* and *C. laminarioides*. *Structure.* Prostrate filaments 40–90 μm in diameter, cells L/D 2–3.5; erect filaments tapering only slightly, median cells 30–90 μm in diameter and L/D 3–7.5. Cells multinucleate; rhodoplasts discoid.

*Reproduction.* Gametophytes dioecious or monoecious. Female axes (Fig. 100B) usually lateral, 4–5 (–13) cells long, the last 4 cells short and the fifth 4–5 times as long as the fourth cell. Subapical cell with 3 periaxial cells, one sterile, one fertile and cutting off an auxiliary cell, and the other (supporting) cell bearing a terminal sterile cell and lateral carpogonial branch (Fig. 100B). The hypogenous and subhypogenous cells do not bear any lateral involucral filaments before or after fertilization. Post-fertilization the carpogonial branch cells fuse and both auxiliary cells are involved in the two-armed fusion cell (Fig. 100C), which cuts off small gonimoblast cells and ovoid terminal carposporangia 20–45 μm in diameter, without
any involucral branchlets. Spermatangial heads (Fig. 100D, E) are 30–50 μm in diameter and L/D 2–3, sessile or on short pedicels on upper parts of erect filaments.

Tetrasporangia (Fig. 100F) are clustered on short pedicels on upper parts of erect filaments, 40–50 μm in diameter, undivided in Australian collections (AD, A52059, A32149).

_Type_ from Riambel, Mauritius (Vaughan 996, on _Cymodocea_); in C. Isotype in AD, A17892.

_Distribution_: Mauritius, South Africa.

Shark Bay, W. Aust. to Seal Bay, Kangaroo I., S. Australia.

Fig. 100. _Tiffaniella cymodoceae_ (AD, A32149). _A_. Prostrate and erect axes. _B_. Fertile axis with procarp system. _C_. Mature carposporophyte with procarp system on left. _D_. Erect axis with spermatangial heads. _E_. Longitudinal section of a spermatangial head. _F_. Erect axis with undivided tetrasporangia. (All as in Gordon 1972, courtesy of _Aust. J. Bot._)

Gordon (1972, p. 121) records T. cymodoceae on Amphibolis, but all specimens in AD are on Codium.

**Genus LOMATHAMNION** Gordon 1972: 125

_Thallus_ tufted and spreading, with prostrate filaments attached by digitate haptera, and erect, simple to sparsely branched, uniseriate erect filaments; epiphytic on Codium. Cells multinucleate.

**Reproduction.** Gametophytes dioecious. Procarps subapical on short lateral branches, the last 3 cells shorter, with 2 periaxial cells, one sterile and the other (supporting) cell bearing a sterile apical cell and a lateral carpogonial branch; the single auxiliary cell divides post-fertilization to produce short gonimoblast filaments with terminal ovoid carposporangia, the 2–4 gonimolobes each with a gelatinous sheath, fusion cell absent, inner and outer involucral filaments absent. Spermatangial heads ovoid, borne on unicellular pedicels on the erect or prostrate filaments. Tetrasporangia are terminal on unicellular pedicels, lateral on the erect filaments, tetrahedrally divided, often appearing cruciate.

**Type species:** _L. epicodii_ Gordon 1972: 127.

A genus of 2 species, the type and _L. capense_ Stegenga (1984, p. 357) from South Africa. _Lomathamnion_ is distinct from other genera of the tribe in having only 2 periaxial cells, as well as having only a single auxiliary cell, lacking a fusion cell, and lacking inner and outer involucres around the carposporophyte.


**FIG. 101**

_Thallus_ dark red-brown, tufted and spreading, 2–4 mm high, with prostrate filaments and erect, simple to sparingly branched, branches (Fig. 101A), 1–4 branches from each cell of prostrate filaments, tapering slightly above. Prostrate filaments attached by digitate haptera; epiphytic on Codium galeatum. Structure. Prostrate filaments 30–45 µm in diameter, cells L/D 1–4; erect filaments with median cells 30–40 µm in diameter, cells L/D 2–6, terminal cells often hair-like. Cells multinucleate; rhodoplasts discoid.

**Reproduction.** Gametophytes dioecious. Female axes (3-)4 (-12) cells long, borne laterally on lower cells of erect filaments or occasionally on the prostrate axes, with the last 3 cells short and the subhypogenous cell 2–3 times as long. Subapical cell bearing 2 periaxial cells, one sterile and one (the supporting cell) with a sterile apical cell and a lateral carpogonial branch (Fig. 101B). Post-fertilization the supporting cell cuts off an auxiliary cell which produces 2–4 gonimoblast cells each dividing to form 3–4 cells which either directly or on subdivision become ovoid carposporangia (Fig. 101C) 25–50 µm in diameter. Very little fusion occurs between cells of the procarp or gonimoblast, and a fusion cell is not produced. The apical cell, sterile periaxial cell, and sterile cell on the supporting cell all normally remain undivided. Spermatangial heads (Fig. 101D, E) ovoid, 40–55 µm in diameter, borne on unicellular pedicels laterally on lower cells of erect filaments or directly on prostrate filaments. Tetrasporangia (Fig. 101A) terminal on unicellular pedicels produced laterally on erect filaments, single or in opposite pairs, 40–50 µm in diameter, tetrahedrally divided but often almost cruciate arranged.

**Type from** Seal Bay, Kangaroo I., S. Aust., epiphytic on Codium galeatum (Gordon, 31.x.1966); holotype and isotypes in AD, A30961.
**Lomatizamnion**

**SPERMOTHAMNIEAE 217**

**Distribution**: Dongara, W. Aust., to Phillip I., Victoria.


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**Fig. 101. Lomatizamnion epicodii** (A, B, AD, A20909; C, AD, A28897; D, E, AD, A30961). A. Prostrate and erect axes with tetrasporangia. B. Mature procarpin system. C. Young carposporophyte. D. Prostrate and erect axes, with spermatangial heads. E. Longitudinal section of a spermatangial head. (All as in Gordon 1972, courtesy of Aust. J. Bot.)
Genus PTILOTHAMNION Thuret ex Le Jolis 1863: 118

*Thallus* usually minute, with prostrate filaments usually attached by digitate haptera, and erect, sparsely branched to pinnate, filaments or axes; most species epiphytic. Cells multinucleate.

*Reproduction.* Gametophytes monoecious or dioecious. Procarps subapical, with the upper two axial cells small and the subhypogenous cell larger, with 2 sterile periaxial cells and a supporting cell with a sterile apical cell and a lateral carpogonial branch. Auxiliary cell producing 2-5 gonimoblast initials which divide 1–3 times, the terminal or most cells becoming carposporangia; fusion cell slight to absent. Sterile procarp cells not dividing, but the hypogenous cell bearing, before or after fertilization, two branchlets which come to surround the carposporophyte. Spermatangial heads ovoid to elongate, sessile or pedicellate, terminal or lateral on erect filaments, composed of central axial cells, periaxial initials and surface spermatangia.

Tetrasporangia sessile or pedicellate on erect filaments, tetratedrally or polyhedrally divided.

**Type species:** *P. plumae* (Dillwyn) Thuret in Le Jolis 1863: 118.

A genus of 6–8 species (see Gordon 1972, pp 129, 135), with 2 species on southern Australian coasts, characterised by a female axis with 2 small cells, an outer involucre of two opposite branchlets from the larger hypogenous cell, no inner involucre from the sterile cells of the procarp, a single auxiliary cell, and the terminal or all cells of the gonimoblast becoming carposporangia.

**KEY TO SPECIES OF PTILOTHAMNION**

1. Erect filaments 15–20 μm in diameter, prostrate filaments 15–30 (-40) μm in diameter; involucral filaments developing on hypogenous cell after fertilization; carposporangia in successive gonimolobes; spermatangial heads terminal; tetrasporangia pedicellate; epiphytic on *Zonaria.* ................................................................. 1. *P. schmitzii*

1. Erect filaments 30–60 μm in diameter, prostrate filaments 25–35 μm in diameter; involucral filaments present on hypogenous cell before fertilization; carposporangia in gonimolobes developing simultaneously; spermatangial heads lateral, sessile; tetrasporangia sessile; epiphytic on *Lenormandia* ........................................... 2. *P. subsimplex*


**FIG. 102A–F**

*Thallus* (Fig. 102A) 0.5–2 mm high, with branched prostrate filaments bearing sparingly branched erect filaments, on the surface or entangled with basal stolose rhizoids of the host. Epiphytic on *Zonaria* (or *Homoeostrichus*), or epizoic, attached by appressed or digitate haptera. *Structure.* Prostrate filaments 15–30 (-40) μm in diameter, cells L/D 1.5–4.5, erect filaments tapering only slightly, 15–20 μm in diameter, cells L/D 2.5–4.5. Cells multinucleate; rhodoplasts discoid.

*Reproduction.* Gametophytes monoecious or dioecious. Female axes (Fig. 102B) apical on erect filaments, with the last 2 cells comparatively short and the hypogenous cell longer and similar to vegetative cells. Procarps on the subapical cell, with two sterile periaxial cells and a supporting cell with a terminal sterile cell and a lateral carpogonial branch with cells of equal size. Post-fertilization fusion of carpogonial branch cells occurs but little other fusion and no fusion cell is formed. The auxiliary cell cuts off cells which form gonimolobes (Fig. 102C) of varying ages, with the cells of one gonimolobe maturing simultaneously into angular carposporangia 20–25 μm across. Sterile cells of the procarp do not divide, but the hypogenous cell produces, after fertilization, two involucral branchlets (Fig. 102C) which branch and curve around the carposporophyte. Spermatangial heads (Fig. 102D, E) occur terminally on erect filaments, slightly ovoid and 30–35 μm in diameter.
Tetrasporangia (Fig. 102F) occur on 1–few-celled pedicels on erect filaments, often forming unilateral series on upper branches, 40–45 μm in diameter, tetrahedrally divided.

**Type** from Bay of Islands, New Zealand; probably lost.

**Distribution:** North I., New Zealand.

In Australia, Eucla, W. Aust., to Flinders, Vic., and around Tasmania.


*P. schmitzii* is commonly found on various species of *Zonaria*, though often overlooked; it also occurs on ascidians. It differs from *P. subsimplex* in having all cells of the carpogonial branch of similar size, all carposporangia in a gonimolobe maturing together, and in the involucral branchlets on the hypogenous cell developing only after fertilization.


**FIG. 102G–K**

Thallus 1–2 mm high, with prostrate filaments bearing sparingly branched erect filaments (Fig. 102G). Attachment by digitate haptera; epiphytic on *Lenormandia*. Structure. Prostrate filaments 25–35 μm in diameter, cells L/D 2–3.5, erect filaments 30–60 μm in diameter and cells L/D 1–3.5, terminal cell obtuse. Cells multinucleate; rhodoplasts discoid.

Reproduction. Gametophytes monoecious or dioecious. Female axes (Fig. 102H) terminating erect filaments, the last 2 cells short, the hypogenous cell larger and bearing 2 lateral branchlets of 1–2 cells before fertilization. Procarps (Fig. 102H) on the subapical cell, with 2 sterile periaxial cells and the supporting cell with a terminal sterile cell and a lateral carpogonial branch with the third and fourth cells larger. Post-fertilization the cells of the carpogonial branch fuse, but only slight further fusion occurs. The auxiliary cell cuts off 2–5 gonimoblast initials which divide to form carposporangia 30–35 μm in diameter, in gonimolobes (Fig. 102 I) which mature simultaneously. Sterile procarp cells do not divide, but the involucral branchlets (Fig. 102 I) on the hypogenous cell branch and completely encircle the mature carposporophyte. Spermatangial heads (Fig. 102) are lateral and sessile on upper cells of the erect filaments, ovoid, 30–40 μm in diameter.

Tetrasporangia (Fig. 102K) are sessile on upper cells of erect filaments, often unilateral, ovoid, 50–65 μm in diameter, tetrahedrally (sometimes appearing decussately) divided.

**Type** from Pennington Bay, Kangaroo I., S. Aust., on *Lenormandia* in sublittoral pools (Womersley, 30. i. 1946); holotype in AD, A32150.

**Distribution:** Only known in southern Australia from the type.


**Genus INTERTHAMNION** Gordon 1972: 135

Thallus with prostrate filaments bearing erect, branched filaments 1–2 mm high, prostrate filaments attached by digitate haptera; cortication absent; cells uninucleate.
Reproduction. Gametophytes dioecious. Female axes terminal on erect axes with the last two cells small and the hypogenous cell larger. Procarp on the subapical cell, with 3 periaxial cells, one sterile, one fertile (with an auxiliary cell) and the supporting cell with a terminal sterile cell and a lateral carpogonial branch. Auxiliary cells 2 per procarp, each producing a gonimolobe with terminal carposporangia. Sterile procarps producing post-fertilization 3 small groups of 3–5 cells each; hypogenous cell producing post-fertilization 4 outer involucral branchlets. Spermatangial heads ovoid, sessile, usually unilateral and adaxial on erect axes. Tetrasporangia pedicellate, on clustered branchlets lateral on erect axes, with small involucral branchlets, tetrahedrally divided.

Type (and only) species: I. attenuatum Gordon 1972: 137, fig. 44.

Interthamnion is most closely related to Spermothamnion, differing in having a relatively elongate hypogenous cell producing 4 post-fertilization laterals, and without a distinct fusion cell; Spermothamnion also has no division of the sterile cells of the procarp.

Interthamnion attenuatum Gordon 1972: 137, fig. 44.

**FIG. 103**

Thallus (Fig. 103A, E) 1–2 mm high, with prostrate filaments producing erect, mostly unilaterally and abaxially (occasionally oppositely) branched, filaments, tapering considerably near their apices. Prostrate filaments attached by digitate haptera; epiphytic on Zonaria. Structure. Prostrate filaments 35–60 μm in diameter, cells L/D 3–9, erect filaments tapering from lower cells 20–60 μm in diameter and L/D 2–5 to upper cells 15–25 μm in diameter and L/D 3–7. Cells multinucleate; rhodoplasts discoid.

Reproduction. Gametophytes dioecious. Female axes (Fig. 103B) terminal, 5–7 cells long with the last 2 cells short, the hypogenous cell larger. The subapical cell bearing three periaxial cells, one sterile, one fertile (producing an auxiliary cell), and the supporting cell with a terminal sterile cell and lateral carpogonial branch. Fusion cell slight, involving both auxiliary cells, with short gonimoblast filaments bearing terminal ovoid to pyriform carposporangia (Fig. 103C) 30–35 μm in diameter. The sterile cells of the procarp produce post-fertilization, 3 small groups each of 3–5 cells and the hypogenous cell bears 4 cells at fertilization which later produce outer involucral filaments (Fig. 103C) around the carposporophyte. Spermatangial heads (Fig. 103D) borne unilaterally on erect branches, pedicellate, ovoid, 25–30 μm in diameter.

Tetrasporangia (Fig. 103E) pedicellate, on laterals of erect branches, with other small branches developing from the basal cell(s) forming a cluster, ovoid, 60–80 μm in diameter, tetrahedrally divided.

Type from Aldinga, S. Aust., on Zonaria spiralis in upper sublittoral pools (Womersley, 11.x.1965); holotype in AD, A29616.

Distribution. Only known from the type specimen and from SE Tasmania.

Known specimens: Arch Rock, E of Ninepin Point, SE Tas., on Zonaria, 8–12 m deep (Barrett, 23.x.1994; AD, A63960). Bruny I. (opposite Gordon), Tas., on Z. angustata, 2–3 m deep (Brown, 10.x.1986; AD, A57825).

Genus SPERMOTHAMNION Areschoug 1847: 334

Thallus with prostrate filaments attached by digitate haptera, and erect, slightly to moderately and irregularly branched filaments, epilithic or epiphytic. Cells multinucleate.

Reproduction. Gametophytes usually dioecious. Procarps subapical on erect filaments, with the upper 3 cells smaller and the subhypogenous cell larger, the subapical cell bearing 3 periaxial cells, one sterile, one fertile and producing an auxiliary cell, and the supporting cell with a sterile apical cell and a lateral carpogonial branch. Fusion cell involving both auxiliary cells and the hypogenous cell, becoming 2-armed with two gonimoblast groups with terminal
carposporangia. Sterile procarp cells not dividing further but the subhypogenous cell usually bearing 4 outer involucral branchlets. Spermatangial heads sessile or pedicellate, ovoid, on upper cells of erect filaments.

Tetrasporangia terminal on short pedicels, becoming clustered, lateral on erect filaments, tetrahedrally divided.

Fig. 103. *Intrathamnion attenuatum* (AD, A29616). A. Thallus with prostrate and erect axes. B. Procarp just post-fertilization, with disconnected trichogyne. C. Mature carposporophyte, with carposporangia and involucral branches from hypogenous cell. D. Longitudinal section of spermatangial head. E. Erect axes bearing branchlets with tetrasporangia. (All as in Gordon 1972, courtesy of Aust. J. Bot.)
**Spermothamnion**

Type species: *S. turneri* (Roth) Areschoug 1847: 334 [= *S. repens* (Dillwyn) Rosenvinge 1924: 298].

A genus of 20–30 recorded species (Gordon 1972, p. 119), but many will probably be placed in other genera when their sexual reproduction is known.

*Spermothamnion* is characterised by the prominent fusion cell incorporating both auxiliary cells and the hypogenous cell, by the lack of an inner involucre from sterile procarp cells, and the presence of outer involucral filaments from the subhypogenous cell.

Two species occur on southern Australian coasts. A third species, *S. miniatum* Huisman (1985), occurs on N.S.W. and Western Australian coasts, and differs from other species in having involucral filaments only from the axial cell below the subhypogenous cell, the female axis being 4 cells long. Other epilithic species in AD cannot be placed in the absence of female plants, but such tufts 1–3 cm high are not uncommon.

**KEY TO SPECIES OF SPERMOTHAMNION**

1. Thallus 1–1.5 mm high, irregularly branched, prostrate filaments 20–35 µm in diameter, erect filaments 20–55 µm in diameter, epiphytic on *Xiphophora chondrophylla* ...
   1. *S. pinnatum*

1. Thallus 1–3 cm high, sparingly and irregularly branched, prostrate filaments 50–100 µm in diameter, erect filaments 65–85 µm in diameter, epilithic, often in sand ...
   2. *S. cymosum*

1. *Spermothamnion pinnatum* Gordon 1972: 114, figs 37, 38A–D.
   *Callithamnion turneri* sensu Sonder 1881: 11.
   *Callithamnion turneri* var. *repens* sensu Harvey 1859b: 334.

**FIG. 104A–F**

*Thallus* (Fig. 104A) 0.5–1.5 mm high, with irregularly branched prostrate filaments producing ascending to erect filaments, usually from each cell, irregularly subdichotomously branched. Prostrate filaments attached by digitate haptera; epiphytic on *Xiphophora chondrophylla*. **Structure.** Prostrate filaments 20–45 µm in diameter, cells L/D 2–3; erect filaments 25–55 µm in diameter, cells L/D 3.5–6, tapering only slightly. Cells multinucleate; rhodoplasts discoid.

**Reproduction.** Gametophytes dioecious. Female axes (Fig. 104B) with 3 small terminal cells, the subapical cell with 3 periaxial cells, one sterile, one fertile producing an auxiliary cell, and the supporting cell with a sterile apical cell and a lateral carpogonial branch. Post-fertilization the two auxiliary cells cut off gonimoblast cells and extensive fusion occurs (Fig. 104C) involving the hypogenous cell, the supporting and fertile periaxial cells, and lower gonimoblast cells with terminal carposporangia (Fig. 104C) 20–40 µm in diameter. The subhypogenous cell produces four, branched, outer involucral filaments (Fig. 104C). Spermatangial heads (Fig. 104D, E) are elongate, 30–40 µm in diameter and L/D 2.5–3.5, sessile on the adaxial side of erect filaments.

Tetrasporangia (Fig. 104A, F) are terminal on short 1 (-2) celled pedicels borne laterally on erect axes, 60–75 µm in diameter, tetrahedrally divided.

**Type** from Southport, Tas., on *Xiphophora chondrophylla* (Wollaston & Mitchell, 27 ii. 1964); holotype in AD, A27713.

**Distribution:** Antechamber Bay, Kangaroo I., S. Aust., to San Remo, Vic., and southern Tasmania.

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SPERMOTHAMNIEAE

Spermothamnion


S. pinnatum probably occurs on Xiphophora spp. throughout their range, especially in Tasmania.


**FIG. 104G**

Thallus (Fig. 104G) densely tufted, 2–4 cm high, with entangled, branched, prostrate filaments producing erect filaments which are sparingly and irregularly to subdichotomously branched. Prostrate filaments attached by digitate haptera; epilithic. Structure. Prostrate filaments 50–100 μm in diameter, cells L/D 5–10; erect filaments 60–85 μm in diameter, tapering only slightly, cells L/D 6–7. Cells multinucleate; rhodoplasts discoid.

Reproduction. Gametophytes unknown.

Tetrasporangia (Fig. 104G) terminal on short pedicels borne laterally on upper cells of erect axes, with further pedicels producing clusters, 50–70 μm in diameter, tetrahedrally (or with 8) divided.

Type from Middleton Bay, King George Sound, W. Aust., on sand-covered rocks; lectotype in Herb. Harvey; TCD (Alg. Aust. Exsicc. 524B); isotype in AD, A18288.

**Distribution:** Rottnest I. to King George Sound, W. Aust., and Vivonne Bay, Kangaroo I., S. Australia.

Lord Howe I.

**Selected specimens:** Vivonne Bay, Kangaroo I., S. Aust., low eulittoral in bay near jetty (Womersley, 30.1.1956; AD, A20061, A20338).

Placement of S. cymosum in Spermothamnion is uncertain in the absence of female plants.

**Tribe RADIATHAMNIEAE** Gordon-Mills & Kraft 1981: 129 by H.B.S. Womersley

Thallus small, epiphytic, eocorticato, attached by a single basal cell or a pectinate holdfast, with a curved primary axis, each cell producing unilaterally secondary branches on the convex side, branches irregularly alternately or oppositely branched with some secondary axes branching as the primary axis; terminal cells rounded or becoming hair-like and caducous; gland cells absent. Cells uninucleate.

Life History triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes dioecious (known mainly in Radiathamnion). Carpogonial branches formed on basal cells of short lateral branchlets on lateral branches, with the auxiliary cell fusing with the fertile axial cell and producing three gonimolobes successively. Spermatangia on elongate heads borne mostly in pairs on cells of laterals, with the spermatangia borne directly on the fertile axial cells, or possibly borne directly on short branchlets.

Tetrasporangia borne on small-celled branchlets on lateral branches, sessile, tetrahedrally divided.
The Radiathamnieae was based on the monotypic genus *Radiathamnon*, distinguished by its vegetative morphology with curved main axes bearing unilaterally laterals from the convex side, this pattern being repeated in lesser branchings. The genus *Ochmapexus*, based on *Callithamnion minimum* Harvey, is here added to the tribe since it has the same basic morphology; sexual reproduction however is not well known (see below). The two genera differ clearly in their hosts, attachment, and in frond details.

**KEY TO GENERA OF RADIATHAMNIEAE**

1. Epiphytic in apical pits of * Laurencia* spp.; attachment by a single basal cell; branchlets alternate on laterals, tapering to hair-like ends ............................... RADIATHAMNION
1. Epiphytic on the surface of *Caulerpa*, *Halopteris* and occasionally other algae; attachment by a distinctive pectinate multicellular holdfast; branchlets opposite or alternate ................................................................. OCHMAPEXUS

**Genus RADIATHAMNION** Gordon-Mills & Kraft 1981: 129

*Thallus* small, epiphytic in the apical pits of * Laurencia* spp., attached by a single basal cell, with a curved primary axis bearing unilaterally secondary branches on the convex side, branches irregularly branched and tapering to hair-like, often caducous, ends. Cells uninucleate. 

*Reproduction.* Gametophytes dioecious. Procarps borne on the basal cell of 2–3-celled laterals, with a 4-celled carpogonial branch; post-fertilization the auxiliary (or supporting) cell fuses with the axial cell and produces a terminal and usually 2 lateral gonimoblasts, surrounded by involucral branchlets from lower axial cells. Spermatangial heads elongate, often in pairs from branchlet cells, with spermatangia cut off directly from axial cells of the heads. 

Tetrasporangia lateral on small-celled branchlets on the lateral branches, sessile, tetrahedrally divided.


**FIGS 105, 107H, 1**

*Thallus* (Fig. 105A) 1–2.5 mm high, red, growing from the apical pit of * Laurencia* spp., with a single prominent basal cell partly within the host tissue, producing a curved or arched main branch (Fig. 105A) 15–25 cells long, with most cells bearing unilaterally a single lateral branch on the convex side; branching dense to open, with laterals subdi- or trichotomously branched, the ends tapering to long hair-like, often caducous, ends. Epiphytic on various * Laurencia* species under moderate to rough-water conditions. 

*Structure.* Basal cell ovoid, 40–70 μm in diameter, cells of primary axis 25–90 μm in diameter and L/D 1–1.5, tapering slightly above, cells of lateral branches 17–40 (-80) μm in diameter and L/D 3.5–11 (often with rows of 1–3 swollen isodiametric cells), decreasing to hair-like cells 8–12 μm in diameter and L/D 10–22. Cells uninucleate; rhodoplasts discoid to elongate.

*Reproduction.* Gametophytes dioecious. Procarps (Fig. 107H) borne on small-celled laterals on the secondary and tertiary branches, with the fourth or fifth subapical cell producing a 2–3 celled filament (terminal cell hair like) with the basal supporting cell bearing a 4-celled carpogonial branch. Post-fertilization the supporting cell may or may not divide to form an auxiliary cell, which produces a terminal and usually 2 lateral gonimoblasts (Fig. 105 B) 100–250 μm across, with ovoid to angular carposporangia 10–18 μm across; a basal fusion cell develops (Fig. 107 I) and several involucral branchlets develop from 1 or 2 cells below the carposporophyte. Spermatangia (Fig. 105C,D) develop on elongate heads 10–12 μm in diameter and L/D 2.5–4.5, occurring mostly in pairs on small-celled branchlets, each with 7–11 axial cells most of which cut off directly 2–4 spermatangia.

Tetrasporangia (Fig. 105E) occur laterally (often unilaterally) on small-celled pectinate branchlets on laterals, often alongside elongate unicells, sessile, slightly ovoid, 35–45 μm in diameter, tetrahedrally, cruciately or decussately divided.
Fig. 105. Radiathamnion speleotis (A, D, E, AD, A52056; B, AD, A42929; C, MELU, K6666). A. Thallus with uniaxial branches on convex side of main axis, and tetrasporangial branchlets. B. Branch with carpogonial branchlets from lower cells. C. Branches with spermatial heads. D. Branches with elongate spermatidial heads, axial cells producing spermatia directly. E. Tetrasporangial branchlets. (C, by G.T. Kraft.)
**Ochmapexus**

Type from Flinders, Westernport Bay, Vic., on *Laurencia filiformis f. heteroclada*, 1–2 m deep on jetty piles (*Kraft & Ricker, 9.v.1978*); holotype in MELU, K6666; isotypes in MELU, AD and UC.

Distribution: Marino, S. Aust., to Flinders, Victoria.


**Genus OCHMAPEXUS** Womersley, gen. nov.

Thallus small, epiphytic on *Caulerpa longifolia* and several other algae or epizoic, attached by complanately branched, pectinate, multicellular holdfasts, with a curved primary axis bearing unilaterally secondary branches on the convex side, branches oppositely or alternately branched, tapering slightly; lesser branches often also unilaterally branched. Cells uninucleate.

Reproduction. Female thalli unknown*. Male thalli doubtfully known; possible spermatangia cut off from cells of short lateral branchlets borne unilaterally on upper branches. Tetrasporangia borne on short lateral branchlets, first terminally and then laterally or in opposite pairs, sessile, tetrahedrally divided.

Thallus parvus, epiphyticus in *Caulerpa longifolia* et in aliquot aliis algis, affixus per haptera complanate ramosa multicellularia, cum axe curvato primario ferente unilaterale ramos secundarios in latere convexo; rami oppositae vel alternate ramosae, exigu decrecentes; rami minores saepe idem unilaterale ramosae. Cellulae gliadi absentes. Cellulae uninnucleatae.

Reproductio. Thalli feminei ignoti. Thalli masculini dubie noti; spermatangia forte abscissa e cellulis ramulorum verticillatorum brevium lateraliumque unilaterali in ramis superioribus.

Tetrasporangia in ramulis brevibus lateralibusque primo terminaliter, et deinde laterali ter vel in paribus oppositis, sessilia, tetraedrice divisa.

Type (and only) species: *O. minimus* (Harvey)Womersley, *comb. nov.*

*Ochmapexus* is named for the distinctive holdfasts, ochma referring to holdfast and pexus to the comb-like arrangement. Although sexual plants are little known, *Ochmapexus* agrees in general morphology with *Radiathamnion* but differs in hosts, in basal attachment, and in thallus details.

**Ochmapexus minimus** (Harvey)Womersley, *comb. nov.*

*Callithamnion minimum* Harvey 1863, synop.: Iv. Sonder 1881: 11.

**FIG. 106**

Thallus (Fig. 106A, B) medium to dark red, 500–1500 μm high, complanately branched with distinctive pectinate, adherent and non-adherent, holdfasts; epiphytic, mainly on *Caulerpa longifolia*. Structure. Main axes curved to straight (Fig. 106A), lateral branches often unilateral on the upper side of the curved axis (Fig. 106B), axial and lateral branch cells bearing a single or often two opposite branchlets (Fig. 106A, B), simple or similarly branched. Axial cells 27–45 μm in diameter and L/D 1.2–1.8, basally shorter, cells of laterals decreasing to 14–20 μm in diameter and L/D 1.2–2 in mid thallus, then to 8–12 μm in diameter and L/D (1-) 2–4 in apical cells of branchlets. Holdfast (Fig. 106C) 80–180 μm across, with two rows of isodiametric cells from the basal axial cell and lying in the plane of the thallus, each cell bearing an elongate cell (with a separate sheath) which divides (occasionally to 2–3 cells) especially on contact with the host and adheres; unattached holdfasts occur frequently on upper branches of the thallus. Cells uninucleate; rhodoplasts elongate to ribbon like, few per cell.

Reproduction. Gametophytes little known.* Possible spermatangial development (Fig. 106B, D) consists of short, branched, rows of smaller isodiametric cells 3–6 μm across on upper thallus cells, but one case also with tetrasporangia.

* AD, A67940, from Marion Bay, Yorke Pen., S. Aust., on *Cystophora monilifera*, drift (*Womersley, 9. x. 1998*) shows carpogonial branches on the basal cells of branches of the laterals, but no later stages.
Tetrasporangia (Fig. 106E, F) on short branchlets, first terminal and with further potential tetrasporangia developing singly or in opposite pairs from 1–2 cells below the mature sporangium, sessile, subspherical to slightly ovoid, 21–34 μm in diameter, tetrahedrally divided.

Type from Port Fairy, Vic., on Caulerpa longifolia (Harvey, Alg. Aust. Exsicc. 525D); lectotype sheet in Herb. Harvey, TCD.

Distribution: Pennington Bay, Kangaroo I., S. Aust., to Gabo I., Vic., and SE Tasmania.


O. minimus occurs particularly on Caulerpa longifolia where vast numbers of plants may be present, and is also known on a variety of other hosts. Most plants are sterile, only few tetrasporangial and sexual thalli being known.

Callithamnion minimum was recorded from New Zealand, epiphytic on Caulerpa brownii, by Adams (1994, p. 250), but her description does not agree with the Australian species.

Tribe CALLITHAMNIEAE Schmitz 1889: 450

by H.B.S. Womersley & E.M. Wollaston

Thallus much branched radially or distichously with a single lateral from each axial or branch cell (except for involucral branchlets from 1–2 cells below the carposporophyte), with determinate, branched, lateral branchlets which may develop into indeterminate laterals; apical cells inconspicuous or clear, dividing transversely; corteication absent or of appressed filaments within or external to the axial cell wall, or of loose rhizoids, with or without a hirsute outer layer of acrinaly orientated filaments; gland cells absent; cells uninucleate or multinucleate.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes usually dioecious, occasionally monoecious. Procarps on intercalary vegetative cells below the branch apices, single or in series a few cells apart, with two opposite periaxial cells, one (the supporting cell) cutting off the 4-celled carpogonial branch. Post-fertilization each periaxial cell cuts off an auxiliary cell and diploid nuclei from the fertilized carpogonium are transferred to each auxiliary cell which divides to form a chain of 3–4 cells, the upper of which develops rounded or furcate-lobed gonimolobes which appear twinned on the branchlets; sterile involucral filaments from cells below the procarp are present or absent. Spermatangial filaments occur on cells of the determinate lateral branchlets, forming one or a few small clusters on each cell, usually adaxial but often spreading around the cell; in some genera forming spermatangial heads.

Tetrasporangia (rarely octosporangia) sessile or pedicellate on cells of the determinate lateral branchlets, usually adaxial, tetrahedrally divided.

The Callithamnieae now includes 5 or 6 genera (Millar 1990, p. 403), of which Callithamnion (with multinucleate cells), from which Aglaothamnion (with uninucleate cells) is sometimes separated, Carpothamnion (see Wollaston 1992), and the new genus Hirsutithallia.
The separation of the first two genera on the basis of number of nuclei per cell is accepted by some authors (eg. Maggs & Hommersand 1993), but is not followed here since there appear to be no other morphological characters correlated with this.

The tribe is characterised by the position of procarps on intercalary vegetative cells, with two opposite periaxial (and auxiliary) cells which produce two (“twinned”) carposporophytes.

**KEY TO GENERA OF CALLITHAMNIEAE**

1. Branches ecorticate or with a slight cortex on lower axes of loose rhizoids or a thin layer of appressed filaments within the axial cell wall ....................... CALLITHAMNION

1. Branches moderately to heavily corticate from near the apices, cortex thick and pseudoparenchymatous or with an outer cortex of moderate to dense anticlinal, short, simple or branched filaments ................................................................. 2

2. Lower branches with an appressed rhizoidal cortex producing an outer cortical tomentum of short anticlinal filaments ...................... HIRSUTITHALLIA

2. Cortex dense and thick from close to apices, of entwined rhizoids becoming pseudoparenchymatous, surrounding a large celled axial filament .................. CARPOTHAMNION

**Genus CALLITHAMNION** Lyngbye 1819: 123

*Thallus* erect, 1–8 (-12) cm high, much branched spirally or alternate distichously, with indeterminate axes and main branches bearing determinate lateral branchlets, with single branchlets from each cell, apex of branches overtopped or not; lower axes corticated or not, cortication by loose rhizoids or appressed filaments; holdfast rhizoidal. Cells uninucleate or multinucleate.

*Reproduction.* Gametophytes usually dioecious, some monoecious. Procarps on intercalary cells below apices of branches, with a pair of opposite periaxial cells, one bearing a 4-celled carpogonial branch; sterile cells absent. Fertilized carpogonium usually dividing vertically and fusing via two connecting cells with each auxiliary cell cut off from both periaxial cells, each then producing a foot cell and upper cells giving rise to twinned carposporophytes which may be rounded or furcate-lobed and tapering. Involutral branchlets absent or present and arising from cell(s) below the procarp. Spermatangial clusters borne on cells of determinate branches, usually 1 or 2 adaxial clusters per cell.

Tetrasporangia sessile or pedicellate, usually one per cell, adaxial on cells of determinate branchlets, tetrahedrally divided.

*Lectotype species:* *C. corymbosum* (Smith)Lyngbye 1819: 125.

*Agalothamnion* was distinguished from *Callithamnion* by Feldmann-Mazoyer (1941, p. 451) by being uninucleate, whereas the latter is multinucleate. Other features used by Feldmann-Mazoyer, such as the form of the carposporophyte, have been found in both genera, and they are separated by some authors, but only on the number of nuclei per cell. Most southern Australian species are uninucleate, except *C. caulescens* which is very similar to *C. shepherdii*, and until other features can be correlated with the nuclear situation and molecular comparisons are done, it seems preferable not to separate the species in 2 genera.

Recognition of species of *Callithamnion* requires presence in each collection of all fertile stages. Collections of female material can be placed as the genus, but male or tetrasporangial specimens only are difficult to identify unless distinctive vegetatively; numerous such collections in AD have been omitted from this account and further species certainly occur on southern Australian coasts.

Identification of the species of *Callithamnion* on southern Australian coasts is restricted by lack of knowledge of the several species of this genus from Rottnest I, named by Harvey.
These include *C. flabelligerum*, *C. multifidum*, *C. crispulum*, *C. pusillum*, *C. scopula* and *C. debile*. Until these can be recollected, with female specimens, some names in current use must remain doubtful. Two other little known species are *C. longinode* Harvey (1863, synop.: liii); Sonder (1881, p. 10); De Toni (1903, p. 1340); Lucas (1909, p. 49), from Warrnambool, Vic., and *C. ovuligerum* Askenasy (1894, p. 16, pl. IV figs 19, 23, 24); De Toni (1903, p. 1340) and Lucas (1909, p. 49) from "Adelaide", S. Australia. Until these are recollected it is not possible to place them, but both are clearly not species of *Callithamnion*.

### Key to Species of *Callithamnion*

| 1. Branching essentially alternately distichous, at least on lesser branches. | 2. Axes and often branch bases with a closely adherent rhizoidal cortex. | 2. *C. pinnatum* |
| 1. Branching radial, not distichous. | 2. Axes without cortication or with loose, corticating rhizoids over the lower cells. | 3. *C. obtipum* |

| 3. Axial cells 70–120 µm in diameter, lower cells of branchlets 30–55 µm in diameter, about half that of the axial cells. | 1. *C. violaceum*. |  |
| 3. Axial cells 160–250 µm in diameter, lower cells of branchlets 40–55 µm in diameter, about 1/4 that of the axial cells. | 3. *C. obtipum* |

| 4. Most lower and/or mid axial cells long (L/D 4–15). | 5. Lower axes 90–130 µm in diameter, cells L/D 8–15; carposporophytes involucrate with branches from lower cells. | 4. *C. circinatum* |
| 4. Most lower and mid axial cells relatively short [L/D 1–4 (-6)]. | 5. Lower axes 45–75 µm in diameter, cells L/D 3–12; carposporophytes with or without involucral branchlets. | 6. *C. pseudobyssoides* |

| 5. Lateral branchlets tapering over 4–8 cells. Lower axes 90–130 µm in diameter, cells L/D 8–15; carposporophytes involucrate with branches from lower cells. | 5. Lateral branchlets tapering gradually over many cells. Lower axes 45–75 µm or 150–500 µm in diameter, cells L/D 3–12; carposporophytes with or without involucral branchlets. | 6. *C. circinatum* |
| 6. Lower axes 45–75 µm in diameter, ecoriculate, cells L/D (3–) 4–8 (–10); carposporophytes rounded and with irregular involucral branchlets from lower cells. | 6. Lower axes 150–500 µm in diameter, corticate by descending rhizoids within the cell wall, mid cells L/D 8–12; carposporophytes rounded, without involucral branchlets. | 7. *C. pseudobyssoides* |

| 7. Terminal branchlet cells 5–8 µm in diameter and L/D 1.5–2.5; cells multinucleate. | 7. Terminal branchlet cells 2.5–5 (–6.5) µm in diameter and L/D (3–) 4–10 (–12); cells uninnucleate. | 6. *C. caulescens* |
| 8. Lateral branchlets 40–65 µm in diameter basally, tapering to 20–30 µm at 3–4 cells below apices; carposporophytes rounded. | 8. Lateral branchlets 30–30 (–35) µm in diameter basally, tapering to 8–12 µm at 2–3 cells below apices; carposporophytes branched with tapering lobes. | 7. *C. shepherdii* |

| 9. Determinate branchlets not well defined, apical cells 3–6 µm in diameter and L/D 2–5, mid axial cells 30–40 µm in diameter and L/D 3–5. | 9. Determinate branchlets well defined, 200–400 µm and 5–10 cells long, apical cells 7–10 µm in diameter and L/D 1–2, mid axial cells 40–60 µm in diameter and L/D 2–3. | 9. *C. byssoides* |


| 10. *C. propebyssoides*. |
**Spongoclonium paradoxum** (Harvey) De Toni 1903: 1363. Lucas 1909: 50; 1927: 466, pl. 32; 1929a: 24. 

**FIGS 107A–D, 108**

**Thallus** (Fig. 108A) erect and spreading, grey-red to red-brown or red-violet, 2–6 cm high, densely tufted and often even-topped, with main axes bearing laterals for several orders. Branches more or less alternately distichous (Fig. 108F), ecoricate, with a prominent gelatinous sheath, lower filaments and pinnules usually unbranched; lower axes with loose descending rhizoids. Attachment by loose rhizoids; epilithic or on small mussels. **Structure.** Lower axes 70–120 (-300) μm in diameter, cells LID (2-) 3-6, lateral branchlets alternately distichous with lower cells 30-55 μm in diameter and LID 0.5-2-4, tapering to 25-35 μm in diameter and L/D 1–3 at 2–3 cells below their apices, ends of apical cells rounded. Cells uninucleate; rhodoplasts ovoid to ribbon-like.

**Reproduction.** Gametophytes dioecious. Procarps (Fig. 107A) borne on axial cells of the branches, with two periaxial cells one of which (the supporting cell) bears the 4-celled carpogonial branch; post-fertilization each periaxial cell cuts off an auxiliary cell (LOSB) and two rounded lobes (Figs 107B, 108C) (150-350 (-450) μm across) of carposporangia 25-35 μm in diameter. Spermatangia (Figs 106C, 107D) are borne in dense clusters on the upper side of (spreading all around) cells of the last two orders of the branchlets, each cluster with a single basal cell bearing 2–3 orders of smaller cells and terminal ovoid spermatangia 1.5–4 μm in diameter.

**Tetrasporangia** (Figs 107D, 108E, F) sessile and adaxial on lower cells of the ultimate branchlets, scattered or on each cell, subspherical to ovoid, 50-75 μm in diameter, tetrahedrally divided.

**Type** from Georgetown, Tas. (Harvey, Alg. Aust. Exsicc. 517); lectotype in Herb. Harvey, TCD.

**Distribution:** Robe, S. Aust., to Western Port, Vic. (Wilson), and around Tasmania.


The type specimen of *Callithamnion paradoxum* from Browns R., Tas. (near Kingston, S of Hobart), in Herb. Harvey, TCD, appears identical with that of *C. violaceum* (both are tetrasporangular). *Spongoclonium scoparium* J. Agardh, type from Western Port, Vic. (Wilson, 13.i.1892) in Herb. Agardh, TCD, is slightly thicker in the branches but otherwise agrees well with *C. violaceum*; the lectotype is tetrasporangular. *Callithamnion scoparium* Hooker (1847, p. 490, pl. 189 fig. III), from the Falkland Is, appears to be a quite distinct species. *Callithamnion violaceum* usually occurs just above low tide level and in pools at this level, occasionally in deep water. It is a dark red to red-violet colour and forms dense tufts.

2. **Callithamnion pinnatum** Womersley, nom. nov.

**Thamnocarpus griffithsioides** J. Agardh 1897: 34. De Toni 1903: 1520.

**Callithamnion griffithsioides** (J. Agardh) Kylin 1956: 398 [NON Sonder 1855: 512 (*Anotrichium griffithsioides*) and Solier in Kützing 1861: 22, pl. 66–f (a *Griffithsia*)].
Fig. 108. *Callithamnion violaceum* (A, B, AD, A55788; C, AD, A64198; D, E, AD, A16354). A. Habit. B. Base of twinned young carposporophytes. C. Branches with twinned carposporophytes. D. Branch with spermatangial clusters. E. Branches with tetrasporangia. F. Pinnate branch with adaxial tetrasporangia.
Callithamnion

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FIG. 109

Thallus (Fig. 109A) erect, red-brown, 3–8 cm high, with a main axis and lateral branches alternately distichous with 2–3 orders of branching, branchlets alternately pinnate (Fig. 109B), ecoricate above but developing an adherent rhizoidal cortex (Fig. 109B, C) of filaments arising from the basal cells of laterals and growing downwards within the wall sheath of axial cells. Attachment probably rhizoidal; probably epilithic. Structure. Lower axes 200–350 μm in diameter, axial cells 100–150 μm in diameter and L/D 1.5–3, adherent rhizoidal cells 15–25 μm in diameter and L/D 2–4 (-6); branchlet pinnules mostly simple (Fig. 109D), with lower cells 45–110 μm in diameter and L/D (1-) 1.5–2 (-3), tapering slightly to cells 35–55 μm in diameter and L/D 1.5–2 at 3–4 cells from their apices, then to small spinous end cells (often lost leaving a cell with a rounded end). Cells uninucleate(?); rhodoplasts discoid.

Reproduction. Carposporophytes with rounded lobes, carposporangia 20–30 μm across, with curved involucral branches from cells just below the carposporophyte. Spermatangia unknown. Tetrasporangia (Fig. 109D) on short pedicels on the pinnules, often 2–3 per pedicel, subspherical, 30–45 μm in diameter, tetrahedrally divided.

Type from Port Phillip Heads, Vic.; (Wilson, 5.ii.1890); lectotype in Herb. Agardh, LD, 20191.

Distribution: Known only from the type and Warrnambool, Vic.


C. pinnatum appears to be a rare but distinctive species, known from only 2 collections. The LD specimens are both tetrasporangial and AD, A22945 is cystocarpic, but carposporophytes have not been seen. The cells appear to be uninucleate, but confirmation of twinned supporting cells and carposporophytes is needed.

C. pinnatum shows some similarity to A. gallicum (Nageli) Halos (see Maggs & Hommersand 1993, p. 99, fig. 33) in its pinnate branching and corticated axes, but differs in having pedicellate tetrasporangia, shorter cells of the branchlets, and carposporophytes probably involucrate.

3. Callithamnion obstipum (Cowling, Kraft & West) Womersley, comb. nov.


Thallus (Fig. 110A) erect, medium red-brown, 1–2 cm high, distichously branched (Fig. 110E), with laterals for 2–3 orders, ecoricate throughout except for loose rhizoidal cortication over lowest few cells. Branchlets markedly slenderer than parent axes. Attachment by a rhizoidal holdfast; epilithic or on jetty piles. Structure. Lower axes 160–250 μm in diameter, cells with a thick wall, L/D 1–1.5 (-2); lateral branchlets prominently alternately distichous with ultimate filaments 6–14 cells long and unbranched, usually with an abaxial branch from the basal cell, lower cells 40–55 μm in diameter and L/D 2–3, tapering to 18–30 μm in diameter and L/D 2–3 at 3–4 cells below apices, then to smaller apical cells with rounded ends. Cells uninucleate; rhodoplasts discoid, ribbon-like in older cells and longitudinally aligned.

Reproduction. Gametophytes dioecious. Procarps borne on axial cells, with two periaxial cells one of which (the supporting cell) bears the 4-celled carposporangial branch; post-fertilization each periaxial cell cuts off an auxiliary cell (Fig. 110B) and 1 or 2 rounded lobes (Fig. 110C) 90–180 μm across of carposporangia 15–25 μm across; a loose involucre of branched filaments develops from 1 or 2 cells below the carposporophyte. Spermatangia (Fig. 110D) on small clusters on ultimate branches, 1–3 per parent cell, branched 2–3 times, spermatangia ovoid, 2–3 μm in diameter.

Tetrasporangia (Fig. 110E) sessile and adaxial on lower cells of the ultimate branchlets, ovoid, 35–55 μm in diameter, sub-decussately to tetrahedrally divided.

Type from Gloucester Reserve, Williamstown, Vic. on Mesophyllum, 3–5 m deep (Kraft & Saunders, 3.iii.1995); holotype in MELU, K10543.
Distribution: Port Lincoln, S. Aust., Williamstown, Victoria (probably to Gabo L, Vic.).


The recently described C. obstipum (as Aglaothamnion obstipum) by Cowling, Kraft & West (1998, p. (33), figs 2–11) is very closely related to A. feldmanniae Halos (1965, p. 126, figs

![Figure 110](image_url)  
*Fig. 110. Callithamnion obstipum (A, AD, A16407; B–E, AD, A58611). A. Habit. B. Young twinned gonimoblast filaments developing gonimolobes. C. Twinned carpogporophytes, each with 2 lobes. D. Young spermatangial branchlets. E. Pinnate branch with tetrasporangia.*
4–6), and may be within the variability of the latter. *A. obstipum* was considered to differ from *A. feldmanniae* in habit, in having prostrate axes, an abaxial branchlet on the basal cell of laterals, and in having tetrasporangia often borne in pairs on parent cells, as well as being characterised by flexing of the bearing cells of the spermatangial clusters. *A. obstipum* does appear to be a more robust species, with apical cells 10–16 µm in diameter, lower cells of laterals 22–45 µm in diameter, and mid to lower cells of main axes 35–120 µm in diameter, compared to 8–10 µm, 15–40 µm and 60–110 µm respectively in *A. feldmanniae* (as in Maggs & Hommersand 1993, p. 97 and slide from Milford Haven, Wales (AD, A67791, sent by C. Maggs).

The basal attachment may provide a minor difference, but the presence or not of an abaxial basal branch on the laterals and in pairing of tetrasporangia is variable in both species. The flexing of cells bearing spermatangial clusters seen in culture does not occur in the single field collection (AD, A58611 — see Fig. 110D) and may be unimportant. For the moment, *A. obstipum* is used rather than *A. feldmanniae*, but further collections and comparisons are clearly desirable.


Thallus (Fig. III A) erect, densely tufted, medium to dark red-brown, 4–12 cm high, ecorticate throughout, with much branched axes and main branches (Fig. III B) bearing radially lateral branchlets from each cell, usually positioned below the cross wall and often becoming further distant as the axial cells elongate; lower laterals usually with recurved branches (Fig. III C). Attachment by rhizoids from lower axial cells; epilithic, on solid substrate or epiphytic on *Heterozostera*. Structure. Lower and mid axes 90–130 µm in diameter, cells L/D 8–15 below, L/D 4–6 in mid thallus, decreasing to upper axial cells 50–80 µm in diameter and L/D (1−) 2–3. Lateral branchlets usually 8–12 cells long with 2–4 branches, tapering over 4–8 cells, lower cells 25–35 µm in diameter and L/D (1−) 2–3, decreasing to 15–20 µm in diameter and L/D 1–3 at 3–4 cells from tips, then tapering to apical cells 6–9 µm in basal diameter, pointed or with rounded ends. Cells uninucleate; rhodoplasts discoid, becoming ribbon like in older axial cells.

Reproduction. Gametophytes probably dioecious. Procarps frequent (often on each second cell) on axial cells near branch apices, with two periaxial cells one of which (the supporting cell) bears the 4-celled carpogonial branch; post-fertilization each periaxial cell cuts off an auxiliary cell (Fig. III D) and rounded groups (100–200 µm across) of carposporangia 25–35 µm in diameter; carposporophytes involucrate (Fig. III E) by simple branchlets from lower cells, *Spermatangia* unknown. Tetrasporangia (Fig. III F) usually adaxial on cells of the branchlets, sessile, subspherical, 90–100 µm in diameter, tetrahedrally divided.
Fig. 111. Callithamnion circinatum (A–C, E, AD, A57453; D, AD, A35021; F, AD, A46048). A. Habit. B. Branch systems. C. Lower branches with circinate lateral branchlets. D. Twinned carposporophytes on axial cell. E. Twinned (unequal) carposporophytes with involucral branchlets from lower cells. F. Branches with tetrasporangia.
Callithamnion

**Type** from Port Noarlunga, S. Aust., 19 m deep on tyre reef (Branden, 26.iii.1987); holotype in AD, A57453.

**Known specimens:** Elliston, S. Aust., 10–11 m deep in bay (Shepherd, 20.x.1969; AD, A35021). Off Crag Point, N Spencer Gulf, S. Aust., 15 m deep (Shepherd, 6.xi.1974; AD, A46048).

*C. circinnatum* appears to be a distinctive species, marked by the tapering determinate branchlets, lower axial cells usually with circinnate branchlets from lower axial cells, and involucral branchlets around the carposporophyte.

5. **Callithamnion pseudobyssoides** Crouan & Crouan 1867: 136.
   
   

**FIG. 112**

*Thallus* (Fig. 112A) erect, red-brown fading to grey, 5–15 mm high, densely tufted and much branched with several axes and laterals of several orders, radially branched, ecoricate throughout. Attachment by loose rhizoids; epilithic. **Structure.** Lower and mid axes 45–75 μm in diameter, cells L/D (3-) 4–8 (–10), lateral branchlets with lower cells 25–45 μm in diameter and L/D 2–4, tapering slightly to 20–30 μm in diameter and L/D 1.5–2 at 3–4 cells below apices, apical cells 10–14 μm in diameter and L/D 1–2, with rounded ends. Cells uninucleate; rhodoplasts discoid, ribbon like in larger cells. **Reproduction.** Gametophytes dioecious. Procarps borne on mid cells of the branchlets, with two periaxial cells one of which (the supporting cell) bears the horizontal 4-celled carpogonial branch; post fertilization each periaxial cell cuts off an auxiliary (Fig. 112B) cell which develops rounded lobes (Fig. 112A) 150–250 μm across; ovoid in diameter and L/D 1–2, with involucral branches from lower branch cells irregularly surrounding the carposporophyte. Spermatangial clusters (Fig. 112C, D) adaxial and profuse on cells of the branchlets, with a larger basal cell cutting off a spreading plate of cells which form initials bearing ovoid spermatangia 2–3 μm in diameter. 

Tetrasporangia (Fig. 112E) sessile and adaxial on cells of the ultimate branchlets, ovoid, 35–55 μm in diameter, tetrahedrally divided.

**Type** from Kervallon, France (Crouan); lectotype in LD.

**Distribution:** Europe.

In southern Australia from South West R. mouth, Kangaroo I., S. Aust.

**Selected specimens:** South West R. mouth, Kangaroo I., S. Aust., rear of reef (Womersley, 17.i.1965; AD, A28990).

The above collection agrees well with descriptions and illustrations of this European species (observed also by Dr Christine Maggs). It is possible that *C. debile* should be a synonym, though Harvey described *C. debile* as having upper distichous branching; however, this is not apparent in the type which appears to be irregularly radially branched throughout. Until fertile female specimens from Rottnest I. or nearby are available, *C. debile* cannot be confirmed as a synonym.

6. **Callithamnion caulescens** (J. Agardh)Womersley, **comb. nov.**


Fig. 112. Callithamnion pseudobryoides (AD, A28990). A. Frond with twinned carpocorophytes. B. Twinned supporting and auxiliary cells producing gonimoblasts. C. Branches with spermangia. D. Spermangial clusters. E. Branches with tetrasporangia.
**Callithamnion**

**FIG. 113**

Thallus (Figs 113A) erect, flaccid and spreading, medium red-brown, 2–6 cm high, densely tufted with several orders of branching grading gradually from lower corticated axes (Fig. 113C) to slender ultimate branchlets (Fig. 113B) in flat-topped clusters, radially branched throughout. Lesser branches irregularly branched from every cell, corticate, lower main branches and axes corticate by descending rhizoids, often spirally twisted around the axial cells, lying within the axial cell wall. Attachment by rhizoids; epilithic or epiphytic. Structure. Apical cells 5–8 μm in diameter and L/D 1.5–2.5, often with a terminal hair, 2–4 subapical cells of similar dimensions. Lower and mid axes, including cortication, 50–500 μm in diameter, cells L/D 8–12 (decreasing to 0.5–2 near the base), corticating rhizoids (8-) 15–25 μm in diameter with cells L/D 6–12. Lower ecorticate branch cells 50–80 μm in diameter and (2-) 3–6, decreasing gradually to 10–20 μm in diameter and L/D 2–3 (8-) at 3–4 cells from apices. Cells multinucleate; rhodoplasts discoid to elongate in small cells, ribbon like and longitudinally aligned in larger cells.

Reproduction. Gametophytes dioecious. Procarps borne on axial cells of the lesser branches, with two periauxial cells, one (the supporting cell) bearing a 4-celled carpogonial branch; post-fertilization each cuts off an auxiliary cell and rounded lobes (Fig. 113E) 180–250 μm across of carposporangia 25–35 μm in diameter; involucral branchlets absent. Spermatangia (Fig. 113D) borne on short branched filaments or clusters, often in series on successive cells.

Tetrasporangia (Fig. 113E, F) sessile on upper branchlets, scattered, ovoid to subspherical, 25–45 μm in diameter, tetrahedrally to decussate/d. Type from Tasmania (Gunn); lectotype in Herb. Agardh, LD, 18430.

**Distribution:** Ardrossan, S. Aust., to Port Phillip, Vic., and N Tasmania.


The type of var. caulescens J. Agardh is densely epiphytic on a filiform alga (a Gracilaria?); it was distinguished by Agardh by the decurrent corticating filaments within the wall sheath of axial cells, and differs from A. byssoides in having coarser axial cells and rounded carposporophyte lobes. Records of C. byssoides from Tasmania (eg. Dixon & Price 1981, p. 117) are probably based on var. caulescens, here recognised as a species.

7. **Callithamnion shepherdii** Womersley, sp. nov.

**FIGS 107E-C, 114**

Thallus (Fig. 114A, B) erect, flaccid and spreading, red-brown, 2–5 (-10) cm high, profusely branched with corticate upper and mid thallus grading from slender, ultimate, irregular branches (not flat-topped) to lower corticated axes. Attachment by rhizoids from base of axes; epilithic or epiphytic. Structure. Apical cells with rounded ends (pointed ends on some lower lateral branchlets) without terminal hairs, 2.5–5 (-6.5) μm in diameter and L/D (3-) 4–10 (-12), subapical cells 4–8 μm in diameter and L/D 4–8, increasing gradually (Fig. 114E, G) to mid thallus cells 10–25 (-60) μm in diameter and L/D 4–6 (-12), with broad sheaths, then to lower cells 200–450 μm in diameter (contents 35–60 μm in diameter) and L/D 1–2, with down-growing rhizoids developing within the broad gelatinous sheaths, from the basal cells of lateral and from the axial cells, and forming a complete cortical layer (Fig. 114C); rhizoids (3-) 5–12 μm in diameter, cells long. Cells uninucleate; rhodoplasts elongate, ribbon like in larger cells.

Reproduction. Gametophytes dioecious. Procarps borne on axial cells of lesser branches, with 2 periaxial cells, one becoming a 4-celled carpogonial branch (Fig. 107E). Post-fertilization...
Each produces an auxiliary cell (Fig. 107E) which develops gonimolobes (Fig. 107G, 114D) developing into irregularly rounded lobes (Fig. 114E) 80–300 μm across of ovoid carposporangia 10–20 μm in diameter; no involucre occurs. Spermatangia (Fig. 114F) borne on short branched filaments or clusters, often in series on successive cells.

Fig. 113. Callithamnion canescens (A39532). A. Habit. B. Branches. C. Cortication of lower axial cells. D. Branch with a procarp with twinned auxiliary cells. E. Twinned carposporophytes.
Tetrasporangia (Fig. 114G, H) sessile on upper branchlets, ovoid to sub-spherical, 25–35 μm in diameter, tetrahedrally to more or less decussately divided.

Thallus erectus, flaccidus, 2–5 (–10) cm altus, ramulosissimus, ecorticatus, supra et corticatus in axibus inferioribus. Affixus per rhizoidea e basi axium; epilithicus aut epiphyticus. Cellulae apicales plerumque finibus rotundatis, sine pilis, 2.5–5 (–6.5) μm diametro et L/D 4–8, cellulae in medio thallo 10–25 (–60) μm diametro et L/D 4–6 (–12), vaginis latis, cellulae inferiores 200–450 μm diametro (contenta 35–60 μm) et L/D 1–2, cum rhizoidea descendentibus intra vagina lata velut stratum completum corticale; rhizoidea (3–) 5–12 μm diametro. Cellulae uninucleatae; rhodoplasta elongata ad taeniformia.


Holotype from American R. inlet, Kangaroo I., S., Aust., 2–3m deep in channel (Kraft, 7.iv.1972; AD, A42399).


The species is named after Dr Scoresby Shepherd, who has contributed greatly to knowledge of our subtidal algae by his SCUBA diving activities. 
C. shepherdii is based on a female type specimen with tetrasporangial specimens known from the same locality. Male and tetrasporangial specimens are known from Waldegrave I., corresponding well in all vegetative features.

C. shepherdii is close to C. caulescens in most features, differing in the latter having multinucleate cells.

8. Callithamnion confertum Womersley, sp. nov.

FIG. 115

Thallus (Fig. 115A) erect, mid red-brown, 5–20 mm high, densely tufted with main axes (Fig. 115B) bearing prominent laterals with branchlets 0.5–1.5 mm long and 2–5 orders of branching, all radially branched and ecorticatus; some branchlets continue growth as laterals. Attachment by tufted rhizoids from the basal axial cells; epiphytic on Caulerpa brownii, Jania sp. and Laurencia sp. Structure. Lower and mid axes 100–180 (–240) μm in diameter, cells L/D 1.5–3, main laterals 60–90 μm in diameter, cells L/D 2.5–4, lateral branchlets (4–) 6–10 cells long, lower cells 40–65 μm in diameter and L/D 1.5–2.5, tapering to 20–30 μm in diameter and L/D 1–2 at 3–4 cells below their apices, apical cells 8–12 μm in diameter and L/D 1–2, ends rounded. Cells uninucleate; rhodoplasts discoid, ribbon like in larger cells.

Reproduction. Gametophytes probably dioecious. Procarps borne on mid cells of the young indeterminate axes, with two periaxial cells one of which (the supporting cell) bears the 4-celled carpogonial branch; post-fertilization each periaxial cell cuts off an auxiliary cell and forms a rounded gonimolobe (Fig. 115C) 100–220 (–360) μm across of carposporangia 15–35 μm in diameter; involucral branches arise from the axial cell below the carposporophyte. Spermatangia unknown. 

Tetrasporangia (Fig. 115D) borne adaxially on cells of the lateral branchlets, sessile, subspherical to ovoid, 40–55 μm in diameter, tetrahedrally divided.

Thallus erectus, 5–20mm altus, confertim caespitosus; axes principales, ferentes laterales prominentes cum ramulis 0.5–1.5 mm longis et 2–5 ordinibus ramificationis, omnes radiatim ramosos ecorticatosque; aliquot ramuli velut laterales etiam crescentes. Affixus per rhizoidea
Callithamnion caespitosa e cellulis basalibus axialibusque, epiphyticus in Caulerpa brownii, Jania sp. et Laurencia sp. Axes inferiores et medias 100–180 (240)μm diametro, cellulae L/D 1.5–3, laterales principales 60–90μm diametro, cellulae L/D 2.5–4, ramuli laterales (4–) 6–10 cellulas longi, cellulae inferiores 40–65μm diametro et L/D 1.5–2.5, contractae ad 20–30μm diametro et L/D 1–2 in 3–4 cellulis sub apices; cellulae apicales 8–12μm diametro et L/D 1–2, extremis rotundatis. Cellulae uninucleatae; rhodoplasta discoidea, taeniformes in cellulis maioribus.

Fig. 115. Callithamnion confertum (AD, A32685). A. Habit. B. Branch with carposporophytes. C. Branch with twinned carposporophytes. D. Branch with tetrasporangia.
Reproduction. Gametophyta probabiliter dioicia. Procarpia e cellulis axium iuvenum indeterminatorum portata, cum 2 cellulis pericentralibus; alter (cellula sustinens) ramum 4 cellularem carpogonialem ferens; post fecundationem quaeque cellula pericentralis cellulam auxiliarem abscindens et faciens gonimolobum rotundatum 100-220 (-360) \( \mu m \) latum carposporangiofum 15-35 \( \mu m \) diametro; ramuli involucrales e cellula axiali sub carposporophyta orti. Spermatangia ignota.

Tetrasporangia adaxialiter in cellulis ramulorum lateralium portata, sessilia, subsphericalia ad ovoidea, 40–55 \( \mu m \) diametro, tetraedrice divisa.

Type from Robe, S. Aust., on Caulerpa brownii in upper sublittoral pools (Womersley, 9 ix.1968); holotype in AD, A32685.

Possible specimens: Safety Cove, Port Arthur, Tas., on Laurencia and Jania, 0-1 m deep (Brown & Kenchington, 16.x.1986; AD, A57738 and A57739 resp.).

Callithamnion confertum appears distinct from other Australian species which have been referred to Callithamnion, but further collections and comparisons with other species are needed. It is named after the congested branching of the laterals.


FIG. 116

Thallus (Figs 116A) erect and spreading, medium red-brown, tufted, 5–15 mm high, main axes weakly defined apically, clearer below, bearing radially shorter lateral branchlets which are branched 2–4 times, ecorticate. Attachment by spreading rhizoids from basal cells of erect axes (Fig. 116B), sometimes producing further erect axes; epiphytic on gelatinous Rhodophyta (e.g. Gloiosaccion, Platomafoliosa, Tsengia comosa).

Structure. Apical cells 3–6 \( \mu m \) in diameter and L/D 2–5, ends of apical cells rounded, increasing to 8–12 \( \mu m \) in diameter and L/D 2–4 at 2–3 cells below their apices, increasing gradually to 30–40 \( \mu m \) and L/D 3–5 in mid cells and in lower axes 80–120 \( \mu m \) in diameter, cells L/D (1–) 1.5–2 (–6), with thick gelatinous walls; lateral branchlets branched 3–4 times, lower cells 20–30 (–35) \( \mu m \) in diameter and L/D 2–3 (–4). Cells uninucleate; rhodoplasts discoid to elongate.

Reproduction. Gametophytes dioecious. Procarps borne on mid cells of the upper axes or main branches, with two periauxial cells one of which (the supporting cell) bears the 4-celled carpogonial branch; post-fertilization each periauxial cell cuts off an auxiliary cell which produces a branched carposporophyte (Fig. 116C, D) with tapering lobes of ovoid carposporangia (10–) 15–30 \( \mu m \) in diameter. Spermatangia (Fig. 116E) borne on short branched filaments 3–4 cells long, ovoid, 1.5–3 \( \mu m \) in diameter.

Tetrasporangia (Figs 116F) sessile on cells of the lateral branchlets, subspherical, 25–45 \( \mu m \) in diameter, tetrahedrally to decussately divided.

Type from Cornwall, England (Arnott); lectotype in TCD (L’Hardy-Halos & Rueness 1990, p. 353). Distribution: Europe.

In southern Australia, from Esperance, W. Aust., to Port MacDonnell, S. Aust.

These specimens appear to agree well with *C. byssoides* in Europe; all collections have been on gelatinous red algae. However, interfertility should be checked following the study of L’Hardy-Halos & Rueness (1990).

10. **Callithamnion propebyssoides** Womersley, *sp. nov*  

**FIG. 117**

*Thallus* (Fig. 117A) 1–2 cm high, medium red-brown, erect and tufted with indeterminate axes bearing radially shorter lateral branches themselves with spirally arranged determinate branchlets (Fig. 117B), ecorticate except possible slight rhizoidal cortication near the base of axes. Attachment by rhizoids from basal cells of erect axes; epiphytic (on *Caulocystis*).  

**Structure.** Apices of axes inconspicuous, apical cells of branches 6–9 µm in diameter and L/D 1–1.5 (2), subapical cells gradually increasing to 10–15 µm in diameter and L/D 1–1.5 in sub spherical to ovoid cells and lower branchlet cells, then to 40–60 µm in diameter and L/D 2–3 in mid axial cells (Fig. 117B, C), with lower cells 80–120 µm in diameter and L/D (1-) 3–4. Determinate branchlets 200–400 µm and 5–10 cells long, with 2–3 orders of branches , apical cells 7–10 µm in diameter and L/D 1–2. Lateral indeterminate branches developing from determinate branchlets. Cells uninucleate; rhodoplasts discoid to elongate in smaller cells, ribbon like in larger cells.  

**Reproduction.** Gametophytes dioecious. Procarps borne on mid cells of upper axes or main branches, with 2 periangial cells, one bearing a 4-celled carpogonial branch; postfertilization each periangial cell cuts off an auxiliary cell which develops a branched carposporophyte (Fig. 117C, D) with deep pyramidal lobes of carposporangia 10–15 µm across; no involucral filaments occur. Spermatangia on small branched clusters on upper cells of determinate branchlets.  

Thallus 1–2 cm altus, erectus, caespitosus, cum axibus indeterminatis et cum ramis ramulos breviores determinatos spiratim ferentibus, ecorticatus. Affixus per rhizoidea e cellulis basalibus axium erectorum; epiphyticus. Apices axium inconspicui, cellulae apicales 6–9 µm diametro et L/D 1–1,5, crescentes ad cellulas ovoideas 10–15 µm diametro et L/D 1–1,5, deinde ad 80–100 µm diametro et L/D (2-) 3–4 in cellulis inferioribus axialibus. Ramuli determinati 200–400 µm et 5–10 cellulas longi, ramosi, cellulis apicalibus 7–10 µm diametro et L/D 1–2. Rami determinati e ramulis determinatis crescentes. Cellulae uninucleatae; rhodoplasta discoidca ad taeniformia.  

**Reproductio.** Gametophyta dioica. Procarpia in cellulis in mediis axibus vel ramis, cum 2 cellulis periangialibus et cum uno ramo carpogoniali; post fecundationem quaeque cellula periangialis cellulam auxiliarem producens et faciens carposporophyrum ramulosum cum lobis profundis carposporangiorum; involucrum absens. Spermatangia in fasciculis parvis ramosisque in ramulis determinatis.  

Tetrasporangia in ramulis sessilia 30–40 µm diametro, decussatim ad tetradrice divisa.  

**Type** from Fisherman Bay, Port Broughton, S. Aust., on *Caulocystis* (uvifera ?), drift (Womersley, 23.viii.1967); holotype and isotype in AD, A31803.  

**Distribution:** only known from the type.  

*C. pseudobyssoides* differs from *C. byssoides* in habit, having shorter, more distinct, determinate branchlets with broader and shorter subapical and lower axial cells. Reproductively however they are similar.

The specific epithet refers to the similarity with *C. byssoides*.  

**Genus HIRSUTITHALLIA** Wollaston & Womersley, *gen. nov.*

*Thallus* erect, 1–20 cm high, much branched with indeterminate axes and main branches clothed with ecorticate, usually determinate, alternately branched branchlets, some continuing
growth as indeterminate branches; branches becoming corticate by appressed rhizoidal filaments from the basal cells of ecorticate branchlets, becoming dense and often 2–4 cells thick below, with the outer cells producing short, simple or slightly branched, anticlinal

Fig. 117. Callithamnion propheystoides (AD, A31803). A. Habit on Caulonystis urifera. B. Branches with lateral branchlets. C. Branches with branched carpogonophores. D. Twinned, branched carpogonophores. E. Branches with tetrasporangia.
filaments forming a sparse to dense hirsute tomentum over the older branches. Gland cells absent. Cells uninucleate, often with further darkly staining globules.

**Reproduction.** Gametophytes dioecious. Procarps formed on cells of ecorticate branchlets, with two periaxial cells, one (the supporting cell) producing a 4-celled carpogonial branch with the first 3 cells horizontal around the supporting cell and the carpogonium and trichogyns directed upwards. Post-fertilization the carpogonium usually divides longitudinally and each cell unites via a small connecting cell with the two auxiliary cells cut off the supporting cell and the other periaxial cell. A gonimoblast initial then produces lobes of carposporangia which may be rounded or conical and furcate one or more times. Species are without or with an involucre of curved, simple or branched branchlets arising from the cell below the procarp. Spermatangial clusters single on cells of ecorticate branchlets, with a single, elongate, anticlinal stalk cell producing several initials which, directly or via further cells, produce terminal spermatangia.

Tetrasporangia produced singly on cells of ecorticate branchlets, sessile, subspherical, tetrahedrally divided.

**Thallus** erectus, multo ramosus; axes indeterminati, rami principales vestiti ramulis ecorticatis, plerumque ramulosis ramosis, aliquot rami indeterminati crescentes; cellulae magis veteres corticati per filamenta appressa et rhizoidealia e cellulis basaliis ramorum ecorticatorum, crescentes dense et saepe crassi infra 2-4 cellulis; cellulae exteriorres efferentes filamenta brevia, simplicia vel leviter ramosa, anticlinia, facientia tomentum sparsum ad densum hirsutum supra ramos magis veteres. Cellulae glandis absentes. Cellulae uninucleatae.

**Reproductio.** Gametophyta dioica. Procarpi in cellulis ramorum ecorticatorum formata cum 2 cellulis pericentralibus; alter (cellula sustinens) ramum 4 cellularem carpo gonialarem faciens, primus 3 cellulis horizontalibus circum cellulam sustinentem et carpogonium et trichogynum sursum directa. Post fecundationem carpogonium longitudinaliter divivsim; quaeque cellula coniungens per cellulam parvam coniunctivam cum 2 cellulis auxiliaribus ex cellula sustente et altera cellula pericentrali absicisa. Lobi carposporangiorum rotundati vel conicales furcatique. Species sine vel cum involucro curvatorum, simplicium vel ramosorum ramulorum, e cellulae infra procarpi. Fasciculi spermatangiales singuli in cellulis ramorum ecorticatorum.

Tetrasporangia singulatim in cellulis ramorum ecorticatorum, sessilia, subsphericalia, tetraedice divisa.

*Type species:* *H. mucronata* Wollaston & Womersley, *sp. nov.*

*Hirsutithallia* is named from the hirsute tomentum of anticlinal filaments, borne on the outer layer of rhizoidal filaments clothing the older axes and branches. While some species of *Callithamnion* have older branches corticated, the cortical filaments are usually much looser and do not produce the striking tomentum of anticlinal filaments characteristic of *Hirsutithallia.* Development of the procarp and carposporophyte are very similar to *Callithamnion* (and *Aglaothamnion* if accepted), but the uninucleate cells would ally *Hirsutithallia* with *Aglaothamnion.* The spermatangial clusters, with a distinctly elongate stalk cell bearing a hemispherical cushion of initials and ultimate spermatangia, also appear distinctive for *Hirsutithallia* and different to *Callithamnion* where more than one spermatangial branch arises from each thallus cell and a prominent, elongate, stalk cell does not occur.

However, two species (*H. formosa* and *H. angustata*), while similar to the other species in cortex characteristics and carposporophyte development, differ in having involucres around the carposporophytes and the spermatangial branches are similar to those in *Callithamnion.* While currently placed in *Hirsutithallia,* their position merits further study.

**KEY TO SPECIES OF HIRSIUTITHALLIA**

1. Cortication commencing close to apices. Carposporophytes without an involucre of filaments from the cell below the procarp. ................................................................. 2
1. Cortication starting some distance from apices. Carposporophytes with an involucre of curved filaments from the cell below the procarp ........................................................... 5

2. Terminal cells of branchlets, especially their walls, mucronate. 1. H. mucronata
2. Terminal cells of branchlets with rounded ends and walls ........................................ 3

3. Determinate branchlets 200–300 μm long, subdichotomous to laterally branched; carposporophytes simple or furcate ................................. 2. H. laricina
3. Determinate branchlets 500–1500 μm long, radially or abaxially branched; carposporophytes with several pyramidal lobes .............................................................. 4

4. Anticlinal cortical filaments profuse, often with 2 from each cell of the longitudinal cortical filaments; determinate branchlets radially branched, basal cells 50–90 μm in diameter; carposporophytes much branched with tapering lobes, carposporangia 20–28 μm in diameter, spermatangial clusters 45–55 μm in diameter, tetrasporangia 40–45 μm in diameter .................................. 3. H. tineta
4. Anticlinal cortical filaments sparse to abundant, usually with only one from each longitudinal cortical cell; determinate branchlets mostly abaxially branched, basal cells 80–130 μm in diameter; carposporophytes each with a pyriform lobe, carposporangia becoming 30–55 μm in diameter, spermatangial clusters 60–130 μm in diameter, tetrasporangia 40–90 μm in diameter ............... 4. H. abaxialis

5. Thallus moderately robust, branching often subdistichous, axial cells L/D 1–1.4, ecorticate branchlets with short laterals 4–8 cells long, cells L/D 1–1.5 .................... 5. H. formosa
5. Thallus slender, branching irregularly radial, axial cells of corticated branches L/D 2–5, all branches increasing gradually in diameter with lower and mid cells L/D 2–4 ................................................................. 6 H. angustata

1. Hirsutithallia mucronata Wollaston & Womersley, sp. nov.

Hirsutithallia CALLITHAMNIEAE 253

Thallus (Fig. 118A) erect, medium to dark red-brown, sometimes grey-red, 5–10 (-16) cm high, densely radially branched usually with several main axes bearing determinate laterals and with a narrowly pyramidal form; cortication commencing close to apices. Holdfast rhizoidal, 0.5–1 mm across; epiphytic on various algae. Structure. Ecorticate determinate branchlets 1.5–2 mm long, subdichotomous at almost right-angles (Fig. 118E, G), basal cells 45–65 μm in diameter and L/D 1.5–2 (2.5), tapering over 10–20 cells to mucronate (especially the apical wall) terminal cells (Fig. 118F, G) basally 8–14 μm in diameter and L/D about 1, occasionally with a slender hair. Axial cells of corticated branches increasing to 200–300 μm in diameter and L/D 1–1.5, becoming densely corticated (Fig. 118B, C) with narrow descending rhizoidal filaments bearing few to dense outer anticlinal filaments 5–8 cells and 100–220 μm long, often branched near their ends. Lateral branches arising by continued growth of determinate branchlets or on their lower cells. Cells uninucleate, with other darkly-staining globules; rhodoplasts elongate to ribbon like.

Reproduction. Gametophytes dioecious. Procarps (Fig. 121A) borne on mid cells of ecorticate branchlets, with two opposite periaxial (supporting) cells, one producing a carpogonial branch; post-fertilization the carpogonium enlarges and divides, and each cell connects with an auxiliary cell (Fig. 121B) via a small connecting cell, then developing rounded carposporangial groups (Figs 118D, 121C, D) from a large basal cell, with further rounded groups often developed; fusion of the supporting cell, auxiliary cell and lower gonimoblast cell usually occurs; mature carposporangia (Fig. 118D) are irregularly ovoid and 10–25 μm across; no involucre occurs. Spermatangial clusters (Fig. 118E, F) 40–65 μm across, with a stalk cell bearing initials which directly or indirectly bear terminal spermatangia.

Tetrasporangia (Fig. 118G) are sessile on mid and upper cells of ecorticate branchlets, subspherical, 40–55 (-60) μm in diameter, tetrahedrally divided.
**Hirsutithallia**

_Thallas_ erectus, 5–10 (-16) cm altus, confertim radiatum ramosus plurumque cum aliquot axibus principalibus laterales ferentibus, anguste pyramidalis. Hapteron rhizoidale 0.5–1 mm latum; epiphyticum. Ramuli ecorticati et determinati 1.5–2 mm longi, subdichotomi ferme rectangulares; cellulae basales 45–65 μm diametro et L/D 1.5–2 (-2.5), decrescentes per 10–20 cellulas ad cellulam mucronatas (praesertim in muro apicali) terminales basi 8–14 μm diametro et L/D circa 1. Cellulae axiales ramorum corticatorum ad 200–300 μm diametro et L/D 1–1.5 crescentes; confertim corticatescentes cum filamentis angustis declinatis rhizoidalis, portantes paucu ad densa ulteriori anticlinalia filamenta 5–8 cellulas et 100–220 μm longa sape ramulosa prope fines. Rami laterales orientes e ramulis determinatis continue crescentibus aut in cellulis inferioribus. Cellulae uninucleatae; rhodoplasta ad tainformia elongata.

**Reproductio.** Gametophyta dioica. Procarpia in mediis cellulis ramulorum ecorticatorum, cum 2 cellulis oppositis pericentralibus (sustinentibus), alter ramum carpoconidalem faciens; post fecundationem carpoconidium auctum et divisum; quaeque cellula cum cellula auxiliari iungens per cellulum parvam coniugentem; deinde evolutus fasciculi conjugati carposporangiacei e cellula magna basali; plurumque conjuncto cellulae sustentis, cellulae auxiliari, cellulae inferioris gonimoblasti, carposporangia matura irregular ovoidea 10–25 μm lata. Fasciculi spermangiacei 40–65 μm lati cum cellulae ferente fasciculus terminalium spermangiatum.

Tetrasporangiaca sessilia in cellulis medio et superiore ramulorum corticatorum, subsphericalia, 40–55 (-60) μm diametro, tetraedice divisa.

**Type** from Pennington Bay, Kangaroo I., S. Aust., drift (Kraft & Min Thein, 3.xii.1971; holotype in AD, A41394).

**Distribution:** Elliston, S. Aust., to Inverloch, Vic., and around Tasmania.


_H. mucronata_ differs from all other species of the genus in having mucronate terminal cells of the branchlets. It has been frequently confused with _H. laricina_, but differs in this manner, in having rounded rather than pyramidal carposporophytes, and in being a more robust species, epiphytic on various algae on rough-water coasts. On the south coast of Kangaroo I. it is common on _Laurencia elata_ but where _Codium fragile_ occurs (SE S. Aust. to Tasmania) it is a common epiphyte on it, though in Tasmania the _H. mucronata_ plants are generally only 1 cm or so high.

**Harvey** included specimens from Port Fairy, Vic. (e.g. Trav. Ser.200 and Alg. Aust. Exsicc. 510D) under _Callithamnion laricinum_ (in NSW, 401736, 401740) but they clearly show mucronate terminal cells.

2. _Hirsutithallia laricina_ (Harvey) Wollaston & Womersley, _comb. nov._

**Thallus** (Fig. 119A) erect, medium red-brown, 2–10 cm high, with a main axis bearing radially branched indeterminate laterals giving a narrowly to broadly pyramidal or spreading form, with terminal and lateral branchlets; cortication commencing from close to the apices. Holdfast 0.5–1 mm across, rhizoidal; usually epiphytic on *Posidonia*. *Structure.* Ecorticate determinate branchlets (Fig. 119F) 200–300 μm long, on corticate or potentially corticate laterals, subdichotomous to laterally branched with basal cells 40–75 (-90) μm in diameter and LID 1,5–2, tapering over 6–12 cells to small terminal cells 6–12 μm in diameter and LID 1, ends rounded and occasionally bearing hairs. Axial cells of corticated branches increasing to 200–600 μm in diameter and LID (1-) 1,5–2 (shorter near the base), becoming densely corticated (Fig. 119B) by narrow, descending rhizoidal filaments arising from the basal cells of lateral branchlets, and bearing few to numerous outer anticlinal filaments 4–6 cells and 50–140 μm long and 12–22 μm in diameter, simple or becoming branched near their ends. Cells uninucleate; rhodoplasts discoid to ribbon like.

**Reproduction.** Gametophytes dioecious. Procarps borne on mid cells of ecorticate branchlets. Carpogonial branches borne on one of the two more or less opposite periaxial cells (Fig. 119C), with the carpogonium post-fertilization dividing longitudinally and each cell uniting with the auxiliary cell cut off from each supporting cell, then dividing to form the goniomolobes (Fig. 119D) which have a sterile basal cell bearing an upper group of carposporangia; the two carposporophytes are rounded to pyramidal in shape or often furcate, tapering from a broader base, and may not develop simultaneously; carposporangia irregularly ovoid, 20–30 (-45) μm across; involucre absent. Spermatangial clusters (Fig. 119E), 30–55 μm across, formed on cells of ecorticate branchlets, with a stalk cell cutting off several initials which may branch again, with ultimate spermatangia. Tetrasporangia (Fig. 119F) sessile, subspherical, borne singly on mid to upper cells of ecorticate branchlets, 45–65 μm in diameter, tetrahedrally divided.

**Type** from Rottnest I., W. Aust., on *Posidonia* ("Zostera" of Harvey); lectotype in Herb. Harvey, TCD (Trav. Set 200).

**Distribution:** Yanchep, W. Aust., to Port Phillip Heads, Victoria.


*H. laricina* is usually epiphytic on *Posidonia*. It has often been confused with *H. mucronata*, which is a more robust species with mucronate terminal cells to the branchlets, common on other algae on rough-water coasts; the latter also has rounded carposporangial groups in contrast to the usually elongate ones in *H. laricina*. Harvey’s Trav. Set 200 and Alg. Aust. Exsicc. 510D from Port Fairy, Vic. are *H. mucronata*, whereas these numbers from Western Australia are *H. laricina*.

Development of the anticlinal cortical filaments appears to be variable. Some specimens from Western Australia, as for Harvey’s 1963 illustration, show very few, whereas they are abundant in other specimens. No other differences between these variations have been recognised.

Harvey’s (1862, pl. 218) record from Port Arthur, Tasmania, may be of a separate species of *Hirsutithallia*.
Fig. 119. Hirsutithallia laricina (A, A9214; B, F, AD, A41582; C, AD, A 24441; D, AD, A55419; E, AD, A50596). A. Habit. B. Corticated branch with anticlinal filaments and ecorticate branchlets. C. Procarp with twinned auxiliary cells. D. Part of a carposporophytes with twinned gonimolobes from the axial cell. E. Cells bearing spermatangial clusters. F. Thallus with tetrasporangia.
3. _Hirsutithallia tincta_ Wollaston & Womersley, sp. nov.

FIG. 120

_Thallus_ (Fig. 120A) erect, 5–10 (-13) cm high, with a main axis bearing radially numerous alternate to irregular laterals with a more or less pyramidal form, cortication commencing close to apices. Holdfast 0.5–1 mm across; epilithic. **Structure.** Ecorticate determinate branchlets (Fig. 120C, G) 500–1500 μm long, subdichotomous, basal cells 50–90 μm in diameter and L/D 1–2, decreasing over 6–15 cells to small ovoid, rounded, terminal cells 4–9 μm in diameter and L/D 1.5–2, often with hairs. Axial cells of corticate branches increasing to 150–450 μm in diameter and L/D 1.5–2, becoming densely corticated (Fig. 120B) by descending rhizoids from the basal cells of ecorticate branchlets, and bearing profuse anticlinal filaments 3–4 (-5) cells and 45–50 (-60) μm long, occasionally branched near their ends and with terminal hairs. Cells uninucleate but with numerous darkly staining globules; rhodoplasts small, irregularly discoid in young cells, more elongate in older cells.

**Reproduction.** Gametophytes dioecious. Procarps borne on mid cells of ecorticate branchlets. Carpogonial branches borne on one of two opposite periaxial cells, with the carpogonium enlarging transversely post-fertilization and dividing longitudinally prior to fusion via connecting cells with the two auxiliary cells cut off from the periaxial (one the supporting) cells. Each auxiliary cell produces a gonimoblast initial which forms irregular, branched, tapering goniomolobes (Fig. 120C, D), with later tapering lobes being produced from the first, forming a much branched carposporophyte; carposporangia irregularly ovoid, 20–28 μm in diameter; involucre absent. Spermatangial clusters (Fig. 120E, F) are 45–55 μm across, borne on cells of the ecorticate branchlets, with a stalk cell which branches 2–4 times with terminal spermatangia.

Tetrasporangia (Fig. 120G) are borne singly on outer cells of ecorticate branchlets, sessile, subspherical, 40–55 μm in diameter, tetrahedrally divided.

_Thallus erectus_, 5–10 (-13) cm altus, axe principalis multos alternatos ad laterales irregulares radiatim ferente, in forma pyramidalis. Hapteron 0.5–1 mm latum, epilithicum. Ramuli ecorticati et determinati 500–1500 μm longi, subdichotomii, cellulae basales 50–90 μm diametro et L/D 1–2, decrescentes ad cellulas parvas ovoideas rotundatas terminales 4–9 μm diametro et L/D 1.5–2. Cellulae axiales ramorum corticatorum ad 150–450 μm diametro et L/D 1.5–2, crescentes, confertim corticales per rhizoidea descendentia e cellulis basaliis ramorum ecorticatorum, ferentes filamenta anticlinalia 3–4 (-5) cellulas et 45–50 (-60) μm longa, interdum ramosa prope extremos pilis terminalibus. Cellulae uninucleatae; rhodoplasta parva, irregulariter disoida ad elongata.


Tetrasporangia singulatim in cellulis exterioribus ramorum ecorticatorum, sessilia, subsphericalia, 40–55 μm diametro, tetraedice divisa.

**Type** from Elliston, S. Aust., 7 m deep (Shepherd, 21.x.1970); holotype in AD, A37575.

**Distribution:** Safety Bay, W. Aust., to Port MacDonnell, S. Australia.

**Selected specimens:** Safety Bay, W. Aust., drift (Womersley, 29.x.1979; AD, A50730). Point Avoid, S. Aust., epiphytic, drift (Womersley, 2.xii.1975; AD, A46885). Almonte Beach, SE of Point Avoid, S. Aust., on _Codium galeatum_ (Lawrence, 21.1.1977; AD, A47883); Seal Bay, Kangaroo I., S. Aust., on _Codium galeatum_, drift (Womersley, 29.x.1966; AD, A31031); Pennington Bay, Kangaroo I., S. Aust., drift (Womersley, 29.x.1966; AD, A30853); Stanley Beach (E of Pennington Bay), Kangaroo I., S. Aust., on _Posidonia_, drift (Womersley, 27.1.1957; AD, A20820); Port MacDonnell, S. Aust., on _Tsengia_, drift (Kraft, 30.x.1986; AD, A57327).

_H. tincta_ is closest to _H. abaxialis_, differing in lacking the abaxial branching, in having more branched carposporophytes, each with several tapering lobes, and in having smaller carposporangia.
Fig. 120. *Hirsutithallia tincta* (AD, A37575). A. Habit. B. Cortication with anticlinal filaments. C. Upper branches with corticate axis and carposporophytes. D. Branched and twinned carposporophytes. E. Spermatanigal clusters, surface view. F. Spermatangial clusters on stalk cells. G. Branch with tetrasporangia.

**FIG. 122**

*Thallus* (Fig. 122A) erect, medium grey-red, 1–5 cm high, with a main axis bearing radial laterals giving a broadly pyramidal form, cortication commencing close to apices. Holdfast 0.2–0.5 mm across, rhizoidal; epiphytic on *Posidonia* and *Amphibolis*. **Structure.** Ecoricate determinate branchlets 650–1500 μm long, subdichotomous or laterally branched (Fig. 122B) mainly abaxially with outer filaments slightly upwardly curved, basal cells 80–130 μm in diameter and L/D (1-) 1.2–1.6, tapering over 10–15 cells (the last 2–5 cells markedly smaller) to small, rounded, terminal cells 5–10 μm in diameter and L/D 2–3, often with terminal hairs. Axial cells of corticated branches increasing to 200–300 (400) μm in diameter and L/D 1–1.5, becoming densely corticated by descending rhizoids from the basal cells of lateral branchlets, with most rhizoid cells bearing an outer anticlinal filament 3–6 (-7) cells and (45-) 60–120 (-150) μm long, simple or occasionally branched. Lateral branches arising on basal to mid cells of branchlets. Cells uninucleate, with no or few darkly-staining globules per cell; rhodoplasts discoid, ribbon like in older cells.

**Reproduction.** Gametophytes dioecious. Procarps borne on basal to mid cells of indeterminate laterals on ecoricate branchlets. Carposporangia borne on one of two opposite periaxial cells, with the carpogonium post-fertilization dividing longitudinally and each cell connecting via a small connecting cell with the auxiliary cells cut off from the two periaxial cells. Each auxiliary cell then divides to produce a gonimoblast initial which forms branched chains of cells enlarging to form pyramidal lobes (Fig. 122C, D) of ovoid carposporangia becoming 30–55 μm in diameter; involucre absent. Spermatangial clusters (Fig. 122E, F) are 60–130 μm across, borne on cells of the ecoricate branchlets, with a stalk cell bearing 2–4 (-5) cells from its outer end, each of which bears 1–3 further series of smaller cells, the terminal ones being spermatangia.

Tetrasporangia (Fig. 122G) are borne singly on cells of ecoricate branchlets, sessile, subspherical, 40–90 μm in diameter, tetrahedrally divided.

Thallus erectus, 1–5cm altus, axe principali laterales radiales ferente, late pyramidalis. Hapleron 0.2–0.5mm latum, rhizoidalaleum: epiphyticus in *Posidonia* et *Amphibolis*; ramuli ecorictati determinatique 650–1500μm longi, subdichotomi vel laterali ramosi abaxialiter filamentis ulterioribus leviter sursum curvatis; cellulae basales 80–130μm diametro et L/D (1-) 1.2–1.6, decrescentes per 10–15 cellulas (extremae 2–5 cellulae insigniter minores) ad cellulas parvas rotundatas terminales 5–10μm diametro et L/D 2–3. Cellulae axiales ramorum corticatorum ad 200–300 (400)μm diametro et L/D 1–1.5 crescentes, dense corticatae per rhizoidea descendentia e cellulis basalis ramulorum laterali, plurumque cellulae rhizoideales ferentes filamentum exteriores anticinali cum 3–6 (-7) cellulis et (45-) 60–120 (-150)μm longum, simplex vel interdum ramosum. Rami laterales orientes in cellulis basalis ad cellulas medias ramulorum verticillatorum. Cellulae uninucleatae; rhodoplasta discoida, taeniformes in cellulis magis maturis.


Tetrasporangia singulatim in cellulis ramulorum ecoricatorum portata, sessilia, subsphericalia, 40–90μm diametro, tetraedice divisa.

*Type* from Tiparra Reef, Spencer Gulf, S. Aust., on *Posidonia sinuosa*, 5 m deep (*Shepherd*, 30.ix.1970); holotype in AD, A37311.

**Distribution:** Only known from Tiparra Reef, S. Aust., on *Posidonia* and *Amphibolis antarctica.*
**Hirsutithallia**  

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Selected specimens:

Tiparra Reef, Spencer Gulf, S. Aust., 5 m deep on *Amphibolis* (Shepherd, 30.ix.1970; AD, A37304), 11 m deep on *Amphibolis* (Shepherd, 5.xi.1971; AD, A38308) and 5 m deep on *Posidonia australis* (Shepherd, 13.vii.1971; AD, A39240).

*H. abaxialis* is named from the abaxial branching of many of the ecorcite branchlets. It differs from *H. laricina* in having longer ecorcite branchlets with basal cells of greater diameter, tapering markedly over the last 2–5 cells, and less branched carposporophytes with larger carposporangia. Collections at Tiparra Reef have been made from May to November.

5. **Hirsutithallia formosa** (Harvey)Wollaston & Womersley, comb. nov.

 Lasiothaliaformosa (Harvey)De Toni 1903: 142l. Lucas 1909: 52; 1929b: 52.  

**FIGS 121E, F, 123**

*Thallus* (Fig. 123A) erect, medium red-brown, (5-) 10–20 cm high, much branched with numerous laterals bearing alternately shorter subdistichous branches with ultimate ecorcite branchlets. Holdfast small, 0.5–1 mm across, rhizoidal; epiphytic on *Amphibolis* and probably epilithic.  

**Structure.** Ecorcite determinate branchlets (Fig. 123B) 1000–1500 (-2000) µm and many cells long, bearing shorter lateral branches alternately and more or less subdistichous, basal cells 60–95 µm in diameter and L/D 1.5–2, often bearing hairs; ultimate branchlets 4–8 cells and 90–180 µm long, alternately branched, basal cells 25–45 µm in diameter and L/D 1–1.5, decreasing to 6–10 µm in terminal cells. Axial cells of corticated branches (Fig. 123B) increasing to 500–700 µm in diameter and L/D 1–1.4, becoming densely corticated by descending rhizoidal filament from the basal cells of lateral branchlets andbearing outer anticlinal filaments 3–6 (-10) cells and 100–180 µm long, at first sparse and separated, below dense. Cells uninucleate; rhodoplasts discoid to elongate, ribbon like or reticulate in older cells.

**Reproduction.** Gametophytes dioecious. Procarps situated 2–4 cells below the apex of ecorcite branchlets, with two opposite periaxial cells, one (the supporting cell) bearing a 4-celled carpogonial branch, the carpogonium dividing post-fertilization and each cell uniting via a connecting cell with an auxiliary cell cut off each periaxial cell (Fig. 123C), which then each produce a primary gonimoblast cell (Fig. 121E) and rounded lobes of ovoid carposporangia 20–30 µm in diameter; involucral filaments (Fig. 123D) develop from cells below the procarp and curve up and around the carposporophytes. Spermatangial clusters on cells of lesser ecorcite branchlets, branched 2–3 times.

Tetrasporangia (Figs 121F, 123E) are borne singly on cells of the ecorcite branchlets, sessile, subspherical, 30–50 µm in diameter.

**Type** from Port Phillip Heads, Vic., (Harvey); lectotype in Herb. Harvey, TCD (Alg. Aust. Exsicc. 515).

**Distribution:** Venus Bay, S. Aust., to Port Phillip Heads, Vic., and the north coast of Tasmania.

Selected specimens:


*H. formosa* is a relatively robust and openly branched species, distinguished (along with *H. angustata*) by the involucre of filaments around the carposporophytes. The cells are shorter and broader than in *H. angustata*, with markedly shorter ultimate branches on the ecorcite branchlets.
6. **Hirsutithallia angustata** (Hooker & Harvey) Wollaston & Womersley, *comb. nov.*


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**Fig. 123. Hirsutithallia formosa** (A, C-E, AD, A20156; B, A64586). A. Habit. B. Corticated axis with eocorticuate branchlets. C. Twinned young carposporophytes on axial cell. D. Branches with carposporophytes. E. Eocorticuate branchlets with tetrasporangia.
**Carpothamnion**

*Spongoclonium angustatum* (Hooker & Harvey) De Toni 1903: 1361. Lucas 1909: 49; 1927: 467, pl. 34 fig. 1; 1929a: 24.

**FIGS 121G–K, 124**

**Thallus** (Fig. 124A) medium to dark red, slender, 5–10 cm high, much branched openly and alternately radially, lightly corticate over lower branches. Holdfast small, 0.2–0.5 mm across, rhizoidal; apparently epilithic. **Structure.** Ecoricate laterals (Fig. 124B, D) and branchlets mostly 0.5–5 mm long, subdichotomous to laterally branched, basal and lower cells (35–) 40–75 μm in diameter and L/D (1.5–) 2–4, decreasing gradually over many cells to 15–25 μm in diameter, then to 3–5 short terminal cells 5–8 μm in diameter and L/D 1.5–2.5, often bearing a hair. Axial cells of corticate branches (Fig. 124E) increasing to 200–350 μm in diameter and L/D 2–5, lightly corticate in central and lower parts of the thallus with descending rhizoidal filaments from the basal cells of ecoricate branchlets; where lightly corticate (Fig. 121G) the rhizoidal filaments are laterally separated, but in lower parts cortication may be of several layers; outer anticlinal filaments are relatively sparse above, upwardly projecting, usually simple, some branched terminally, 4–8 (-10) cells and 100–300 μm long, but denser below. Cells uninucleate; rhodoplasts discoid to elongate. ribbon like in older cells.

**Reproduction.** Gametophytes dioecious. Procarps (Figs 121H, 124B) borne on axial cells 3–6 cells below branch apices which continue development, with a pair of opposite periaxial cells, one being the supporting cell of a 4-celled carpogonial branch. Post-fertilization the carpogonium enlarges transversely (Fig. 121I), with a nucleus in each end, but apparently does not divide. Auxiliary cells are cut off from the supporting cell and the other periaxial cell, and fusion occurs with each via small connecting cells. Each auxiliary cell produces a gonimoblast initial (Figs 121J, 124D) which produces successive rounded lobes of carposporangia, the terminal lobes developing first; mature carposporangia ovoid, 20–30 μm across. Mature carposporangiates (Fig. 124C,D) 200–350 μm across, surrounded by a lax involucre of 3–6 branched, curved, filaments from the axial cell(s) below the procarp, with the apical filament remaining above the fertile axial cell; the involucre is initiated very soon after fertilization. Spermatangia (Fig. 124E,F) on 1–3 laxly branched clusters (20–40 μm across) of ovoid cells on upper cells of ecoricate branchlets and on anticlinal filaments, usually one (occasionally 2) cluster per cell with a larger, isodiametric basal cell. Tetrasporangia (Figs 121K, 124G) occur on cells of ecoricate branchlets and occasionally on the anticlinal outer cortical filaments, sessile, subspherical, 30–45 μm in diameter, tetrahedrally divided.

**Type** from Tasmania (prob. Georgetown) (Gunn); in BM.

**Distribution:** N Spencer Gulf, S. Aust., to Port Phillip Heads, Vic. (Wilson) and N and SE Tasmania.


*H. angustata* is the slenderest, most laxly branched species of *Hirsutithallia*, with typical cortication on the older branches and axes only. It differs from other species (except *H. formosa*) in having an involucre around the carposporangiates, and also in having more laxly branched spermatantial branchlets, attached by isodiametric cells.

**Genus CARPOTHAMNION** Kützing 1849: 668

*Thallus* erect, 2–32 cm high, much branched irregularly, with ecoricate apical tufts of slender, alternate, spirally branched axes and determinate lateral branchlets, with dense, pseudoparenchymatous, rhizoidal cortication from shortly below the apical tufts, surrounding a large celled axial filament; holdfast first discoid, developing branched haptera. Cells uninucleate.
Reproduction. Gametophytes dioecious. Procarps on intercalary cells of ecoricate axes, with two opposite periaxial cells, one bearing a 4-celled carpogonial branch; sterile cells absent. Fertilized carpogonium fusing with both auxiliary cells via connecting cells, producing twinned carposporophytes with basal foot cells; involucral branchlets absent. Spermatangia borne on cells of determinate branchlets, with initials cutting off intermediate cells and then spermatangia. Tetrasporangia borne on cells of the determinate branchlets, sessile, tetrahedrally divided.

Type species: *C. gunnianum* Kützing 1849: 668.

*Thamnocarpus* Harvey (1844, pl. 662), a generally used name for this genus, was proposed for conservation by Silva (1950, p. 270), but this proposal was not accepted and the name remains as *Carpothamnion* Kützing. The type species was described in detail by Wollaston (1992), who recognised a second species from Africa.

*Carpothamnion* is characterised by callithamnoid reproduction but with a dense, pseudoparenchymatous cortex surrounding the large axial filament, arising shortly below the apices.


**FIGS 125, 126**

*Thallus* (Fig. 125A) erect, dark red-brown, 4–32 cm high, cartilaginous with usually one irregularly branched axis and well developed lateral branches (Fig. 125B), becoming heavily corticated (Fig. 125C,D) from close to apices and 1–2 mm in diameter. Holdfast discoid, becoming hapteroid, 0.5–6 mm across, pseudoparenchymatous; epilithic. **Structure.** Apices when young (or proliferous from older branches) with alternately spirally branched filaments 1–2.5 (-4) mm long, forming apical tufts or short laterals (Fig. 125B) when undamaged but easily lost; cells of young axes 20–40 μm in diameter and L/D (0.5-) 1–2, lateral branchlets basally branched with long unbranched ends, 20–35 μm in diameter with cells L/D 3–5. Rhizoidal cortication (Fig. 126A) commencing close to branch apices from basal cells of determinate laterals, becoming dense and pseudoparenchymatous, with an outer layer of smaller cells; rhizoids 5–12 μm in diameter, cells L/D 4–10, outermost cells isodiametric, 4–8 μm across. The axial filament gradually enlarges to (150-) 250–500 μm in diameter, cells L/D 1–1.5 (-2), and remains very conspicuous in section of the branches. Cells uninucleate; rhodoplasts discoid to elongate.

**Reproduction.** Gametophytes dioecious. Procarps (Figs 125E, 126B) borne on axial cells of the ecoricate apical tufts, with two opposite periaxial cells often 2–3 axial cells apart. One periaxial bears a 4-celled carpogonial branch, and post-fertilization (Fig. 126C) each periaxial cuts off an auxiliary cell and fusion of the carpogonium with both occurs via connecting cells; twin gonimoblasts, each with a foot cell, are initiated, forming rounded, lobed, carposporophytes (Fig. 126D) 100–200 μm across with carposporangia 25–30 μm in diameter. Spermatangia (Figs 125F, 126E) occur in groups on cells of the branchlets, with clusters of initials producing about 4 cells each of which bears outwardly 3–4 spermatangia. Tetrasporangia (Figs 125G, 126F) are borne on cells of the branchlets, singly or with a second younger one, sessile, ovoid, 30–45 μm in diameter, tetrahedrally divided.
Carpothamnion

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**Type** from Port Arthur, Tas. (*Gunn*); lectotype in Herb. Harvey, TCD.

**Distribution:** Houtman Abrolhos, W. Aust. (Huisman 1997), to Phillip I., Vic., and around Tasmania.


*C. gunnianum* is not common but occurs in scattered localities along southern Australia, from shallow (probably shaded) to deep water. It is readily recognised by the delicate terminal tufts on young or actively growing plants and the very dense cortication of the large axial cells on older branches.

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**Fig. 126.** *Carpothamnion gunnianum* (A–D, AD, A42663; E, AD, A35964; F, AD, A32506). A. Early cortication of axis by rhizoids from basal cells of branchlets. B. A procarp with 2 periaxial cells and a 4-celled carpogonial branch. C. Young twinned gonimoblasts with persistent carpogonial branch. D. Twinned (uneven) carposporophytes. E. Spermatangial clusters. F. Branchlet cells with tetrasporangia. (All as in Wollaston 1992, courtesy of Phycologia.)
Tribe COMPSOTHAMNIEAE Schmitz 1889: 450
by H.B.S. Womersley and E.M. Wollaston

*Thallus* erect, 5–20 cm high, much branched complanately, largely or partly distichously, usually with long lateral branches on the axes, with a single, lateral, determinate branchlet on each cell, some of which become indeterminate; apical cells dividing alternately obliquely or more or less transversely; axes and branches corticated below with loose rhizoids from the basal cells of lateral branches; one genus (*Haloplegma*) net like, flat and irregularly complanately branched; gland cells absent. Cells multinucleate.

*Life history* triphasic with isomorphic gametophytes and tetrasporophytes.

*Reproduction.* Gametophytes dioecious. Procarps borne on 2–3 cells of short lateral axes, 2–5 or more cells below the apex which may develop further, with 2 or 3 periaxial cells, one bearing a 4-celled carpogonial branch and another a short 1–3-celled sterile branch; supporting cell with or without a sterile cell. Post-fertilization the auxiliary cell produces 2–5 gonimolobes becoming rounded groups of carposporangia. Carposporophyte with some fusion of basal cells but not a distinct fusion cell, surrounded by simple or branched involucral filaments derived from the axial cell(s) below the carposporophyte or sterile cells of the procarp. Sporogonic heads borne on cells of the determinate branchlets, sessile or pedicellate, ovoid to elongate, with an axial filament (sometimes with a terminal hair) producing whorls of initials and ultimate spermatangia. Tetrasporangia borne on cells of the determinate branchlets, sessile or pedicellate, ovoid to subspherical, tetrahedrally divided with occasional octosporangia.

The Compsothamnieae includes four or five genera, two (*Dasythamniella*, including *Compsothamnionella*, and *Haloplegma*) in southern Australia, *Compsothamnion* in the Northern Hemisphere, and probably *Antarcticothamnion* which Moe & Silva (1979) referred to a separate tribe but Gordon-Mills & Wollaston (1980) consider should be placed in the Compsothamnieae. *Gymnophycus* Huisman & Kraft (1983) is also considered a probable member of the tribe. The tribe is characterised by procarps borne on somewhat unlimited apices 3 to many cells long, with such apices often lengthening slightly after procarp formation. The procarps have 2 or 3 periaxial cells with a single carpogonial branch and usually a short sterile filament on one periaxial cell. The spermatangia are typically formed in heads. Norris (1985, p. 61) following Itôno (1977, p. 43), mistakenly stated that *Compsothamnionella* has a "Pleosporium-type of procarp structure". The latter is distinct in this respect and is placed in the Spongoclonieae.

**KEY TO GENERA OF COMPSOTHAMNIEAE**

1. Thallus distichously branched, densely corticated by rhizoidal filaments .................. DASYTHAMNIELLA

   1. Thallus flat and complanately branched, with a net-work of internal filaments bearing short clusters of surface filaments ........................................... HALOPLEGMA

**Genus DASYTHAMNIELLA** Silva 1970: 942

*Thallus* erect, 5–25 (-50) cm high, with distichous, lateral, indeterminate branches for several orders, developed from determinate branchlets and becoming densely corticated by lax rhizoidal filaments from shortly or more distantly below the branch apices. Active indeterminate apices distichously branched, apical cells dividing obliquely to transversely; lateral determinate branchlets ecorticate, basally branched, terminally unbranched, cells short. Cells multinucleate (2–10 small nuclei per cell).

*Reproduction.* Gametophytes probably dioecious. Procarps borne on the third and often also the fourth cell of short, 3–8-celled, lateral branches, with 2 (-3) periaxial cells, one bearing...
a sterile cell and a 4-celled carpogonial branch. Carposporophyte with fusions between basal cells and with 1–4 successive rounded gonimolobes, with or without separate involucral branchlets (apart from lower determinate branchlets), all cells becoming carposporangia. Spermatangia on distinct clusters borne adaxially on branchlets (unknown in type species).

Tetrasporangia sessile or on 1–5-celled pedicels, sometimes clustered by branching from pedicels, situated on determinate ramuli, tetrahedrally divided.

Type species: *D. setosa* (J. Agardh) Silva 1970: 942 [= *D. dasyura* (Harvey) comb. nov.]

*Antarcticothamnion* Moe & Silva (1979, p. 402) is closely related to *Dasythamnietta* but differs in branching pattern, origin of lateral indeterminate branches which arise on main axes as verticils, in binucleate carposporangia and in having polysporangia; the female reproduction in both genera is very similar.

The active apices usually with oblique cell divisions, and the procarpal axes of 3–8 cells with one (or two) procarps on the third and fourth cells, place *Dasythamnietta* in the *Compsothamnieae*. All the species included below are similar in this respect to the type species, *D. dasyura*. *Dasythamnietta* is now considered to include *Compsothamnietta* Ilono (1977, p. 42) and differs from *Compsothamnion* (see Westbrook 1930 and Gordon-Mills & Wollaston 1990) in having usually only 2 periaxial cells on the female axis and developing only a single auxiliary cell compared to 2 in *Compsothamnion*.

Harvey (1863, synop.: ii) had grouped 4 of the species now referred to *Dasythamnietta*, plus species of *Spongoclonium*, in his Section 1. *Dasythamnion* of Callithamnion.

**KEY TO SPECIES OF DASYTHAMNIELLA**

1. Mature determinate branchlets 0.5–3 mm long, more or less complanately branched with unbranched ends 200 μm –2 mm long; tetrasporangia pedicellate ........................................ 2

2. Determinate branchlets 1–3 mm long, basally branched with unbranched ends 1–2 mm and 20–50 (70) cells long; cells isodiametric (L/D 1–1.5) . 1. *D. dasyura*  
   2. Determinate branchlets 0.5–1 (1.5) mm long, alternately branched with unbranched ends (40) 200–600 μm and (3) 5–17 cells long, cells elongate, L/D 1.5–3 (4) .............................................................................................................. 3

3. Thallus fastigate, much branched with erect lateral branches but without prominent spreading laterals; lateral branchlets lax and not or scarcely overlapping; cortication relatively slight on lower axes .............................................................. 2. *D. latissima*  
   3. Thallus with prominent, spreading, lateral branches, densely branched with overlapping branchlets with curved pinnules; cortication becoming dense on lower axes and lateral branchlets .............................................. 3. *D. sollastoliana*  

4. Lower cells of determinate branchlets 30–40 μm in diameter and L/D 0.8–1, tapering to 15–20 μm in diameter in subapical cells ................. 4. *D. plumigem*  
   4. Lower cells of determinate branchlets 15–25 μm in diameter and L/D 1–2, tapering to subapical cells 6–9 μm in diameter and L/D 2–3 ........................................ 5. *D. superbiens*  

1. **Dasythamnietta dasyura** (Harvey) Womersley, *comb. nov.*  
FIGS 127, 129A

*Thallus* (Fig. 127A) erect, medium to dark red-brown, 5–20 (-30) cm high, with a well developed and densely corticated main axis and laterals (usually 1–10 cm long) for 2–4 orders, more or less distichously branched, ultimate branches often plumose; axes 1–3 mm in diameter. Holdfast conical, 2–10 (-15) mm across, rhizoidal; epilithic. *Structure.* Active apices (Fig. 127B) with cells dividing by transverse to slightly oblique walls (usually oblique at laterals), distichously alternately branchcd, apical cells 15–25 μm in diameter and LID 1–1.5, axial cells increasing from 40–60 μm in diameter and LID 1–1.5 (-2) shortly below apices to 100–200 μm in diameter and LID 0.8–2 in lower thallus. Determinate branchlets 1–3 mm long, simple or basally branched 1–3 times, ultimate filaments (Fig. 127C) becoming 1–2 mm and 20–50 (-70) cells long, tapering only slightly until near their ends, 25–45 μm in diameter with cells LID (0.7-) 1-1.5 (-2). Indeterminate lateral branches developing from determinate branchlets. Lower and mid axes and branches heavily corticated by entwined rhizoids 12–25 μm in diameter with cells LID 1-5, produced from basal cells of laterals. Cells multinucleate; rhodoplasts discoid.

*Reproduction.* Gametophytes dioecious. Procarps (Fig. 127D) on usually the third and often the fourth cell (Fig. 129A) of short branches 4–5 cells long, with two periaxial cells, the first (supporting) cell cutting off a sterile ceil and a 4-celled carpogonial branch; the sterile periaxial cell may also cut off an apical cell. Carposporophytes with basal cells fusing but without a distinctive fusion cell; gonimolobes (Fig. 127E) 1-4, 300–750 μm across, successively developed, rounded, carposporangia 10–25 μm across; carposporophytes terminal on short lateral branches, densely surrounded by curved branchlets from lower cells. Spermatangia (Fig. 127F) ovoid, 27–45 μm in diameter and LID 1.8-2.1. Tetrasporangia (Fig. 127G) on pedicels 1-5 cells long, becoming clustered by branching from pedicels, situated on lower to mid cells of determinate ramuli, subspherical, 25–45 μm in diameter, tetrahedrally divided (very rarely octosporangia).

*Type* from Port Phillip Heads, Vic. (Harvey); lectotype (Harvey, Trav. Set 426); also Alg. Aust. Exsicc. 505, in Herb. Harvey, TCD.

*Distribution:* Gulf St Vincent, S. Aust., to Port Phillip Heads, Vic., and S Tasmania.


*Type* setsoum J. Agardh is represented in Herb. Agardh by a single specimen (Encounter Bay, S. Aust., Hussey, L.D., 18868). It is a robust and old specimen of *D. dasyura*. The species is an elegant and well-marked taxon with its distichous thallus and plumose branch ends, developing long unbranched filaments with short cells in the determinate branchlets.


*Phlebothamnion latissimum* (Harvey) Kützing 1849: 656; 1862: 3, pl. 8a, b.


FIGS 128, 129B–E

*Thallus* (Fig. 128A) erect and tufted, red-brown, 5–18 cm high, fastigiate with one to few axes and tufted erect laterals. Branching regularly alternate and mostly distichous for 2-4 orders, corticated on lower axes. Holdfast 3–8 mm across, rhizoidal; epiphytic (often on shells). *Structure.* Apical cells dividing obliquely, increasing from 10–15 μm in diameter and L/D 1–2 to 500–600 μm in diameter and L/D (1.5-) 2–3 (-4) in the
Fig. 128. *Dasythamniella latissima* (A, AD, A64251; B-D, G, AD, A35579; E, F, A46255). A. Habit. B. Apex of indeterminate axis with more or less distichous laterals. C. A 4-celled branch with a procarp on left and young (2-celled) sterile branch on right. D. A 7-celled branch with young carposporophyte above cell 6, opposite a 4-celled sterile branch. E. A carposporophyte below the branch apex, surrounded by involucral branches from lower cells. F. Branchlets with spermatangial heads. G. Branchlets with tetrasporangia.
central part of the axes. Determinate branchlets 1–2 mm long, alternately distichous (Fig. 128B) but later becoming slightly spiral, not or slightly overlapping, with unbranched ends 200–600 μm and 8–17 cells long; cells in median parts (10-) 20–45 (-60) μm in diameter and L/D (2-) 3–4. The apical cell and ends of the axes are always emergent and never overtopped by lower laterals. Rhizoidal cortication is sparse above but denser and spongy below, the rhizoids entwined and connected by lateral pit-connections, increasing the axis diameter to 1–2 mm. Lateral indeterminate branches developing by continued growth of determinate laterals. Cells multinucleate; rhodoplasts discoid to elongate, ribbon like in larger cells.

Reproduction. Gametophytes dioecious. Procarps (Fig. 129B) borne on the third to fifth cell of short, 3–8-celled branches (Fig. 128C), with the fertile central cell bearing two periaxial cells, one (the supporting cell) cutting off a terminal sterile cell and a 4-celled, curved, carpogonial branch; the other periaxial cell forming a short sterile branchlet of 3–5 cells. An auxiliary cell is produced from the supporting cell and cuts off 2–4 successive gonimolobe initials (Fig. 129C) developing rounded groups of carposporangia (Fig. 128D, E) 180–350 μm across, each carposporangium angular and (15-) 20–25 μm across. The mature carposporophyte is surrounded by an involucre (Fig. 128E) of normal and additional curved lateral branchlets from the 2–3 axial cells just below the procarp; basal cells of the carposporophyte fuse somewhat but without forming a distinctive fusion cell. Spermatangial clusters (Fig. 128F, 129D) cylindrical, borne adaxially on the lower cells of branchlets, 25–45 μm in diameter and L/D 1.5–4, with 3–7 axial cells producing whorls of cells with ultimate spermatangia.

Tetrasporangia (Fig. 127G, 128E) are usually borne adaxially on lower cells of branchlets, pedicellate, 30–45 μm in diameter, tetrahedrally divided.

Type from Georgetown, Tas. (Gunn 1308); lectotype in BM.


Compsothamnionella huismanii Gordon-Mills & Wollaston is identical with the earlier described Callithamnion latisimum Harvey from Tasmania. The species occurs in relatively calm water habitats, whereas Dasythamniella wollastoniana is usually found on open coasts. Two collections listed by Gordon-Mills & Wollaston as C. huismanii (AD, A44558 and A28896) are now referred to D. wollastoniana; both are from open coasts, and one (AD, A55680 from Blanche Harbor, S.Aust., female only) differs from D. latissima in having 2 carpogonial branches per procarp, and the trichogynes with a prominent bulbous swelling. Determination of this taxon awaits further material. The Kangaroo I. specimen (AD, A32978) is tetrasporangial only.

3. Dasythamniella wollastoniana * (Harvey)Womersley, comb. nov.


FIG. 130

Thallus (Fig. 130A) erect, spreading, medium to dark red-brown, 5–15 cm high with 1–3 corticate main axes and prominent spreading, corticate lateral branches 1–5 cm long, with dense, overlapping lateral branchlets. Holdfast 2–8 mm across, rhizoidal; epilithic or epiphytic. Structure. Branching at apices (Fig. 130E) alternate and distichous, apical cells dividing slightly to distinctly obliquely, increasing from 10–25 μm in diameter and L/D 1–2 to 200–300 μm in

* This name is based on that of Archdeacon J.R. Wollaston at Albany, W. Aust., great great grandfather of Elise M. Wollaston, co-author of this account.
Dasythamniella diameter and L/D 1.1.5 (-2) in axial cells in lower parts. Indeterminate lateral branches developing from determinate branchlets and usually more or less distichously arranged, but determinate branchlets not clearly distichous due to crowding and curving of pinnules; branchlets dense and overlapping, with unbranched ends 40–100 μm and 3–8 cells long, pinnules curved and unbranched with median cells (20–) 30–50 μm in diameter and L/D (1–) 1.5–4, growing ends of axes and branchlets emergent or often overtopped by laterals from below. Rhizoidal cortication commencing on mid to upper axes, with lower axes becoming 1–2 mm in diameter, rhizoids loosely to densely entwined. Cells multinucleate; rhodoplasts elongate, ribbon like in larger cells and orientated lengthwise.

Reproduction. Gametophytes dioecious. Procarps borne on short 3–7-celled branchlets (Fig. 130B), with the fertile central cell bearing two periaxial cells, one (the supporting cell)
cutting off a terminal sterile cell and a 4-celled carpogonial branch, the other periaxial cell forming a short sterile branchlet of 2–4 cells. The auxiliary cell cuts off 3–4 successive gonimolobe initials giving rounded groups 100–200 μm across (Fig. 130C) of ovoid carposporangia 10–15 μm across; basal carposporophyte cells fuse and enlarge, with broader pit connections. Curved branchlets from cells below the carposporophyte form an involucre. Spermatangial heads (Fig. 130D) are borne adaxially on lower cells of branchlets, ovoid, 12–22 μm in diameter and L/D 2–3.

Tetrasporangia (Fig. 130E) adaxial on pinnules of branchlets, pedicellate, subspherical, 25–45 μm in diameter, tetrahedrally divided.

Type from Middleton Bay, King George Sound, W. Aust.; holotype in TCD (Harvey, Trav. Set 329).

Distribution: King George Sound, W. Aust., to Port Phillip Heads, Victoria.


The type material of S. wilsonianum J. Agardh, from Port Phillip Heads, Vic. (Wilson), in LD (16868), includes two specimens and appears to be identical with S. wollastonianum. J. Agardh had previously referred these specimens to the latter species, and his description separates S. wilsonianum only on superficial characters. Specimens of D. wollastoniana show the typical reproductive features of Dasythamniella, but differ in habit from D. laisissima.

4. Dasythamniella plumigera (Harvey)Womersley, comb. nov.

Spargoclonium plumigerum (Harvey)J. Agardh 1894a: 118.

FIGS 129F–H, 131

Thallus (Fig. 131A) medium to dark red-brown, 5–25 cm high, alternately distichously and complanately branched for 4–5 orders, usually with a single main axis 2–3 mm in diameter; branches terete, 0.5–1 mm in diameter above, becoming heavily corticated and densely covered with branchlets. Holdfast conical, rhizoidal, 2–5 mm across; epitheca, Structure. Apices (Fig. 131B, E) of indeterminate branches with short apical and subapical cells 10–18 μm in diameter and L/D 0.8–1.2, with oblique divisions and alternate distichous branchlets, emergent, axial cells increasing to 30–50 μm in diameter and L/D 1–1.4 some 10–20 cells below the apices and to 300–500 μm in diameter and L/D (1.2) 2–4 (-6) in lower thallus. Cortication of axes and lateral branches commences close to the apices, by rhizoids from the basal cells of laterals, becoming dense and with the outer cells producing short, branched, anticlinal filaments 350–500 μm long and 20–30 μm in diameter, cells L/D 1–1.5. Lateral branches developing by branchlets becoming indeterminate. Determine branchlets 500–900 μm long, covering most branches, at first distichously branched but their secondary branches often at other angles, with curved unbranched ends 100–200 μm and 10–15 cells long when mature, cells 30–40 μm in diameter basally and L/D 0.8–1, tapering slightly to 15–20 μm in subapical cells. Cells multinucleate; rhodoplasts discoid, elongate in larger cells.

Reproduction. Gametophytes probably dioecious. Procarps (Figs 129F, G, 131C) borne on axial cells near branch apices, often on 2–3 (-4) successive cells with the first procarp on a cell 2–4 cells below the apex and a further 1–3 cells bearing procarps as the axis elongates.
Each fertile axial cell produces 2 periaxial cells at right angles, the first formed producing a small sterile cell and an upwardly curved 4-celled carpogonial branch. Post-fertilization each periaxial cell cuts off an auxiliary cell and both may be diploidised via a small connecting cell, then dividing to a foot cell and upper gonimoblast cell which develops successive rounded gonimolobes (Fig. 131D) 200–500 μm across of ovoid carposporangia 12–22 μm in diameter; basal cells fuse with broader pit connections. The periaxial sterile cell and the second periaxial divide further into short sterile branchlets, but only one carposporophyte develops at each apex, with an involucre of branchlets on lower cells. Spermatangia unknown.

Tetrasporangia (Figs 129H, 131E) are sessile or rarely with a single stalk cell, on cells of the determinate branchlets, subspherical, 35–65 μm in diameter, tetrahedrally divided (rarely octosporangia).

Fig. 131. Dasythamniella plumigera (A–C, AD, A32333; D, E, AD, A32369). A. Habit. B. Indeterminate axis with lateral branchlets. C. Procarp on short branch. D. Carposporophyte with 3 gonimolobes. E. Branch with tetrasporangia.
Lectotype from Western Port, Vic. (Harvey); in Herb. Harvey, TCD (Alg. Aust. Exsicc. 507H).

Harvey in his protologue also recorded the species from Cape Liptrap, Port Fairy and Cape Shank, all in Victoria. The lectotype is very similar in form (reversed) to Harvey’s Pl. 285, fig. 1.

Distribution: West L, Victor Harbor, S. Aust., to Cape Liptrap (Harvey), Vic., and SE Tasmania.

Selected specimens: Toad Head, West L, S. Aust., 18 m deep (Shepherd, 24.x.1966; AD, A31572).

Bridgewater Bay, Vic., drift (Beauglehole, 26.xii.1950; AD, A15654).

Lady Julia Percy Is., Vic., 8-13 m and 8-12 m deep (Shepherd, 5,i.1968; AD, A32463 and 3.i.1968; AD, A32333 resp.). Port Fairy, Vic., drift (Womersley, 25.i.1967; AD, A31737).

Granville Harbour, W Tas., 3-10 m deep (Blackman 79-31, 28.i.1979; AD, A65859).

Fluted Cape, Bruny L, Tas., 10-15 m deep (Shepherd, 12.ii.1972; AD, A61380).

5. Dasythamniella superbiens (Harvey)Womersley, comb. nov.


FIG. 132

Thallus (Fig. 132A, B) red-brown, 7-20 (-50) cm high, with long, spreading lateral indeterminate branches for 3-4 orders, all distichously branched, covered with determinate branchlets which are relatively persistent and subdistichously to irregularly branched; lower axes corticated with loose rhizoids which also bear determinate branchlets. Holdfast discoid, rhizoid al, 2-3 mm across; epilithic. Structure. Indeterminate apices (Fig. 132E) with apical cells 4-6 μm in diameter and L/D 1-1.5, dividing by more or less horizontal cross walls (oblique on cells bearing branches), increasing gradually to 200-500 μm in diameter and L/D 1-2 in the lower thallus; corticating rhizoids arising from basal cells of lateral branches, becoming 20-45 μm in diameter with cells L/D 2-4. Determinate branchlets markedly slenderer than older indeterminate branches, 120-300 μm long and branched 4-7 times, unbranched ends 50-180 μm and 4-8 cells long, lower cells 15-25 μm in diameter and L/D 1-2, tapering gradually to cells just below apices 6-9 μm in diameter and L/D 2-3; some determinate branchlets develop into indeterminate branches. Cells multinucleate; rhodoplasts elongate in younger cells, becoming ribbon like in larger cells.

Reproduction. Gametophytes probably dioecious. Procarps (Fig. 132C) on axial cells below the apices but axial filament above often slightly restricted in growth, with 3 periaxial cells, one bearing a 4-celled carposporangial branch and a second developing a short 1-2-celled sterile branch. Carposporophytes (Fig. 132D) with a slight basal branched, fusion cell and 2-4 successively developed lobes each 150-350 μm across of ovoid carposporangia 10-20 μm across, surrounded by branched involucral branchlets from cells below the carposporophyte. Spermatangia unknown.

Tetrasporangia (Fig. 132E) borne on cells of determinate branchlets, sessile, 18-30 μm in diameter, tetrahedrally divided.

Type from Western Port, Vic. (Harvey); lectotype in Herb. Harvey, TCD (Alg. Aust. Exsicc. 506).

Distribution: Only known from Western Port, Vic., and Elliston, S. Aust.

Known specimens: The type and Elliston, S. Aust., 10-11 m deep in bay (Shepherd, 20.x.1969; AD, A35050).

Harvey (1863, synop.: li) in his type description cited only “Alg. Exsicc. n. 511 (ex parte),” having listed C. brownianum var. majus also under 511. The lectotype in TCD is numbered 506, the number given in Harvey’s 1857 list. MEL has two sheets (504225, 1007342) from Phillip L., Vic., numbered 400 from Harvey’s Travelling Set. These are probably isotypes.
Dasythamniella is apparently a rare alga, known only from Western Port, where it has not been collected since Harvey, and from Elliston. The occurrence of 3 periaxial cells on the female axis indicates that further comparisons with Compsothamnion are needed, but apparently only a single auxiliary cell occurs.

Fig. 132. Dasythamniella superbiens (A, MEL, 1007342; B, C, AD, A34951; D, E, AD, A35050). A. Habit of MEL isoelectotype. B. Habit. C. Procarp on eighth cell of short branch. D. Carposporophyte. E. Branch with tetrasporangia.
Genus HALOPLEGMA Montagne 1842: 258

Thallus erect, flat and complanately branched, flabellate to lobed to much branched, spongy, margins usually smooth, holdfast rhizoidal with a short terete stipe. Structure. Blades with numerous fringing apices, slightly more prominent primary apices separated by several similar secondary apices, apical cells with more or less transverse cross walls. Apical filaments producing mainly opposite lateral filaments in the plane of the thallus which unite with those of adjacent filaments to form rectangular meshes of a network, with alternate cells of the apical filaments producing filaments towards the surfaces which produce small surface clusters forming a felt like cover to the thallus. Cells multinucleate.

Reproduction. Gametophytes dioecious. Carpogonial branches borne on the cells of short branches on lower cells of the surface clusters. Carposporophytes positioned just above the blade surface, with several rounded gonimolobes developing successively, all cells forming carposporangia, and loosely surrounded by filaments of the surface clusters. Spermatangial heads borne on the cells of the surface clusters, ovoid, with axial cells of the heads bearing whorls of cells which cut off spermatangia. Tetrasporangia terminal on cells or short branches on the surface clusters, tetrahedrally divided.

Type species: H. duperreyi Montagne 1842: 258, pl. 7 fig. 1.

A genus of probably 3 species, the type and H. preissii Sonder, both of which are known from southern Australia, and H. anweri Shameel & Nizamuddin (1972) from Pakistan.

Although the details of procarps have not been described for the type species, reproduction of H. preissii indicates that Haloplegma is best placed in the Compsothamnieae.

KEY TO SPECIES OF HALOPLEGMA

1. Thallus 400–600 µm thick, flat and lobed but relatively little branched, surface clusters 45–100 µm long with terminal unbranched rows of 2–4 cells, 8–14 µm in diameter
   .................................................................................................................. 1. H. duperreyi

1. Thallus mostly 1–2 mm thick, complanate and becoming much branched with flat lobes, surface clusters 400–700 µm long with curved, unbranched filaments 250–500 µm and 15–25 cells long, 18–30 µm in diameter
   .............................................................................................. 2. H. preissii


FIG. 133

Thallus (Fig. 133A) red-brown to grey-red, flat and complanately branched, 1–10 cm high, flabellate to lobed, becoming divided or lacerate, lobes expanding upwards to (1–) 2–4 cm broad, mostly 400–600 µm thick, margins smooth to slightly ruffled. Stipe 2–5 mm long, 1–2 mm in diameter, holdfast 2–8 mm across, rhizoidal; epiplithic or on shells (one specimen on old axes of Doxoxysa bulbochaete). Structure. Marginal apices (Fig. 133B) regularly fringing the blades, with primary apices and filaments separated by numerous secondary apices from lateral filaments. Apices with alternate laterals (Fig. 133D) from 3–6 cells below the apical cells, walls more or less transverse, apical cells 10–18 µm in diameter and L/D 1–1.5. Laterals of apical filaments uniting with next adjacent filaments to form a rectangular network (Fig. 133B), with other irregular filaments, the outer cells developing short branch clusters (Fig. 133C, D). Cells of internal filaments 25–45 µm in diameter and L/D 3–7, outer clusters 45–100 µm long with ovoid basal cells 15–30 µm in diameter, branched 1–3 times with terminal unbranched rows of 2–4 cells, 8–14 µm in diameter, isodiametric to slightly ovoid. Cells multinucleate; rhodoplasts discoid to elongate, ribbon like in larger cells.

Reproduction. Gametophytes not observed.
**Haloplegma**

Tetrasporangia (Fig. 133E) terminal on cells of outer clusters, subspherical to slightly ovoid, 20–40 μm in diameter, tetrahedrally divided.

*Type* from Martinique, West Indies; in Herb. Montagne, PC? (not located in 1952).

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**Fig. 133. Haloplegma duperreyi** (A, D, AD, A39281; B, C, E, AD, A51052). A. Habit. B. Frond margin, with 3 primary filaments separated by several secondary filaments, with rectangular networks of inner cells. C. Surface view of frond. D. Longitudinal vertical section showing apical divisions, lateral branches from alternate axial cells, and short surface clusters. E. Tetrasporangia on lower cells of short surface clusters.
**Haloplegma**

**Distribution**: West Indies, tropical and subtropical Indian Ocean, Japan, NW Aust., Qld, and Lord Howe I.

In southern Australia, known from Elliston, N Spencer Gulf, Kangaroo I., and Robe and Nora Creina, S. Aust.


Specimens from Elliston and N Spencer Gulf are well developed and 8–15 cm high, occurring in moderately deep water with considerable current flow, whereas those from rough-water coasts (Vivonne Bay, Robe and Nora Creina) occur in heavily shaded pools or caverns and are often only 1–2 cm high. Few of these specimens are fertile but they appear to agree well vegetatively with *H. duperreyi*; tetrasporangia have been observed in AD, A51052.

Details of the female reproduction have apparently never been described, though Taylor (1950, p. 513) records carposporophytes for the genus.


*Rhodoplexia preissii* Harvey in W. J. Hooker 1844, pl. 613.

*Haloplegma cornu-damae* Kützing 1862: 19, pl. 63a–c.

**FIGS 134, 141 D**

*Thallus* (Fig. 134A) red-brown, flat and complanately branched, (5–) 10–20 cm high, much branched with main branches 5–10 mm broad bearing laterals marginally of various sizes for 3 or 4 orders, mostly 1–2 mm thick, ultimate branches lobed to pointed, margins smooth, surface felt like. Stipe 2–20 mm long, 1–3 mm broad, holdfast rhizoidal, 2–10 mm across; epilithic or epiphytic on *Amphibolis*. Structure. Marginal apices regularly fringing the blades (Fig. 134B) but not conspicuous due to overtopping by long, curved filaments of the surface clusters; rectangular network filaments present but not conspicuous, cells 35–55 μm in diameter and L/D 3–8 (20). Surface clusters (Fig. 134C) 400–700 μm long, basally branched but with long, unbranched, curved, gently tapering ends 250–500 μm and 15–32 cells long, cells 18–30 μm in diameter and L/D 1–1.5. Cells multinucleate; rhodoplasts discoid to elongate.

Reproduction. Gametophytes dioecious. Carposporophytes (Fig. 141D) borne on short branches on lower cells of surface clusters, details uncertain. Carposporophytes (Fig. 134D) lying within and loosely surrounded by filaments of the surface clusters, with 3–5 rounded gonimolobes 400–700 μm across, all cells forming ovoid carposporangia 10–20 μm in diameter. Spermatangial heads (Fig. 134E, F) terminal on the unbranched filaments of the surface clusters, ovoid, 25–35 μm in diameter, with 5–8 axial cells bearing whorls of cells producing spermatangia.

Tetrasporangia (Fig. 134G) terminal on short branches from the lower to mid cells of the (otherwise) unbranched surface filaments, slightly ovoid, 20–45 μm in diameter, tetrahedrally divided.

**Type** from W. Aust. (*Preiss*); holotype in Herb. Harvey, TCD?

**Distribution**: Widespread in tropical waters, especially the Indian Ocean.

In southern Australia, from Shark Bay, W. Aust. (Huisman *et al.* 1990, p. 96) to Walkerville, Vic., and around Tasmania.

*H. preissii* is a common alga on rough-water coasts of southern Australia, ranging from shaded pool situations to deep water. Var. *flabelliforme* Harvey (1859b: 330) from near Georgetown, Tasmania, appears to be only a slender form of the species, and *H. cornu-damae* is typical of the species.

Weber-van Bosse (1913, p. 136) recorded *H. preissii* from Cargados Carajos (N of Mauritius); this tropical locality is well outside the Australian distribution and the specimen should be checked, especially as to similarities with *H. anweri* Shameel & Nizamuddin (1972, p. 434). Cribb (1983, p. 92) refers the W.v. Bosse record to *H. duperreyi*.

**Tribe SPONGOCOLONIEAE** Schmitz 1889: 450

by H.B.S. Womersley and E.M. Wollaston

**Thallus** erect, 5-30 cm high, much branched usually with long axes and lateral branches, apices conspicuous or not, usually overtopped by branchlets from below, axes and branches loosely corticated below with rhizoids from basal cells of laterals; ecor ticate lateral branchlets more or less determinate, some becoming indeterminate; gland cells absent. Cells multinucleate.

**Life history** triphasic, with isomorphic gametophytes and tetrasporophytes.

**Reproduction.** Gametophytes dioecious. Carpogonial branches borne on the subterminal cell of short, 31-5)-celled, branchlets, with 2 periaxial cells on the third cell; the 3 sterile cells (terminal and 2 periaxial cells) enlarging and becoming rounded after fertilization. The subterminal cell cuts off an auxiliary cell which produces successive, rounded, gonimolobes of carpogonia and, a loose involucre of filaments develops from axial cells below the carpogonophyse which terminates a lateral branch. Spermatangial heads are borne on branchlet cells, sessile or pedicellate, ovoid to elongate, with a row of axial cells bearing whorls of cells producing outer spermatangia.

Tetrasporangia or polysporangia occur on cells of the lateral branchlets, sessile or pedicellate, subperipheral to oviod, with 4 or 32-40 spores.

The tribe Spongoclonieae includes probably three genera, *Spongoclonium*, *Pleurosposorum* and *Lophothamnion*. It is characterised by the 3-celled female axis with carpogonial branches on the subterminal cell, a single auxiliary cell, and the 3 sterile cells enlarging, becoming rounded, but not dividing. This distinctive cell arrangement has been interpreted by Kylin (1925, p. 58), Ardé *et al.* (1982, p. 13), Norris (1985, p. 60) and Wollaston (1990, p. 21) as having the apical cell pushed aside to become one of the periaxial cells, and the subapical cell cutting off a supporting cell which forms a sterile cell and a 4-celled carpogonial branch; a
second sterile periaxial cell is cut off opposite the first periaxial (originally apical) cell. If this
development occurs, it is not easily seen, and in many cases it appears that the two periaxial
cells (which occur almost simultaneously and are of similar size and shape) are both cut off
the third cell of a fairly straight 3-celled axis, and the carpogonial branch directly from the
second cell. Carpogonial branches are borne directly on cells of the whorl-branchlets in the
Antithamnieae and Heterothamnieae, and it would not be surprising for them to be borne
directly on cells of a female axis which then act as supporting cells. While this suggested
displacement is not convincingly evident in all southern Australian species, the situation of 3
rounded and enlarged sterile cells is a conspicuous feature of Spongoclonium and the tribe
Spongoclonieae.

Mesothamnion shows essentially the same reproduction as Spongoclonium and cannot
be satisfactorily separated generically, as having a not or only slightly corticated thallus (as
does S. australicum, described below). Mesothamnion is here considered a synonym of the
older genus Spongoclonium.

The genus Lophothamnion is here kept separate from Pleonosporium, both bearing
polysporangia instead of tetrasporangia. Some species of Spongoclonium (e.g. S. australicum,
S. brownianum) which typically bear tetrasporangia do very occasionally show further divisions
to octosporangia but are here considered distinct from species which uniformly bear multi-
spored (32 or more) polysporangia. In contrast to the view of Norris (1985, p. 61), the distinction
between tetra (rarely octo)sporangia and multispored polysporangia is considered an adequate
generic separation. Lophothamnion is separated from Pleonosporium by its dense, radially
and spirally branched thallus, with overtopped apices, in contrast to the distichously branched
thallus with exserted apices of the type species (P. borreri) and most other species of
Pleonosporium. Norris (1985, p. 60) claims species of Pleonosporium are either spirally or
distichously branched, but this does not occur, apparently, within any one species.

KEY TO GENERA OF SPONGOCLONIEAE

1. Thalli much branched, occurring subtidally. Tetrasporophytes with tetrahedrally divided
tetrasporangia, very rarely octosporangia ...................................... SPONGOCLONIUM
1. Thalli forming dense, dark red-brown, lower eulittoral tufts. Tetrasporophytes with
polysporangia of 32-40 spores ........................................... LOPHOTHAMNION

Genus SPONGOCLONIUM Sonder 1855: 515

Thallus erect, 5–30 cm high, much branched irregularly with or without prominent axes,
densely corticated at least on mid and lower axes by branched, entwined, rhizoids produced
from the basal cells of laterals, forming moderate to thick spongy axes, plus an outer cortex of
lax, branched filaments variable in length; axial and branch cells each producing a single,
radially or distichously branched, branchlet or ultimate ramulus. Cells multinucleate.

Reproduction. Gametophytes dioecious. Procarp systems enclosed in a gelatinous sheath,
carpogonial branches borne on the subterminal cell of short, lateral, 3 (-5)-celled branches,
with 2 periaxial cells on the third cell; the three sterile cells (terminal cell and 2 periaxial
cells) enlarge and become rounded. Post-fertilization the auxiliary cell produces successive,
rounded, gonimolobes and a loose involucre of filaments develops from axial cells below the
carposporophyte, which is terminal on a lateral branch of 4–10 cells. Spermatangial heads are
borne on branchlet cells, sessile or pedicellate and ovoid to elongate, with 4–8 axial cells
bearing branched whorls with ultimate spermatangia.

Tetrasporangia occur on branchlet cells, sessile or pedicellate, subspherical to ovoid,
tetrahedrally divided.

Type species: S. conspicuum Sonder 1855: 515.

A genus of 10–15 species (including species placed in Mesothamnion), with 4 species on
southern Australian coasts. The features of Spongoclonium conspicuum have been clarified
by Wollaston (1990) and 2 other species (S. brownianum and S. fasciculatum) show the features of the type species, together with a newly described species.

Several other species were placed under Spongoclonium by J. Agardh (1892, pp. 39–42) and De Toni (1903, pp. 1357–1364), followed by Lucas (1927). These are now placed in other genera as follows:

- S. wollastonianum is Dasythamnilla wollastonianana [including S. wilsonianum].
- S. dasyurum is Dasythamnilla dasyura [incl. D. setosa].
- S. latissinum is Dasythamnilla latissima.
- S. angustatum is Hirusatihallia angustata.
- S. violaceum is Callithamnion violaceum [including S. paradoxum and S. scoparium].

**KEY TO SPECIES OF SPONGOCOLOMNIUM**

1. Thallus slender, corticated only slightly below. ..................................... 4. *S. australicum*

1. Thallus robust, heavily corticated on axes and lateral branches ........................................ 2

2. Axes densely corticated to near the apices, clothed with simple or basally branched branchlets decreasing only slightly in diameter from 20–30 μm basally to (10–) 14–22 μm in diameter near their apices; tetrasporangia on 1–3-celled pedicels ................................................................. 1. *S. conspicuum*

2. Axes moderately to densely Corticate in mid and lower parts, eCorticate over the upper 20–40 cells; tetrasporangia sessile or pedicellate ................................................ 3

3. Branchlets in fascicles, basally branched, straight to slightly curved, basally 10–22 μm in diameter, apical cells 8–13 μm in diameter; tetrasporangia usually sessile ............................................. 2. *S. fasciculatum*

3. Branchlets curved, basally 25–55 (-100) μm in diameter, apical cells 12–20 μm in diameter; tetrasporangia sessile or often pedicellate ............................................. 3. *S. brownianum*


**Reproduction.** Gametophytes dioecious. Carpogonial branches (Fig. 136B) borne on short, 3-celled, lateral branches on limited indeterminate branches along the main laterals. The subterminal cell cuts off a 4-celled carpogonial branch (Fig. 136B), with the third cell bearing 2 opposite sterile periauxial cells; a distinct gelatinous sheath encloses the fertile axis, and the three sterile cells (apical, and 2 periauxial) enlarge considerably and become rounded, often remaining visible in mature carposporophytes (Figs 135C, 136C). Post-fertilization an auxiliary cell is cut off from the supporting cell and the gonimoblast cell develops several rounded gonimolobes successively (Fig. 135C), lobes (150-) 200–400 μm across, carposporangia ovoid, (15-) 20–30 (-50) μm in diameter. Axial cells below the developing carposporophyte produce
Spongoclonium an involucre of filaments. Spermatangial heads (Figs 135D, 136D) are borne on cells of branchlets in mid to upper parts of the thallus. Each head has 1–2 stalk cells and is 20–45 μm in diameter and 50–70 μm long, with an axis of 8–10 cells bearing whorls of 2–4 cells, the terminal initials producing ovoid spermatangia 2–2.5 μm in diameter.

Tetrasporangia (Fig. 136E) are borne on outer cells of the branchlets, on 1–3-celled pedicels (which may branch and form further tetrasporangia), subspherical and 25–45 (–55) μm in diameter, tetrahedrally divided.

Type from Cape Liptrap, Victoria (Mueller, 1853); holotype missing from MEL, 1007336 (see Wollaston 1990, p. 21).

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

**Spongozonium**

**Spondoglonieae**


*S. conspicuum*, and its relationships with the superficially similar *Lasiothallia hirsuta*, have been clarified by Wollaston (1990).


**FIG. 137**

**Thallus** (Fig. 137A) erect, medium to dark red-brown, 10–30 cm high, irregularly branched (Fig. 137B) with one to a few main axes and strongly developed main laterals, densely corticated in mid and lower parts but branches ecoricate for many cells below their apices. Holdfast rhizoidal, 5–12 mm across; epilithic or on Amphibolis. **Structure.** Axial cells 50–120 μm in diameter near apices, 130–250 μm in diameter below and L/D 2–7, longer basally within the cortication; each axial cell bearing a single, spirally arranged, ecoricate, basally branched, branchlet, often clustered or fasciculate but readily denuded in parts, tapering from 10–22 (–30) μm in diameter basally, cells L/D 4–6, to 8–13 μm in diameter, cells L/D 4–5, near their apices; cortical rhizoids (10–) 20–40 μm in diameter, cells L/D 4–6. Cells multinucleate; rhodoplasts discoid.

**Reproduction.** Gametophytes dioecious. Carposgonial branches 4-celled, borne on the subterminal cell of short, lateral, 3-celled branchlets, with the third cell bearing 2 sterile perialarial cells; the 3 sterile cells enlarge and become rounded. Following fertilization, the auxiliary cell produces successive, rounded, gonimolobes (Fig. 137B, C) 130–350 μm across with carposporangia 10–20 μm in diameter, and a loose involucre of filaments develops from axial cells below the carposporophyte. Spermatangial heads (Fig. 137D) are borne on cells of branchlets in the mid to upper thallus. Each head is sessile (without a stalk cell), 50–70 (–90) μm long and 40–50 μm in diameter, with an axis of 6–8 (–10) cells bearing whorls of cells and ultimate spermatangia 2–3 μm in diameter.

Tetrasporangia (Fig. 137E) occur on branchlets in the mid and upper thallus, sessile, subspherical to slightly ovoid, (20–) 40–50 μm in diameter, tetrahedrally divided.

**Type** from Port Phillip Heads, Vic. (*Wilson*); holotype in Herb. Agardh, LD, 18629.

**Distribution:** Port Houton, W. Aust., to Westernport Bay, Vic., and the N coast of Tasmania.


The holotype of *S. fasciculatum*, as for all herbarium specimens of the species, adheres closely to paper and is difficult to study; it appears to be a somewhat denuded cystocarpic specimen.

*S. fasciculatum* is closely related to *S. conspicuum*, differing in being less strongly corticated with upper branches largely ecoricate, in having more fasciculate branchlets which
taper gently throughout their length, in sessile spermatangial clusters, and in sessile tetrasporangia.


![Fig. 137 Spongoclonium fasciculatum (A-D, AD, A20152, E, AD, A28854).](image_url)

**FIGS 136F–J, 138**

*Thallus* (Fig. 138A) erect, medium red-brown, 3–15 cm high, irregularly alternately branched, usually with a main axis and well-developed laterals, corticated with rhizoids on mid and lower parts, ecorticate above. Holdfast rhizoidal, 2–8 (-12) mm across, epiphytic on *Posidonia, Amphibolis* or larger algae, or epilithic. Structure. Axial cells 27–55 μm in diameter near apices and L/D 1.5–2, 200–700 μm in diameter and L/D 2–4 below, bearing spirally arranged ecorticate branched branchlets tapering from 25–55 (-100) μm in diameter, cells L/D 2–3, to 12–20 (-27) μm in diameter, cells L/D 1.5–3 (-4), near their apices, upper parts usually curved (Fig. 138B); cortical rhizoids 10–20 μm in diameter, cells L/D 3–8 (-12). Cells multinucleate; rhodoplasts discoïd to elongate.

Reproduction. Gametophytes dioecious. Carpogonial branches (Fig. 136F) borne on the subterminal cell of fertile axes 4 to several cells long, the subterminal cell bearing the 4-celled carpogonial branch and the third cell bearing 2 opposite, sterile, periaxial cells (Fig. 138C), with the terminal and 2 sterile periaxial cells enlarging and becoming rounded. Post-fertilization the supporting cell cuts off an auxiliary cell and the carpogonium cuts off two connecting cells, with the carpogonial branch cells partially fusing. The auxiliary cell cuts off an apical gonimoblast initial which produces a first gonimolobe (Fig. 136G), then successively 3 or 4 more (Figs 136H, 138D), each 180–540 μm across, with subspherical carposporangia 10–27 μm in diameter; the supporting cell and sterile cells of the procarp fuse to form a darkly-staining triangular mass with 3 projecting cells. The fourth cell of the fertile axis and lower axial cells produce curved involucral filaments around the carposporophyte. Spermatangial heads (Figs 136I, 138E) are elongate, 35–50 μm in diameter and L/D 2–4, sessile on lower cells of the branchlets, with 5–8 axial cells and outer spermatangia 2–3 μm in diameter. Tetrasporangia (Figs 136J, 138F) are borne on lower cells of the branchlets, sessile or on 1–2-celled pedicels (which may produce a further tetrasporangium or a small fascicle), subspherical, 25–50 μm in diameter, tetrahedrally divided (rarely octosporangia).

Type from “Rottnest, Fremantle and King George Sound”, W. Aust.; lectotype tetrasporangial (Harvey, Trav. Set 264) from King George Sound, in TCD.

Distribution: North Beach, Perth, W. Aust., to Flinders, Vic., and SE Tasmania.


In TCD there are several specimens of Harvey’s Trav. Set 264, including two from King George Sound, one tetrasporangial and one male. The former is selected as lectotype since Harvey originally described tetrasporangia.

*S. brownianum* differs from *S. fasciculatum* in dimensions of the broader branchlets, in producing procarps on relatively longer axes, and in having tetrasporangia either sessile or pedicellate.

*S. brownianum* var. majus Harvey (1863, synop.: ii) from W. Aust. and Port Fairy, Victoria [lectotype Alg. Aust. Exsicc. 511, from Swan R., W. Aust. (Clifton)] appears to be only a larger form with denser branching.


**FIGS 139, 141A, B**

*Thallus* (Fig. 139A) erect, flaccid, red-brown to grey-red, 1–8 (-12) cm high, much branched with slender axes and irregular laterals (Fig. 139B), older axes often loosely corticated.
Fig. 139. *Spongoclonium australicum* (AD, A66797). A. Habit. B. Branch with laterals and branchlets. C. Branchlets with two procarp systems. D. Carposperophyte with rounded sterile cells (arrows). E. Branchlets with spermatangial heads. F. Spermatangial heads. G. Branchlets with sessile tetrasporangia.
with rhizoids. Holdfast small, rhizoidal, 2–5 mm in diameter; epilithic or epiphytic on seagrasses or various algae. Structure. Axis radially branched, apices inconspicuous, each axial cell with a single more or less determinate lateral branchlet. Axial cells 20–40 μm in diameter and L/D 2–4 near apices, increasing to 150–300 μm in diameter and L/D (1–) 2–4 (-5) near the base; lateral branchlets 0.4–1 mm long (some developing as indeterminate laterals), basal cells 25–40 μm in diameter and L/D (2–) 3–4, decreasing gradually to 10–15 μm in diameter and L/D 2.5–5 (–8) in subterminal cells. Corticating rhizoids relatively few, descending from basal cells of lateral branchlets, slender, 10–20 μm in diameter with long cells. Cells multinucleate; rhodoplasts discoid to elongate and branching, becoming ribbon-like in larger cells.

Reproduction. Gametophytes dioecious. Procarps (Figs 139C, 141A, B) borne on short special lateral branches on upper branches, 3 cells long with the subapical cell bearing directly a 4-celled carpogonial branch and the third cell bearing two opposite perialxial cells which remain undivided; the 3 sterile cells (apical and perialxial) enlarge and become rounded (Fig. 139D). Post-fertilization the auxiliary cell is apparently cut off the subterminal (supporting) cell and 3–4 successive rounded gonimolobes 200–450 μm across are produced, each with all cells becoming ovoid-angular carposporangia 10–22 μm in diameter; curved involucral branchlets arise from the axial cell below the female branchlet. Spermatangial heads (Fig. 138E, F) usually adaxial on cells of branchlets, 25–45 μm in diameter and L/D 1.5–2.5, sessile, with 3–4 axial cells each cutting off several cells producing spermatangial initials and ovoid spermatangia 1.5–2.5 μm in diameter.

Tetrasporangia (Fig. 139G) borne on successive cells of branchlets, usually adaxially, sessile, subspherical to ovoid, 25–45 μm in diameter, tetrahedrally divided, occasionally further divided (to octosporangia).

Thallus erectus, flaccidus, 1–8(–12) cm altus, ramosissimus axibus gracilibus et lateralibus irregularibus; axes magis veteres laxe corticati. Hapteron parvum rhizoidale, 2–5 mm diametro epilithicum vel epiphyticum in maris graminibus vel algis. Structure. Axis radiatim ramosus, apicibus inconspicuis; omnes cellulae axiales ramulo singuli par minusve deterterminates. Cellulae axiales 20–40 μm in diametro et L/D 2–4 prope apices, crescentes ad 150–300 μm diametro et L/D (1–) 2–4 (-5) prope basim; ramuli laterales 0.4–1 mm longi (aliaque velut laterales indeterminati evolutentes); cellulae basales 25–40 μm diametro et L/D (2–) 3–4, gradatim decrescentes ad 10–15 μm diametro et L/D 2.5–5 (–8) in cellulis subterminalibus. Rhizoidea corticalia relativo paucia descendentia e cellulis basalibus ramorum lateralium gracilis, 10–20 μm diametro longis cellulis. Cellulae multinucleatae; rhodoplastes discoidei ad elongati et ramos, tenuiformes in cellulis maioribus.


Tetrasporangia in ramorum successivis plerumque adaxialia sessilia, subsphericalia ad ovoidea, 25–45 μm diametro, tetraedrice divisa, interdum plus in octosporangia divisa.

Type from Muston, American R. inlet, Kangaroo I., S. Aust., 3 m deep on Heterozostera (J. Lavers, 7.ix.1996); holotype in AD, A66797.


Lophothamnion SPONGOCLONIEAE 297


This lightly corticated species might be placed in the genus Mesothamnion Börgesen, but as noted above there are no reproductive differences between this genus and Spongoclonium, which is here considered to include Mesothamnion. It differs from the type species, M. caribaeum Börgesen (1917, p. 208, figs 194–200) in being a larger plant, more corticated, and having generally longer axial cells.

**Genus LOPHOTHAMNION J. Agardh 1892: 42**

*Thallus* erect, 5–15 cm high, much branched with one to several main axes and lateral branches, bearing basally branched lateral branchlets with long, unbranched terminal parts; axes corticated below by entwined rhizoids from the basal cells of branchlets or laterals. Active apices spirally branched, usually surrounded by lower mature branchlets. Cells multinucleate.

**Reproduction.** Gametophytes dioecious. Carpogonial branches borne on the subterminal cell of short, 3-celled branches, with a carpogonial branch of 4 small cells, and the third cell bearing two sterile periaxial cells; post-fertilization the 3 sterile cells enlarge and become rounded, and the auxiliary cell produces 1–4 successive rounded gonimolobes, with the carposporophyte becoming surrounded by involucral branchlets from below. Spermatangial heads are borne on lower cells of lateral branchlets, elongate-ovoid.

Polyosporangia sessile on lower cells of lateral branchlets, subspherical, with about 32 spores.

**Type species:** *L. comatum* J. Agardh 1892: 43 [= *L. hirtum* (Hooker & Harvey) Womersley].

*Lophothamnion* is closely related to *Spongoclonium*, having very similar procarps and carposporophytes, including enlarged and rounded sterile cells as in *Spongoclonium*, but differs in having polyosporangia (32–40 spores) instead of tetrasporangia. This conspicuous difference in sporangia (*Spongoclonium* having typically 4 spores per sporangium, very rarely with 8) is considered a satisfactory difference to separate the 2 genera.

**Lophothamnion hirtum** (Hooker & Harvey) Womersley, comb. nov.

*Callithamnion hirtum* Hooker & Harvey in Harvey & Hooker 1845: 192, pl. 78 fig. 2.

*Pleosporium hirtum* (Hooker & Harvey) Laing 1905: 393, pl. 27 fig. 1. Adams 1994: 252, pl. 93 upper right.

*Lophothamnion comatum* J. Agardh 1892: 43.


**FIGS 140, 141C**

*Thallus* (Fig. 140A) erect, flaccid, dark red-brown, 5–15 cm high, densely and irregularly spirally branched (Fig. 140B) with one to several main axes and prominent lateral branches with dense rhizoidal cortication on mid and lower axes (1–2.5 mm in diameter) and laterals; ecorcicate lateral branchlets spirally arranged, 1–2 mm long, with long, curved, unbranched terminal branches. Holdfast conical, rhizoidal, 2–25 mm across; epilithic. **Structure.** Axial cells 50–60 μm in diameter and L/D 1.5–2 above, increasing to 200–300 μm in diameter and L/D 1–2 (-4) below. Lateral branchlets basally branched 1–5 times with long ends tapering only slightly, (20-) 30–50 (-60) μm in diameter with cells L/D (1-) 1.5–2 (-3), terminal cells with rounded ends. Cells multinucleate; rhodoplasts discoid, densely aggregated.

**Reproduction.** Gametophytes dioecious. Carpogonial branches (Fig. 141C) of 4 small cells, on the subterminal cell of short, 3-celled lateral branches and the third cell bearing two sterile periaxial cells; post-fertilization the 3 sterile cells enlarge and become rounded (Fig. 140C) and the auxiliary cell produces 1–4 successive rounded gonimolobes (Fig. 140D) 200–600 μm across of ovoid carposporangia (10-) 20–50 μm in diameter; carposporophytes become
Fig. 140. Lophothamnion hirtum (AD, A66723). A. Habit. B. Branch with branchlets and carposporophytes. C. Young carposporophyte with 3 rounded sterile cells (arrows) and young gonimoblasts. D. Mature carposporophyte with involucral branchlets. E. Spermatangial heads. F. Branchlets with polysporangia.
surrounded by numerous involucral branchlets from cells below them. Spermatangial heads
(Fig. 140E) elongate-ovoid, sessile on lower cells of branchlets, 30–60 μm in diameter and
L/D 2–3 (–4), with 4–5 axial cells producing whorls and ultimate spermatangia.

Polysporangia (Fig. 140F) usually adaxial on lower cells of branchlets, sessile, 
subspherical, (50-) 80–120 (–140) μm in diameter, with 32–40 spores.

Type from the Auckland Is; holotype in Herb. Hooker, BM.

Distribution: New Zealand (S North I. to Auckland Is).
Cape Carnot, S. Aust., to Warrnambool, Vic., and around Tasmania.


There is no apparent difference between the Australian *L. comatum* and the earlier named *C. hirtum* from the Auckland Is, now well known from the southern part of New Zealand and common in the lower eulittoral on Stewart I.

J. Agardh (1892, p. 43) gave “australes Novae Hollandiae et Tasmaniae” as the original localities for *L. comatum*, and in LD are specimens from Port Fairy, Vic., and Orford, Tas. (Meredith), as well as ones from Port Elliot, S. Aust. (Hussey) probably received after the original description. A Port Fairy specimen is selected as lectotype, with two isolectotypes. *L. comatum* is a common species on lower intertidal rock, especially from Robe eastwards and eastern Tasmania.

Tribe MONOSPOREAE Schmitz & Hauptfleisch 1897: 483, 488

by J.M. Huisman & H.B.S. Womersley

*Thallus* erect, uniseriate, eocortic, subdichotomous or alternately branched radially or distichous, or polychotomous below; attachment by unicellular, simple or lobed rhizoids from lower cells of erect or semiprostrate main axes. Cells multinucleate, apical cells dividing transversely, usually overtopped by lateral filaments.

*Life history* directly from propagules or triphasic with isomorphic gametophytes and tetrasporophytes.

*Reproduction*. Asexual propagules ovoid, of 1–3 (–4) cells, sessile or pedicellate, multinucleate, liberated and germinating as a whole.

Gametophytes dioecious. Procarps borne on subapical cells of short axes, with 2 or 3 periaxial cells (one bearing a 4-celled carpogonial branch) and 1 or 2 auxiliary cells, producing 1–3 gonimolobes with all cells becoming carposporangia; fusion cell from the carpogonial branch present or absent. Sterile cells of the procarp usually form an inner involucre after fertilization, and outer involucral branches may arise from 1 or 2 cells just below the procarp (*Deucalion* and *Tanakuellea*).

Tetrasporophytes with tetrahedrally divided sporangia or polysporangia.


The tribe Monosporeae was recognised by Huism & Gordon-Mills (1994) to include 7 genera, 5 of which are here considered to occur on southern Australian coasts. The other two are *Monosporus*, based on *M. pedicellatus* (J.E. Smith) Solier in Castagne (1845, p. 242) which is unknown reproductively apart from monosporangia and uncertain reports of tetrasporangia, and *Desikacharyella* Subramanian (1984) from the southern coast of India. The Australian *Monosporus australis* is here transferred to *Mazoyerella* (see below).

The genera of the Monosporeae are grouped together by their possession of multinucleate, 1–3 (–4)-celled asexual propagules, similarities in habit with subdichotomous to alternate branching and relatively large multinucleate cells, and similarities in the procarp and post-fertilization structures. Gametophytes are now known in most genera (except *Monosporus*),
sometimes only in culture, and are usually rare. However, propagules are usually present and distinctive for each genus.

**KEY TO GENERA OF MONOSPOREAE**

1. Propagules unicellular, with a single elongate stalk cell; procarps with 2 periaxial cells; polysporangia with 8 or 16 spores ....................................................... MAZOYERELLA

2. Propagules uni- to tri-cellular, usually with an elongate, short discoid or 1–2 isodiametric stalk cells; procarps with 3 periaxial cells; tetrasporangia or polysporangia ................. 2

3. Propagules of 3 subequal cells and with a short stalk cell; carposporophyte with only outer involucral filaments present, from hypogenous and subhypogenous cells ..................................................................................................................... DEUCALION

4. Propagules with a single, discoid, basal cell; both inner and outer involucral filaments present ........................................................... TANAKAELLA

5. Propagules with a small trapeziform basal cell and 2 short stalk cells; inner involucral filaments only present ................................................... GUIRYELLA

Genus MAZOYERELLA Gordon-Mills & Womersley 1974: 134

*Thallus* erect, subdichotomous, slender, attached from prostrate or erect axes by rhizoids; cells multinucleate.

*Reproduction.* Propagules ovoid, unicellular with a single, elongate stalk cell.

Gametophytes dioecious. Procarps on subterminal cells of short axes, with 2 periaxial cells, one bearing a 4-celled carpogonial branch and also a sterile terminal cell; post-fertilization slight fusion of the carpogonial branch cells occurs, a single auxiliary cell is cut off from the supporting cell, and 2 or 3 successive gonimolobes develop. The sterile cells of the procarp form inner involucral filaments, and the hypogenous cell of the fertile axis develops a vegetative branch. Spermatangial heads occur on upper thallus cells.

Polysporangia are sessile on upper thallus cells, subspherical, with 8 or 16 spores.


*Monosporus australis* is here transferred to Mazoyerella as the second southern Australian species, following observations by Huisman of the procarp structure and spermatangial heads in culture (Huisman & Gordon-Mills 1994, p. 87). Unfortunately no post-fertilization stages were seen, but the known sexual and polysporangial reproduction is identical with that of comparable stages in *Maz. arachnoidea* apart from absence of involucral filaments from the sterile procarp cells; this development may well be dependent on fertilization.

The genus *Monosporus* is now restricted to the type species *M. pedicellatus*, for which sexual reproduction is unknown and only tetrasporangia are reported, and possibly *M. indicus* Bergesen (1931) – see also Ballantine (1996, p. 12, figs 1–3) and Bucher & Norris (1995, p. 15), and M. inkyui Kim & Choi (1996), although the latter has the propagule morphology of Tanakaella. Monosporus is discussed by Huisman & Kraft (1982, p. 189).

**KEY TO SPECIES OF MAZOYERELLA**

1. Thallus much branched, upper filaments very slender, 4–16 μm in diameter ................................................................. 1. *Maz. arachnoidea*
1. **Thallus subdichotomously branched, filaments robust, (20-) 40–150 μm in diameter in upper and mid cells .................................................. 2. **Maz. australis

*Corynospora arachnoidea* Harvey 1859b: 333.  

**FIGS 142A–D, 143A–D**  
Thallus (Fig. 142A) dark red-brown, erect, 0.5–4 (-5) cm high, forming slender, much branched tufts, subdichotomously branched every 1–3 (-6) cells (Fig. 142B); prostrate filaments absent. Attachment by elongate multicellular rhizoids from lower axial cells. Epiphytic on *Dasya villosa* or probably epilithic.  

**Structure.** Apical and upper cells 4–16 μm in diameter and L/D 4–20, median cells (20-) 25–50 μm in diameter and L/D 4–10, lower cells 100–250 μm in diameter and L/D 4–10. [Lower cells in one collection (AD, A41085) 250–450 μm in diameter with corticating rhizoids within the cell wall.] Cells multinucleate; rhodoplasts discoid to elongate, reticulate in larger cells.  

**Reproduction.** Propagules (Figs 142B, 143B) on unicellular stalks on cells of erect filaments, single celled, elongate-ovoid, (40-) 60–90 μm in diameter, multinucleate.  
Gametophytes dioecious. Procarps (Fig. 143B) on the subapical cell of short 2-celled axes on a larger subhypogenous cell which develops a lateral branch, with 2 periaxial cells, one (the supporting cell) bearing a 4-celled carpogonial branch and a terminal sterile cell. Post-fertilization the auxiliary cell produces usually 3 gonimolobes 40–160 μm across of ovoid carposporangia 15–30 μm in diameter, and the sterile procarp cells (apical, sterile periaxial and supporting sterile cell) produce slender involucral filaments around the young carposporophyte (Fig. 142C). Spermatangial heads (Fig. 142D) sessile on upper cells, slightly elongate, 25–35 (-55) μm in diameter, with usually 4 axial cells (Fig. 143C) producing initials radially and outer spermatangia. Polysporangia (Fig. 143A, D) occur on upper cells, sessile, subospherical, 35–65 μm in diameter, with 8 or 16 spores.  

**Type** from Georgetown, Tas. (Harvey); lectotype in Herb. Harvey, TCD.  

**Distribution:** Troubridge Light to American R. inlet, Kangaroo I., S. Aust., and N Tasmania.  


Collection AD, A37361, from Elliston, S. Aust., was incorrectly placed by Gordon-Mills & Womersley (1974, p. 127) under *M. arachnoidea*, but separated by Huisman & Gordon-Mills (1994, p. 82) as the type of *Tanakaella itonoi*.  

2. **Mazoyerella australis** (Harvey) Huisman & Womersley, comb. nov.  

**FIGS 142E–H, 143F, F**  
Thallus (Fig. 142E) medium to dark red, erect, 5–9 cm high, corticulate, subdichotomous and often flabellate. Attachment by short descending rhizoids from basal cells; epiphytic or possibly epilithic. **Structure.** Apical cells 20–80 μm in diameter and L/D 2–10, increasing to 120–150 μm in diameter and L/D 3–6 in the central thallus and 200–600 (-800) μm in diameter.
and L/D 4–10 near the thallus base. Cells multinucleate; rhodoplasts discoid to elongate, ribbon like in larger cells.

**Reproduction.** Propagules (Fig. 142F, G) arising on subapical cells, when mature with a stalk cell 40–70 μm long and 35–60 μm in diameter, subtending an ovoid propagule 70–120 μm in diameter and 180–270 μm long, with the parent cell developing a lateral branch so that the propagule appears axillary. Propagules with 20–50 nuclei and numerous small vacuoles, stalk cell with 4–5 nuclei.

Gametophytes known only in culture. Female axes (Fig. 143E) of 2 cells and a larger hypogenous cell. Subapical cell with 2 periauxial cells, one (the supporting cell) bearing a 4-celled carpogonial branch and a terminal sterile cell. Post-fertilization stages unknown. Spermatangial heads (Figs 142H, 143F) ovoid, sessile, 90–100 μm in diameter, with 5–6 axial cells bearing whorls of cells and ultimate spermatangia.

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Polysporangia (142G) subspherical to slightly ovoid, situated in branch axils, 90–120 μm in diameter, with 8 spores.

*Lectotype* from Rottnest I., W. Aust. (Harvey); in Herb. Harvey, TCD (Trav. Set 344).

**Distribution:** Rottnest I., W. Aust., to Westernport Bay, Victoria.


**Genus** Deucalion Huisman & Kraft 1982: 178

*Thallus* erect, ecorticate, with a central axis bearing alternate distichous lateral branches for 2 orders, the third order largely adaxially branched, attached by the basal cell and rhizoids from the lower cells; cells multinucleate.

**Reproduction.** Propagules 3-celled, ovoid, with the central cell larger than the apical and basal cells, borne on a short stalk cell.

Gametophytes dioecious. Procarps on the subterminal cell of a 2–3-celled axis, with 3 periaxial cells, one being a supporting cell with a carpogonial branch and a terminal sterile cell. Post-fertilization 2 auxiliary cells are formed with the sterile procarp cells remaining undivided but a branched involucre arising from the hypogenous and subhypogenous cells; carposporophytes with 2 gonimolobes developed from the 2 auxiliary cells. Spermatangial heads formed in adaxial series on lateral branchlets.

Polysporangia are borne on lower cells of branchlets, sessile, with 24–36 spores.

**Type species:** Deucalion levringii (Lindauer) Huisman & Kraft 1982: 179, figs 2–20.

A monospecific genus distinguished by the distichous habit, presence of 3 periaxial cells on the subapical cell of the female axis, two auxiliary cells, an outer involucre, polysporangia and 3-celled propagules.


**FIGS 143G, H, 144**

*Thallus* (Fig. 144A) erect, red-brown, 4–10 cm high, complanately branched with alternately distichous laterals for 2 orders, the third order largely adaxially branched. Attachment by the basal cell and rhizoids from the 3–4 lowest cells of the main axes; epilithic or on mussels. **Structure.** Apical cells 35–55 μm in diameter and L/D (1-) 2–4, dividing transversely, increasing to median cells 160–220 μm in diameter and L/D 1.5–2.5 and 250–380 μm in diameter and L/D (1-) 4–6 in lower cells. Cells multinucleate; rhodoplasts discoid to elongate, ribbon like in larger cells.

**Reproduction.** Propagules (Fig. 144B, E) 3-celled, ovoid, with the central cell larger than the apical and basal cells, 100–150 μm in diameter and 200–280 μm long, borne on a short (L/D 1.5–2) stalk cell in branch axils.

Gametophytes dioecious. Procarps (Fig. 143G) on subterminal cells of a 2 or 3-celled axis, with 3 periaxial cells, one being a supporting cell with a 4-celled carpogonial branch and a terminal sterile cell. Post-fertilization an outer involucre of branched filaments arises from the hypogenous and subhypogenous cells. Carposporophytes (Fig. 144C) of 2 gonimolobes from 2 auxiliary cells. Spermatangial heads (Figs 143H, 144D) in adaxial series on lateral branches, sessile, elongate, with axes 5 cells long, cutting off spermatangia directly or via initials.

Polysporangia (Fig. 144E) on upper ends of lower cells of branchlets, sessile, subspherical, 80–100 μm in diameter, with 24–36 spores.
Type from Pihama, Taranaki, New Zealand, drift (Lindauer, 10.ii.1946); holotype in Herb. Lindauer, AKU, 7165. Isotypes distributed in Algae Nov.-Zel. Exsicc. No. 325.

Distribution: New Zealand.

In southern Australia, from Portland to Flinders, Western Port, Vic., E Tasmania and to Port Hacking, N.S.W.


Fig. 144. Deucalion levringii A, B, E, MELU, 23825; C, MURU, JH2035; D, culture from MELU, 23824). A. Habit. B. Filaments with 3-celled propagules. C. Carposporophyte with 2 gonimolobes and involucral filaments. D. A spermatangial head. E. Filaments with a propagule and a polysporangium. (A, B, D, E, as in Huisman & Kraft 1982, courtesy of J. Phycol.; C, as in Huisman & Gordon-Mills 1994, courtesy of Phycologia.)
Anisoschizus MONOSPORAE 307


Deucalion levingii was considered by Huisman & Kraft (1982, p. 179) to be a recent adventive from New Zealand.

Genus ANISOSCHIZUS Huisman & Kraft 1982: 185

Thallus erect, ecoricate, of slender much branched filaments arising from prostrate axes attached by rhizoids. Cells multinucleate.

Reproduction. Propagules ovoid, 2-celled with the upper cell larger, borne on a very short stalk cell.

Gametophytes dioecious. Procarps borne on the subapical cell of a 2-celled axis on a larger hypogenous cell, with 3 periaxial cells, one being the supporting cell with a 4-celled carpogonial branch and an apical sterile cell. Post-fertilization auxiliary cells are cut off the supporting cell and the opposite periaxial cell and each develops 2–3 gonimolobes. Carpogonial branch cells fuse and sterile procarp cells each produce 1–3 branched inner involucral filaments enveloping the carposporophyte. Spermatangial heads are borne singly on median cells of the thallus.

Polyosporangia occur in branch axils, subspherical, with 8 spores.

Type species: A. propaguli Huisman & Kraft 1982: 185.

Anisoschizus is a monospecific genus, named and distinguished by the propagules with 2 unequal cells.


FIGS 145A–D, 146A–C

Thallus (Fig. 145A) erect, 3 mm to 4 cm high, red-brown, slender and much branched subdichotomously, arising from short prostrate filaments attached by septate rhizoids; epilithic, on timber, or epiphytic on Sporochnus. Structure. Apical cells 10–25 μm in diameter and L/D 4–7, median cells 40–60 μm in diameter and L/D 3.5, lower and prostrate filament cells 50–130 μm in diameter and L/D 2–4. Cells multinucleate; rhodoplasts elongate, ribbon like in larger cells.

Reproduction. Propagules (Fig. 145B, D) 2-celled, ovoid with the upper cell larger and 90–120 μm in diameter, borne on a short stalk cell on the upper end of branch cells.

Gametophytes dioecious. Procarps (Fig. 146A) borne on the subapical cell of short 2-celled axes, with the hypogenous cell bearing an elongate lateral cell. Subapical cell with 3 periaxial cells, one (the supporting cell) bearing a 4-celled carpogonial branch and a sterile cell. Post-fertilization, 2 auxiliary cells are cut-off from the supporting cell and the opposite periaxial cell, and via connecting cells each develops 2 or 3 sequential gonimolobes 80–150 μm across, with ovoid carposporangia 16–30 μm in diameter. Carpogonial branch cells fuse and sterile cells of the procarp (apical, sterile periaxial and supporting sterile cells) produce 1–3 branched inner involucral filaments (Fig. 145C) which envelop the carposporophyte (Fig. 146B). Spermatangial heads (Fig. 146C) occur on adaxial ends of median thallus cells, elongate-ovoid, 25–35 μm in diameter.

Polyosporangia (Fig. 145D) occur on the upper end of cells, subspherical, 40–60 μm in diameter, with 8 spores.

Type from Portsea Pier, Port Phillip Bay, Vic. (Huisman, 29.viii.1980); holotype in MELU, 23826.

Distribution: Hopetoun, W. Aust., to Western Port, Victoria.
Fig. 145. A–D. Anisoschizus propaguli (A, B, D, MELU, 23826; C, MELU, Kraft7440). A. Habit of holotype. B. A 2-celled propagule. C. Carposporophyte with 2 gonimolobes and involucral filaments. D. Filaments with a young propagule, a mature polysporangium and a juvenile one (lower right) at the tetra stage. E, F, Tanakaeila ilonoi (AD, A37361). E. Habit of holotype on Kallymenia cribrosa. F. Filaments with propagules. (A, B, D, as in Huisman & Kraft 1982, courtesy of J. Phycol.; C, E, F, as in Huisman & Gordon-Mills 1994, courtesy of Phycologia.)
Selected specimens: Hopetoun, W. Aust., on Sponochmus, 3–4 m deep (Kraft, 16.viii.1979; MELU).
Daly Head, Yorke Pen., S. Aust., on Sponochmus radiciformis, drift (Woelkerling, 26.iii.1967; AD, A31408).
Warrambool, Vic., on S. radiciformis, drift (Kraft, 11.i.1984; MELU, Kraft 7440). Flinders, Western Port, Vic., on pier (Huisman & Gabrielson, 3.ix.1981; MELU, 24020).

Genus TANAKAELLA Itono 1977: 46

Thallus erect, small, eocorticke, much branched irregularly subdichotomously from prostrate basal filaments, attached by branched haptera. Cells multinucleate.

Reproduction. Propagules ovoid, single celled, with a single small discoid basal cell.
Gametophytes dioecious. Procarps borne on the subapical cell of short axes, with 3 periaxial cells, one (the supporting cell) bearing a 4-celled carpogonial branch and a terminal sterile cell. Post-fertilization the supporting cells cuts off an auxiliary cell which produces successive gonomolobes, and 3 inner involucral filaments are formed from the apical cell, one periaxial cell, and either the second periaxial or the apical cell on the supporting cell. Spermatangial heads occur on median cells of the thallus.

Tetrasporangia occur on axial cells, subspherical, tetrahedrally divided.


T. japonica Itono, from Mageshima, Japan, was placed by Itono in the Sphondylonthamnieae, but transferred by Huisman & Gordon-Mills (1994, p. 85) to the Monosporeae.

Silva et al. 1996: 430.

FIGS 145E, F, 146D, H, 147A–C

Thallus (Fig. 145E, F) red-brown, 1–5 mm high, forming small erect tufts, subdichotomously branched, from prostrate basal filaments. Attachment by branched haptera; epiphytic on Kallymenia cribrosa and Thamnophyllis lacerata. Structure. Apical cells 8–15 μm in diameter and L/D 6–15, dividing transversely, median and basal cells (20-) 40–100 μm in diameter and L/D 4–10. Cells multinucleate; rhodoplasts discoid.

Reproduction. Propagules (Figs 145F, 146D, E, 147A) borne laterally on upper cells, single celled, ovoid, 55–90 μm in diameter, with a single small discoid basal cell.
Gametophytes dioecious. Procarps (Fig. 146F) borne on the subapical cell of short axes, with 3 periaxial cells, one acting as the supporting cell and bearing a carpogonial branch and a sterile cell; hypogenous cell larger, with a lateral vegetative branch. Post-fertilization only the supporting cell cuts off an auxiliary cell, which produces 3 successive gonomolobes (Figs 146G, 147B) 80–220 μm across, with isodiametric carposporangia 20–25 μm across. The apical cell, supporting sterile cell, and one of the sterile periaxial cells divide and form 3 inner involucral groups around the carposporophyte, and loose outer involucral filaments develop from cells below the fertile axis. Spermatangial heads (Figs 146H, 147C) are borne on upper adaxial ends of median thallus cells, ovoid, 30–45 μm in diameter.
Tetrasporangia borne on upper ends of axial cells, subspherical to slightly ovoid, 20–30 μm in diameter, tetrahedrally divided.

Type from Elliston, S. Aust., on Kallymenia cribrosa, 7 m deep in bay (Shepherd, 21.x.1970); holotype in AD, A37361, isotypes distributed in “Marine Algae of southern Australia” No. 597.


Genus GUIRYELLA Huisman & Kraft 1992: 128

Thallus erect, small, ecoricate, irregularly branched, with a prostrate base attached by rhizoids with digitate haptera. Cells multinucleate.

Reproduction. Propagules with a large ovoid cell and a short, trapeziform, basal cell, borne on a 2-celled stalk.

Gametophytes dioecious. Procarps borne on the subapical cell of short axes, with 3 periaxial cells, one (the supporting cell) bearing a 4-celled carpogonial branch and a sterile terminal cell, with the hypogenous cell larger. Post-fertilization the supporting cell and adjacent periaxial cell cut off auxiliary cells each of which produces a gonimolobe. The sterile procarp cells each produce a short involucral branchlet. Spermatangial heads occur on the laterals.

Tetrasporangia occur on cells of the laterals, subspherical, tetrahedrally divided.


Guiyella is characterised by the propagules with a large ovoid spore and short trapeziform basal cell, on a 2-celled stalk, 3 periaxial cells and short involucral branchlets from the sterile cells of the procarp, and tetrahedrally divided sporangia.

The genus is monospecific.


FIGS 146 I, J, 147D–H

Thallus (Fig. 147D) erect from a prostrate base, dark red-brown, 2–10 mm high, much branched irregularly radially with sub dichotomous 4–6-celled laterals from most cells and indeterminate axes every 2–5 cells, mature axes more or less alternately distichous, apices overtopped by laterals. Attachment of prostrate filaments by unicellular rhizoids with digitate haptera; epiphytic on Dictyotales. Structure. Apical cells 10–16 μm in diameter and L/D 2–6, lower cells of determinate laterals 10–30 μm in diameter and L/D 6–10, cells of indeterminate laterals and axes 45–75 μm in diameter and L/D 2–6; prostrate axes 50–180 μm in diameter, cells L/D 3–4. Cells multinucleate; rhodoplasts discoid to elongate.

Reproduction. Propagules (Fig. 147E, H) 2-celled, ovoid, 100–140 μm in diameter with the basal cell trapeziform, terminating short indeterminate branches with a 2-celled stalk, with the upper propagule cell much larger than the lower.

Gametophytes dioecious. Procarps (Fig. 146 I) borne on the subapical cell of short axes, with 3 periaxial cells, one acting as the supporting cell and bearing a carpogonial branch and a sterile cell, and a larger hypogenous cell. Post-fertilization the supporting cell and adjacent periaxial cell cut off auxiliary cells, with 2 connecting cells from the carpogonium, carpogonial branch cells fuse and later degenerate. Each auxiliary cell produces a gonimolobe (Figs 146J, 147F) 200–300 μm across, of ovoid carposporangia 35–50 μm in diameter. Sterile procarp cells (apical, sterile periaxial and supporting sterile cells) each divide once to produce short 2-celled branches; no other involucral branches occur. Spermatangial heads (Fig. 147G) are ovoid, 30–50 μm in diameter, on cells of laterals, with 2–3 axial cells bearing whorls of cells with outer spermatangia.

Tetrasporangia (Fig. 147H) occur on the upper ends of cells of laterals, subspherical with thick wall sheaths, 60–80 μm in diameter, tetrahedrally divided.

Type from Pelsaert Group, Houtman Abrolhos, W. Aust., on Dictyota naevosa, 20 m deep (Kraft & Huisman, 14.x.1990); holotype in MELU, A38705.
Distribution: Houtman Abrolhos to Rottnest I., W. Aust., and Tiparra Reef to Port Noarlunga, S. Australia.


Tribe BORNETIEAE Baldock & Womersley, tribus nov.
by R.N. Baldock & H.B.S. Womersley

*Thallus* subdichotomously to unilaterally branched, or primarily prostrate with several erect filaments arising from a creeping filament, ecorcitate, attached by rhizoids from the basal cell(s); cells elongate, cylindrical, usually relatively large (2–3 mm long); gland cells absent. Cells multinucleate, with crystalline inclusions; rhodoplasts discoid, numerous, scattered or in chains.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes dioecious. Female axis lateral, consisting of a larger basal cell and 5–6 (-8) small cells. Procarp systems 2 (-3), arising successively from subapical cells, each consisting of a supporting cell bearing a terminal sterile cell often dividing to form a 2-celled non-functional carpogonial branch, and a lateral, functional 4-celled carpogonial branch; a further sterile periaxial cell opposite the supporting cell, often dividing to form a 2-celled non-functional carpogonial branch. Following fertilization, further axial cell development usually ceases and the supporting cell divides so that the auxiliary cell is intercalated between sterile cells and residual supporting cell; fusion cell incorporating the auxiliary cell, residual supporting cell, lower gonimoblast cells, and possibly the axial cell at the level of the fertilized procarp, becoming stellate and bearing terminal, clavate carposporangia on slender processes. Involucral branches arising from the large basal and lower 2 small cells of the fertile axis and surrounding the carposporophyte in a condensed 1/4 spiral pattern, forming a characteristic basket-shaped structure. Spermatangial heads ovoid to elongate, sessile, borne singly and unilaterally on the inner side of subdichotomous branches of lateral, basket-like, condensed systems tending branching in a 1/4 spiral pattern.

Tetrasporangia borne singly or more commonly in clusters in similar condensed branch systems to the spermatangial heads, sessile (except possibly *B. secundiflora*), tetrahedrally divided.

*Thallus* subdichotome usque unilateraler ramosus, aut filis erectis et fila repenti, ecorcitate, fixus per rhizoida e basali cellula (aut cellulis); cellulae elongatae, cylindrices, plerumque reative magnae (2-3 mm longae), multinucleate.

Reproductio. Gametophyta dioicta. Axis femineus lateralis, cellula maiore basali et 5–6 (-8) cellulis parvis, Systemata procarpii 2 (-3) successive orientia et cellulis subapicalibus, quodque cum sustinente cellula ferente cellulum terminalem sterilem (saeppe faciens ramum 2 cellularem nonfungentem carpogonialem) et ramum lateralem fungentem 4 cellularem carpogonialem; deinde cellula steriles et periaxialis, opposita cellulum sustinentem, saeppe faciens ramum 2 cellularem nonfungentem carpogonialem. Post fecundationem systemata procarpi cellulas axiales piertumque non plus crescentia; cellula sustinens dividers sic velut cellula auxiliaris iacens inter cellulas steriles et residualem cellulum sustentem; cellula coniunctionis includens cellulum auxiliarum, cellulum manentem et sustentem, cellulas inferiores gonimoblasti et interdum cellulum axialem apud procarpium fecundatum, stellatescens et ferens carposporangia terminalia clavata in processibus gracilibus. Rami involucres e cellula magna basali et 2 parvis cellulis inferioribus axilis fertillis, et einges carposporophytem, faciens structuram corbiformem. Capita spermatangia ovoidea usque elongata, sessilia, portata singulatim et unilateriter in latere interiore ramorum subdichotomorum systematibus lateribus corbiformibus condensis.
Tetrasporangia portata singulatim aut plerumque in fasciculis in systematibus condensis et similibus capitibus spermantaligious, plerumque sessilia, tetraedrice divisa.

**Type** (and only) *genus: Bornetia* Thuret 1855: 159.

A monogeneric tribe of 5 species; the type from Mediterranean and European coasts, *B. binderiana* from southern Australia, *B. tenuis* from southern Australia and possibly South India and South Africa, *B. repens* from South Africa, (Siegenia 1985b, p. 163), and *B. californica* from Pacific North America (Abbott 1971, p. 349).

The establishment of the tribe, represented solely by *Bornetia* was presaged by Baldock & Womersley (1968, p. 209).

The position of *Bornetia* within the Ceramiaceae is problematic. The several non-functional carpogonial branches of 2 cells and functional ones of 4 cells, associated with procarps produced successively along the fertile axis, resembles the Wrangelieae developmental line proposed by Kylin (1930, p. 76). However, *Bornetia* lacks whorl-branchlets, fertile procarps are initiated subapically and supporting cells are periaxial cells and not axial cells; these features place it closer to the Ceramieae developmental line.

Superficially, *Bornetia* resembles the Griffithsieae because of its large, uniseriate, multinucleate cells, subdichotomous branching, and the basket-shaped involucre around carposporophytes; several species have been ascribed previously to *Griffithsia*. *Bornetia* lacks synchronous branchlets which Millar (1986, p. 95) considers unique to the Griffithsieae; reproductively, *Bornetia* is closer to the Sphondylothamnieae (as defined by Gordon 1972, p. 47) in its extended fertile axis, and large gonimoblast fusion cell bearing terminal carposporangia. However, *Bornetia* differs significantly from the Sphondylothamnieae: it lacks whorl branchlets, has an extended female axis of 6 (-8) cells with 2 (-3) procarp systems bearing non-functional carpogonial branches, lacks an inner involucre about the carposporophyte and bears spermatangial heads and tetrasporangia in lateral, condensed, subdichotomous branch systems.

Kylin (1956, p. 370) and Hommersand (1963, p. 333) characterised the Spermothamnieae, in which they included *Bornetia*, by the presence of terminal carposporangia on the fusion cell. Members of this tribe are typically small, often epiphytic with prostrate axes which may be intermingled with filaments of host plants, and although similar to *Bornetia* in lacking whorl-branchlets, cells are small with fewer nuclei. This contrasts with the robust thalli, free prostrate axes and relatively large cells with numerous nuclei of *Bornetia*. The involucre surrounding the carposporophyte in the Spermothamnieae as defined by Gordon (1972, p. 112) develops from sub-hypogenous or hypogenous cells whereas in *Bornetia* it arises from 3 cells (large basal and lower 2 small cells of the fertile axis). In the Spermothamnieae, procarps are single and invariably subapical, and 2 auxiliary cells may be produced. The successive development of subapical procarp systems along a potentially indeterminate axis in *Bornetia* is a unique feature sufficient to separate it from the Spermothamnieae.

**Genus BORNETIA** Thuret 1855: 159

With the characters of the tribe.

**Type species:** *B. secundiflora* (J. Agardh)Thuret 1855: 159, pls 1, 2.

A genus of 5 species, worldwide in distribution.

**KEY TO SPECIES OF BORNETIA**

1. Thallus robust, flabellate, branching mostly unilateral; cells large, 500–900 μm in diameter, L/D 2–4 .......................................................... .................................................. 1. *B. binderiana*
2. Thallus delicate, tufted, branching subdichotomous; cells 200–250 μm in diameter, L/D 5–8 .......................................................... .................................................. 2. *B. tenuis*

4.xii.1968; (Baldock, AD, A62651). Codium galeatum, Dawson (1961, p. 417) recorded it from El Salvador. These records refer to a species of
D’Emrecasteaux Reef, Great Australian Bight, S. Aust .. on
Selected specimens:
needs checking.
AI3937), and drift
Griffithsia.
AD,

thallus (Fig. 148A) light to medium red, 3–9 (-13) cm high, lax and flabellate, subdichotomously and mostly unilaterally branched at intervals of 1–2 cells, more distantly near the base. Attachment by an erect basal cell which in some plants produces short rhizoidal cells. Structure. Upper cells 500–900μm in diameter and L/D 2–3, lower cells 600–700 μm in diameter and L/D 2–4. Cells multinucleate: rhodoplasts discoid.

Reproduction. Gametophytes dioecious. Female axis of 6–8 small cells (Fig. 149A) borne on a larger basal cell containing crystalline inclusions, arising adaxially in the position of a lateral branch; involucral branches arising from the larger basal and lower 2 small cells of the fertile axis in a 1/4 spiral pattern, unbranched or subdichotomously branched once; basal involucral cells oblong, radiating horizontally, bearing 1 (-2) erect, elongate, incurved cells terminally, producing a basket-shaped condensed branch system (Fig. 149C); 2 (-3) procarp systems produced successively from subapical cells in a 1/4 spiral pattern, each consisting of 1(-2) periaxial sterile cell(s) often developing into 2-celled non-functional carpogonial branch(es), and a supporting cell bearing a lateral, recurved, 4-celled carpogonial branch and apically a sterile cell or a non-functional 2-celled carpogonial branch. Following fertilization in the first formed (lowest) procarp system, the supporting cell divides to form an auxiliary cell (Fig. 149B) which is intercalated between the non-functional carpogonial branch and residual supporting cell (see Baldock & Womersley 1969, p. 200) and this divides forming 1-2 gonimolobes. Fusion cell stellate, 200–270 μm across, produced from the auxiliary cell and densely branched lower gonimoblast cells; carposporangia (Fig. 149D, E), granular, ovoid-lachrimiform, 42–55 μm in diameter and L/D 1.6–2, with several vacuoles radiating from a single, central nucleus, borne at first on subdichotomous chains of cells, ultimately at the end of slender processes from the fusion cell (Fig. 149D). Spermatangial heads, sessile, elongate, 130–140 μm in diameter and L/D 2.5–3, single (-2) and apical on 3 (-5) small angular cells which branch laterally in a 1/4 spiral pattern producing a further angular cell and 1 (-3) large elongate, incurved involucral cells resulting in a basket-shaped, compressed branch system (Fig. 149F); heads not exceeding the length of the involucre.

Tetrasporangia sessile, in clusters of 2–4, borne in comparable positions to spermatangial heads in similar condensed lateral branch systems with a 1/4 spiral branching pattern (Fig. 149G), the terminal cells of which form incurved involucres; sporangia ovoid, 53–85 μm in diameter, tetrahedrally divided (Fig 149H).

Type from W. Aust. (probably near Fremantle)(Press); lectotype in MEL, 502123 from “Swan River”.

Distribution: Champion Bay, W. Aust. (Huisman & Walker 1990, p. 419) to Port Phillip, Victoria, usually epiphytic on red algae at moderate depths.


Abbott (1946, p. 442) credited B. binderiana (as Griffithsia) to the Hawaiian Islands, and Dawson (1961, p. 417) recorded it from El Salvador. These records refer to a species of Griffithsia. The record of Børgeesen (1945, p. 16) for Mauritius is also doubtful and the specimen needs checking.

**FIGS 148B–E, 150**

*Thallus* (Fig. 148B) tufted, dark red, 3–7 cm high, epilithic or epiphytic. Filaments subdichotomous at intervals of 2–3 cells, ecorticate, attached by rhizoids at the base. **Structure.** Cells linear, usually 200–250 μm in diameter and L/D 5–8. Cells multinucleate; rhodoplasts discoid.

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In Figs 149, 150, axial cells are numbered from base up to reflect continuing growth.
Reproduction. Gametophytes dioecious. Procarp systems 2 (-3), produced in succession subapically on an adaxial, lateral fertile axis consisting of a larger basal cell (furcate apically) and 5–7 small cells (Fig. 150A); sometimes a separate larger basal cell is not cut off from the vegetative axis, but a constriction forms a basal region (Fig. 150B, C). Procarp systems each consist of a supporting cell bearing apically a sterile cell which often develops into a 2-celled non-functional carpogonial branch, and laterally a recurved, functional 4-celled carpogonial branch, and also a sterile periaxial which develops into a 2-celled non-functional carpogonial branch. Carposporangia terminal (Fig 148C), granular, clavate, densely cytoplasmic, with several vacuoles radiating from a single, central nucleus; 30–40 μm in diameter and L/D 1.7–1.9, radiating from a stellate fusion cell (Fig. 150D); carposporophyte surrounded by 1 (-2)-celled involucral branches, sometimes cells furcate apically (Fig. 150B), cut off from the basal and lower two cells of the fertile axis, or the lowest branch(es) may arise as prolongations of the basal region when no separate basal axial cell occurs (Fig. 150C). Spermatangial heads...
(Fig 148D) sessile, elongate, 70–81 μm in diameter and L/D 1.8–3, single and apical on the inner sides of oblong cells of lateral, condensed, subdichotomous branch systems produced in a 1/4 spiral pattern, the larger elongate, incurved terminal cells of which provide a basket-shaped involucre (Figs 148E, 150F), the terminal cells of which form incurved involucres as with spermatangial heads; globose, 60–65 μm in diameter, tetrahedrally divided.

Type from Grange Beach (Adelaide), S. Aust., drift (Baldock, 23.i.1965); holotype (tetrasporangial) and isotypes (tetrasporangial and male plants) in AD, A28632.


B. tenuis vegetatively resembles small Anotrichium spp (Griffithsieae) in its fine, ecorticate, subdichotomous filaments, but is distinctive reproductively, particularly in the basket-shaped male and tetrasporangial structures.

B. tenuis was recorded from Coffs Harbour, N.S.W. (Millar 1990, p. 412, fig. 49E, F), and South India (Krishnamurthy & Thomas 1971, p. 36, figs. 15–18.44,45), although the cells in the latter record are less elongate. Norris & Aken (1985, p. 60, fig. 22) attributed this species to South Africa on the basis of single fertile male specimen, although the involucral cells were significantly smaller relative to the spermatangial heads in their specimen.

Tribe GRIFFITHSIEAE Schmitz 1889: 449

by R. N. Baldock

Thallus of subdichotomous indeterminate branches (trichotomous in Calliclavula) generally arising subapically, but from lower thallus parts in Halurus and Calliclavula; a range of determinate laterals initiated simultaneously ("synchronic") from the upper shoulders of cells; filaments ecorticate or loosely clothed with rhizoids near the thallus base; cells relatively large, 0.14–2.3 mm in diameter, L/D 1–9, cylindrical to globose; gland cells absent. Cells multinucleate, often with prominent crystalline inclusions; rhodoplasts discoid, numerous, scattered or in chains.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes dioecious. Female axis lateral, 3-celled, subapical cell bearing a procarp system of a lateral sterile cell and a supporting cell with an apical sterile cell and 1(-2) lateral, recurved, 4-celled carposporogonal branch(es); fusion cell columnar, formed from the auxiliary cell, residual supporting cell and lower gonimoblast cells, bearing 1–3 gonimolobes apically, most cells of which form globose, ovoid or clavate carposporangia. Involutural branches synchronic, 1–2-celled, arising from the hypogenous cell of the fertile axis, forming a cupulate involucre about the carposporophyte. Spermatangia on pedicellate heads, or on numerous minute fascicles clustered in the constrictions between vegetative cells towards the apex of filaments, or as a terminal mass on swollen vegetative apical cells; naked, or associated with 1-celled involucral branches arising from the fascicles, or encircled by a palisade-like synchronous involucre produced in a whorl from the vegetative cell bearing the spermatangia.

Tetrasporangia pedicellate or in minute fascicles, similar in position to spermatangia, naked or with involucral branches as for spermatangia, tetrahedrally divided.

Type genus. Griffithsia C. Agardh 1817:xxviii. (See Silva 1980, p.134 for orthographic conservation.)
The Griffithsieae are readily recognised by their naked, uniseriate filaments of large cells, and include 6 genera of which *Anotrichium* (6 of 14 species) and *Griffithsia* (10 of 27 species) are well represented in southern Australia, and *A. planatum* and the monotypic *Baldockia* (Millar 1990, pp. 406–8) are endemic to the eastern coast of Australia.

Millar (1986 p. 93) considered the simultaneous initiation of determinate branches (synchronic laterals) as the definitive feature of the Griffithsieae, and later separated the genera on the basis of branch ontogeny (Millar & Abbott 1997, p. 95). The various forms of synchronic branches fit an evolutionary reduction series proposed by Baldock (1976, p. 567), and refined and expanded by Millar (1986, p. 94) and Searles & Schneider (1989, p. 732):

(a) whors of subdichotomous, pigmented, relatively robust branches which may bear tetrasporangia or spermatangial clusters basally (*Halurus, Baldockia*),
(b) whors of pigmented, relatively delicate cells ("villous laterals" of Millar 1990, p. 90) (*Calliclavula, Ossiella*),
(c) whors (*Anotrichium tenue, A. secundum, A. barbatum*) or clusters (*Griffithsia, Anotrichium* spp.) of colourless, polychotomous, hair-like branchlets ("trichoblasts" of Baldock (1976); "villous whorl-branches" of Millar (1986, p. 95)), which are usually caducous, but may bear tetrasporangia or spermatangial clusters on their permanent, enlarged, pigmented basal cells in *Anotrichium barbatum* (Maggs & Hommersand 1993, p. 179),
(d) whors of pedicels bearing tetrasporangia or spermatangial heads (*Anotrichium tenue, A. secundum*), considered remnant basal cells of the *A. barbatum* type by Joly (1956, p. 29) and Baldock (1976 p. 571), although this is disputed by Kim & Lee (1991, p. 20) for *A. tenue*.
(e) involucral branches of carposporophytes, whorled (*Anotrichium, Baldockia, Halurus, Ossiella*) or abaxial (*Griffithsia*) from hypogenous cells, and
(f) involucral branches of tetrasporophytes produced in a whorl from the vegetative cell bearing the masses of tetrasporangial fascicles (*G. antarctica* group of *Griffithsia*).

In *Anotrichium towinna* and *Griffithsia balara*, lateral branches of restricted growth are produced sequentially in a whorl of 3–4 from the upper shoulders of cells near the apices of axes of indeterminate growth. Although morphologically these resemble the robust synchronic laterals of *Halurus* and to a lesser extent the more delicate ones of *Ossiella* and *Calliclavula*, they are a modification of the subdichotomous pattern of main axes, and are not homologous to synchronic determinate laterals.

**KEY TO GENERA OF GRIFFITHSIEAE**

1. Vegetative axial cells in mid thallus generally large, 0.35–4 mm in diameter and L/D 1–5, cylindrical to ovoid-globose; hair-like synchronic laterals in pairs flanking female fertile axes, caducous. Female axis with a small, discoid hypogenous cell bearing 2-celled synchronic involucral branches in an abaxial arc, the lower cell small, the upper cell elongate and incurved. Spermatangia and tetrasporangia in clusters on numerous minute whorled fascicles in the constrictions between vegetative cells, associated with inflated involucral cells or naked ................................................................. *GRIFFITHSIA*

2. Vegetative axial cells in mid thallus smaller, (0.04-) 0.2–0.6 (-0.9) mm in diameter and L/D 1.7–10, elongate-cylindrical; synchronic hair-like laterals whorled, or clustered adjacent to female axes, persisting until carposporophytes mature. Female axis with cylindrical hypogenous cell enlarging to become pyriform-clavate, similar in length to a vegetative cell and bearing a cupulate whorl of 1-celled, elongate, synchronic involucral branches. Spermatangial heads single and terminal or subterminal and adaxial on large, clavate pedicels, in synchronous whors (*A. tenue, A. secundum*), or single and adaxial from the upper parts of vegetative cells; involucral cells absent. Tetrasporangia single, terminal or subterminal and adaxial on pedicels, in a synchronous whorl of 8–12 (*A. tenue, A. secundum*), or in adaxial clusters of 1–4; involucral cells absent ........................................................................................................... *ANOTRICHIUM*
**Genus GRIFFITHSIA** C. Agardh 1817: xxviii

*Thallus* erect, tufted or flabellate; indeterminate branches subdi-(tri-)chotomous, ecorticate or clothed at the thallus base with recurrent anastomosing rhizoids; cells large, 0.14–4 mm in diameter and L/D 1–9, cylindrical to ovoid-globose; filaments often constricted at the nodes or moniliform; synchroic hair-like laterals usually in pairs, flanking female fertile axes, caducous. Cells multinucleate, rhodoplasts discoid, scattered or in chains; cytoplasm containing large crystalline inclusions.

**Reproduction.** Gametophytes dioecious. Female axis lateral, adaxial, of 3 small, discoid cells, confined to the constriction between vegetative cells, bearing a subapical procarp system consisting of a lateral, abaxial, sterile cell and adaxially a supporting cell bearing apically a sterile cell and laterally 1(-2) recurved, 4-celled carpogonial branch(es); hypogenous cell remaining small, becoming semi-circular when viewed from above as a result of producing 5–13 two-celled synchroic involucral branches in an abaxial arc, the lower cell of each branch small, the upper cell elongate and incurved, forming a hemi-cupulate involucre. Spermatangia on masses of minute whorled fascicles in the constrictions between vegetative cells near the thallus apex, fascicles naked or associated with an involucre of inflated cells borne on the fascicles peripheral to clusters, or developed as a whorl of reniform, 1-celled synchroic branches from the vegetative cells bearing the fascicles, and forming a palisade-like involucre.

Tetrasporangia without prominent hyaline sheaths, borne in groups of 2–several on masses of minute whorled fascicles in similar positions and involucral patterns to the spermatangia, tetrahedrally divided.

**Type species:** *G. corallina* C. Agardh 1817: XXVIII.

A genus of some 27 species, worldwide in distribution, divided into subgeneric groups by Baldock (1976, pp. 545–6) on the basis of tetrasporangial features.

**KEY TO SPECIES OF GRIFFITHSIA**

1. Tetrasporangial and spermatangial clusters without an involucre ................. 1. *G. leges*  
1. Tetrasporangial clusters with an involucre .................................................. 2

2. Cells in mid thallus ovoid-globose to pyriform, 0.8–4 mm in diameter and L/D 1–3, filaments moniliform or much constricted between cells, ecorticate. Tetrasporangial, and in some species spermatangial, fascicles peripheral to clusters bearing inflated involucral cells (inconspicuous and equal in size to a mature tetrasporangium in *G. pulvinata*), vegetative cells adjacent to the reproductive structures normal in size, persistent (*G. corallina* group) ........................................ 3

2. Cells in mid thallus cylindrical to doliform, 0.3–0.9 mm in diameter and L/D 2.5–4.5, filaments rarely constricted between the cells, often clothed near the thallus base with rhizoids. Spermatangial and tetrasporangial fascicles enclosed by palisade-like involucres each produced as a synchroic whorl of 1-celled branches from the vegetative axial cell; vegetative cells adjacent to reproductive structures conspicuously swollen; axial filaments above spermatangial and tetrasporangial clusters often caducous leaving the involucre as an apparently terminal cupulate structure (*G. antarctica* group) ................................................................. 8

3. Cells clavate-obovoid, thallus forming small, dense, pulvinate masses of crowded, erect filaments on rocks. Carposporophytes restricted to upper parts of the thallus, appearing terminal, flanked by 1–3 swollen vegetative cells; spermatangial involucre absent. Tetrasporangial involucral cells of similar size to mature tetrasporangia ...... 2. *G. pulvinata*  
3. Cells ovoid-globose, branching loose or spreading, thallus moniliform. Carposporophytes lateral in the constriction between vegetative cells, or axillary in branch dichotomies; spermatangial involucre present or absent. Tetrasporangial involucral cells larger than mature tetrasporangia ........................................................................................................... 4

4. Thallus subdichotomous, radially branched, of irregularly branched laterals. Carposporophytes lateral in constrictions between vegetative cells or in terminal branch dichotomies ................................................................. 5

5. Thallus 9–26 cm high, spreading, branched many times; cells in mid thallus allantoid or cylindrical with slightly swollen ends, cylindrical only near the thallus base ......................................................................................................................... 5, G. ovalis

5. Thallus 1–14 cm high, branched 3–5 times; cells in mid thallus globose or ovoid ...... 6

6. Thallus light red, spreading, epiphytic on seagrasses. Cells near the mid thallus ovoid, clavate in lower thallus parts. Tetrasporangia large, 80–108 (–130) μm in diameter, with an involucr of narrow-clavate cells, inflated involucral cells only in fascicles peripheral to each sporangial cluster ........................................ 5. G. ovalis

6. Thallus medium dark red, loosely branched, epithec or epiphytic. Cells in mid thallus globose-ovoid. Tetrasporangia 50–80 μm in diameter, with an involucr of ovoid or inflated cells, irregularly furcate or lobed ........................................ 7

7. Thallus 8–14 cm high, branching lax; often growing in deeper water; cells in mid thallus globose-ovoid, 3–4 mm in diameter, and L/D 1.5–2. Spermatangial fascicles naked. Tetrasporangial fascicles involucrate, bearing either ovoid sterile cells about the same size as tetrasporangia or clavate involucral cells 50–60 μm in diameter and L/D 2–3 ........................................................................................................................ 6 G. grandis

7. Thallus 1.5–4.5 (–8) cm high, branching spreading, several times subdichotomous; growing in the lower eulittoral to 5 m depth; cells globose, often with a short proximal neck (ampulliform), in mid thallus 1.6–2.5 mm in diameter. Spermatangial fascicles involucrate or naked. Tetrasporangial fascicles bearing large, swollen, reniform involucral cells often apically furcate, 210–490 μm in diameter and L/D 2–3 ............................. 7. G. monilis

7a. Plants usually epiithic from the lower eulittoral to 2 m depth. Each supporting cell bearing a single carpogonial branch; carposporophyte involucral of 4–6 branches; spermatangial fascicles naked ............... 7a. G. monilis var. monilis

7b. Plants invariably epiphytic in the upper sublittoral to 5 m depth. Each supporting cell bearing a pair of carpogonial branches; carposporophyte involucral of 9–13 branches; spermatangial fascicles bearing large, clavate, apically furcate, involucral cells ......................................................... 7b. G. monilis var. cineta

8. Thallus irregularly branched with long axes bearing whorled laterals of limited growth ................................................................. 8. G. bolata

8. Thallus irregularly subdichotomous or distichous, without whorled laterals of limited growth ................................................................................................................................. 9

9. Thallus dark red; branching essentially radial, irregularly subdichotomous; axes bearing irregular, dense, lateral tufts, in lower parts twisted together and entwined with rhizoids, rope-like; laterals sparse in the lower thallus, consisting of a few spreading, virgate, sub-dichotomies; cells in mid thallus 0.5–0.8 mm in diameter and L/D 3–4 ......................................................................................................................... 10. G. gunniana

Griffithsia antarctica Hooker & Harvey *sensu* Harvey 1859b: 332. Sonder 1881: 11.

**PLATE 1 fig. 2; FIGS 151A, B, 152A–D**

**Thallus** (Pl. 1 fig. 2; Fig. 151A, B) dark red, coarse, 2.5–17 (-20) cm high; eulittoral plants stiff and sometimes erect, forming extensive mats with filaments more or less adpressed, deeper plants more openly branched, irregularly subdichotomous. Attachment by a wad of twisted and anastomosing rhizoids from cells near the thallus base; epilithic. **Structure.** Filaments gradually attenuate towards obtuse apices, slightly constricted at the nodes, loosely clothed with rhizoids below. Cells cylindrical to dohiform, 0.4–0.8 mm in diameter and L/D 2–4.

**Reproduction.** Gametophytes dioecious. Female axis 3-celled, flanked by 2 pairs of minute hair-like synchrochous laterals, subapical but displaced laterally by continued growth of the apical cell. Procarp systems (Fig. 152B) subapical, each with a sterile lateral cell and supporting cell bearing 1(-2) sterile cells apically and 1(-2) lateral, recurved carpogonial branches of 4 cells; hypogenous cell producing abaxially 6–10 two-celled involucral branches; the sub hypogenous cell swollen towards its upper end (Fig. 152A). Post-fertilisation fusion cell columnar, bearing 1–3 gonimolobes terminally, most cells of 480–1500 µm in diameter. Sporangia borne on numerous, minute fascicles clustered in the constrictions between swollen, obovoid and globose cells 750–1250 µm in diameter at the base of a short lateral branch 3–6 cells in length, similar in appearance to those associated with tetrasporangial clusters (see Fig. 152C); filaments including globose cells above fascicles often caducous, so that mature fascicles appear terminal on the basal ovid cells which become 880–1500µm in diameter; fascicles initially polychotomous, later laterally branched; involucral cells absent.

**Tetrasporangia** borne on numerous minute fascicles in the constrictions between ovoid and globose cells at the base of short laterals (Fig. 152C) with the upper cells often caducous; involucral absent. Fascicles producing clusters (Fig. 152D) of 2–6 lachromiform tetrasporangia 46–88 µm in diameter.

**Type** from W. Aust. (probably near Fremantle) (Harvey); the holotype (Harvey, Trav. Set 146) is missing from TCD; lectotype (Baldock 1976, p. 541) Harvey Alg. Aust. Exsicc. 496A.

**Distribution:** Fremantle, W. Aust. to Wilsons Prom., Victoria and Bass Strait.


*G. teges* is a ubiquitous and common species growing in coarse mat-like strata from the lower eulittoral-upper sublittoral, on jetty piles and rock, and to a depth of 21 m, generally on rough-water coasts.

In vegetative features *G. teges* closely resembles *G. antarctica* from sub-antarctic regions, and sterile plants can be confused with this species; *G. teges* usually produces a wad of rhizoids at the thallus base and eulittoral plants grow in coarse clumps and mats, whereas in *G. antarctica*...
branching is more open and few rhizoids are produced. Reproductively, G. teges resembles G. antarctica Hooker & Harvey in that masses of spermatangial and tetrasporangial fascicles lack involucral cells.


**PLATE I fig. 3; FIGS 151C, 152E–H, 153A**

*Thallus* (Pl. 1 fig. 3; Fig. 151C) medium to dark red, 1–3 cm high, filaments erect, subdichotomous several times, ecorticate, forming dense pulvinate masses. Attached at the base by anastomosing rhizoids; epilithic. *Structure*. Cells (Fig. 152G) globose near the thallus apex and 750–900 (±1200) μm in diameter, in mid and basal thallus (Fig. 153A) clavate to obovoid, 1–2 (±2.1) mm in diameter and L/D 2–3.

*Reproduction*. Gametophytes dioecious. Female axis 3-celled, subapical but displaced laterally by continued growth of the vegetative apical cell, flanked by a pair of hair-like synchronic laterals. Procarp systems (Fig. 152E) subapical, each with a sterile lateral cell, and supporting cell bearing a sterile cell apically and a lateral, recurved carpogonial branch of 4 cells. The inner of two connecting cells, cut off from the carpogonium after fertilisation, fuses with the supporting cell (Fig. 152E), which cuts off an apical auxiliary cell; post-fertilisation fusion cell columnar, bearing 1–3 gonimolobes terminally, most cells of which become ovoid carpogonium 25–30 μm in diameter; hypogenous cell producing abaxially 9–12 (±14) 2-celled involucral branches (Fig. 152F), of which the larger, incurved apical cells are occasionally furcate, 325–350 μm in diameter and L/D 1.8–2. Growth of the vegetative axis is often arrested during procarp development, and 1–4 vegetative laterals arise from the vegetative subapical cell, displacing the carpogonial hypha to an apparently terminal position (Fig. 152G). Spermatangia borne on numerous, minute fascicles from the subapical cell and occasionally the cell below, clustered in the constrictions between the cells; involucral absent. A fascicle is at first polychotomous, but elongation of some cells establishes an axis of 3–4 terete cells bearing 1–4 polychotomous branches, the end cells of which each produce 1–2 spermatangia.

Tetrasporangia borne in cell constrictions on numerous minute fascicles 1–3 times dichotomous with small, terete cells, each of which produces a whorl of 1–6 lachrimiform tetrasporangia, 55–88 μm in diameter, or a 1-celled involucral branch (Fig. 152H) equal in size to a tetrasporangium. The sterile involucral cells stain lightly, in contrast to sporangia, which stain densely and divide when quite small.

*Type* from Port Elliot, S. Aust., in the upper sublittoral on granite rock (Baldock, 4.v.1963); holotype and isotypes in AD, A26365.

*Distribution*: Streaky Bay, S. Aust. to Port Phillip Heads, Victoria.


*G. pulvinata* is common in small, low, cushion-shaped masses on rock in the upper sublittoral to lower eulittoral, usually in shaded positions. Shepherd & Womersley (1971, p. 166) recorded this as a *nomen nudum* for Pearson I., South Australia.

*G. pulvinata* reproducitively belongs to the G. monilis group and some intergrades with sparse branching and inflated cells resemble G. monilis and G. pilalyea. However, the erect filaments, pulvinate habit, clavate cells towards the thallus base (see Fig. 153A, B, E), and the small involucral cells of the tetrasporangial fascicles readily distinguish *G. pulvinata*. 

**FIGS 151D, 153B, G–J**

*Thallus* (Fig. 151D) light red, complanately and flabellately branched, regularly subdichotomous, 1.7–4.5 cm high, constricted between cells, ecoricate. Attached by slender rhizoids from the thallus base; epilithic. *Structure*. Cells (Fig. 153B) near the thallus apex ovoid-globose, 0.6–0.9 mm in diameter and L/D 1–1.5, in the mid thallus obovoid-pyriform, 0.8–1.0 mm in diameter and L/D 1.8–2.8, but near the thallus base cylindrical, 0.4–1.1 mm in diameter and L/D 2.5–4.

*Reproduction*. Gametophytes dioecious. Female axes (Fig. 153G) of 3 small, discoid cells, arising subapically but quickly displaced to axillary positions in the forks of dichotomies by the development of further vegetative laterals, resulting in regular ranks of carposporophytes across the thallus (Fig. 153B). Procarp systems subapical, each with a sterile lateral cell and a supporting cell bearing a sterile cell apically and laterally a recurved carpogonial branch of 4 cells; hypogenous cell producing abaxially 7–10, 2-celled, syncrinal involucral branches, of which the larger, incurved, apical cells are ovoid, 110–365 μm in diameter and L/D 1.3–2; post-fertilisation fusion cell columnar, bearing 1–3 gonimolobes terminally, most cells of which produce globose-ovoid carposporangia 45–50 μm in diameter. Spermatangia borne on numerous minute fascicles from upper ends of cells near the thallus apex, clustered in the constrictions between cells; involucre absent. A fascicle at first (Fig 153H) resembles an immature synchronic hair-like lateral, with an urceolate cell producing 4–5 laterals which become terete and bear di-polychotomous branches of small cells producing 1–2 spermatia terminally (Fig. 153 I).

Tetrasporangia produced successively on whorls of minute fascicles in similar positions to spermatangial fascicles; fascicles innermost in a cluster each consist of an urceolate cell (Fig. 153J) producing successively 2–7 lachrimiform tetrasporangia tetrahedrally divided; outermost fascicles each producing an inflated, incurved, ovoid-clavate involucral cell 90–156 μm in diameter and L/D 1–1.3, 2–3 times the size of a tetrasporangium, and forming a composite involucre about clusters.

*Type* from Nora Creina, S. Aust., upper sublittoral pools, shaded (Womersley, 3.ix.1971); holotype and isotypes in AD, A39552—“Marine Algae of southern Australia” No. 176.

*Distribution*. Known only from the south-east of S. Aust., in heavily shaded sublittoral rock pools, and just below low water level.


*G. pilalyea* is very similar reproductively to *G. monilis*, but the vegetative cells (Fig. 153B, E) are smaller and ovoid, and the thallus is distinctly flabellate with a regular and complanate branching pattern.


*Griffithsia corallina* C. Agardh var. *tasmanica* Kützing 1849: 659.


Griffithsia


FIGS 153C, K, L, 154A

**Thallus** (Fig. 154A) light red, spreading, 9–26 cm high, subdichotomous many times, ecorticate, filaments constricted between cells and apically attenuate. Attached by rhizoids from basal cells; epithitic. **Structure.** Cells (Fig. 153C) in upper thallus globose-ovoid, 1–1.5 mm in diameter and L/D 1.9–2.2; in mid thallus allantoid, or cylindrical with swollen ends (bone-shaped), 1.4–2.2 mm in diameter and L/D 1.7–3; basal cells cylindrical, 0.6–1.6 mm in diameter and L/D 2.8–4.

**Reproduction.** Gametophytes dioecious. Female axes 3-celled, associated with whorls of 12–17 polychotomous, hair-like, synchronous laterals, displaced laterally by continued growth of the vegetative apical cell. Procarp systems subapical, each with a sterile lateral cell and a supporting cell with an apical sterile cell and lateral 4-celled, recurved carpogonial branch; the inner of two post-fertilisation connecting cells fusing with the supporting cell which cuts off an auxiliary cell; post-fertilisation fusion cell columnar (Fig. 153L), bearing 1–3 gonimolobes terminally, most cells of which produce ovoid-clavate carposporangia, 35–55 μm in diameter. Carposporophytes lateral in the constrictions between cells (Fig. 153K).

Two carposporophyte types exist, separated on their involucral branches. **Type A** produces 7–10 involucral branches in which the larger terminal cells are 320–450 μm long, regular and incurved (Fig. 153K).

**Type B** produces 5–6 involucral branches with terminal cells 540–850 μm long, furcate or distinctly irregularly lobed (Fig. 153L).

Hair-like syncyclic laterals are successively produced and shed so that carposporophytes may be surrounded by several whorls in various stages of development. Spermatangia borne on numerous minute fascicles from the upper shoulders of usually only subapical vegetative cells, clustered in the constriction between cells. Initially a syncyclic whorl of 6–8 fascicles resembling the initials of hair-like syncyclic laterals develops, but this is soon followed by the production of numerous other fascicles, each consisting of an ovoid basal cell 10–20 μm in diameter bearing 5 branches dividing polychotomously 4–6 times, in which the terminal cells produce 1–2 spermatangia; involucral cells absent.

Tetrasporangia occur on numerous whorls of minute fascicles clustered in constrictions of cells near the thallus apex (Fig. 153C), inner fascicles consisting of short pedicels 40–50 μm long bearing a whorl of 3–7 lachrimiform tetrasporangia 55–67 μm in diameter, produced successively, and tetrahedrally divided; outermost fascicles also each bearing 1(2)-inflated, incurved 1-celled involucral branches, 110–180 μm in diameter and L/D 1.5–2, forming a composite palisade-like involucre about clusters.

**Type** from “Ad Novam Hollandiam”; in PC.

**Distribution:** Swan River, W. Aust. to Tasmania, India and St Paul Island, Indian Ocean.


A species of large plants with allantoid cells, related to the *G. monilis* Group reproducitively, growing in estuarine conditions, 2–5 (22) m deep, commonly on seagrasses. The record of Borgesen (1934, p.42) from the Arabian Sea is doubtful, and although Adams (1983, p. 2) considered the species naturalised in Stewart Island, N.Z., this may have been confused with *G. (Pandorea) traversii*. 

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**Griffithsia GRIFFITHSIEAE 329**

Sonder 1881: II.


**FIGS 151E, 153D, M, N**

*Thallus* (Fig. 151E) light red, 3–4 (–6.5) cm high, branching spreading, 3–4 times subdichotomous, ecoricate. Attached by rhizoids from the basal cell; epiphytic on sea grasses or algae. **Structure.** Apical and subapical cells globose, 0.3–1.4 mm in diameter, cells in mid thallus ovoid, 2.5–3.0 mm in diameter and L/D 1.5–2; at the thallus base clavate, 1.2–1.8 mm in diameter and L/D 2–3; filaments highly constricted between cells, rapidly attenuate-truncate apically (Fig. 153D).

**Reproduction.** Gametophytes dioecious. Female axes 3-celled, subapical, but displaced laterally by the continued growth of the vegetative axis, flanked by numerous, caducous, hair-like synchronic laterals. Procarp systems subapical, each with a sterile lateral cell and a supporting cell bearing a sterile cell apically and a recurved carpogonial branch of 4 cells laterally; hypogenous cell producing abaxially 8–12, 2-celled synchronic involucral branches, of which the larger, incurved apical cells are 300–390 μm in diameter and L/D 2.5–3; post-fertilisation fusion cell columnar, bearing 1–3 gonimolobes terminally, most cells of which form large, ovoid carposporangia 60–70 μm in diameter. Carposporophytes lateral in the constrictions between cells (Fig. 153D). Spermatangia borne on numerous, minute fascicles from upper shoulders of cells near the thallus apex, clustered in the constrictions between cells; involucre absent.

Tetrasporangia borne on whorls of minute fascicles produced successively on most cells near the thallus apex, tetrahedrally divided. Fascicles innermost in a cluster (Fig. 153M) each consist of an urceolate cell producing successively 3–5 globose tetrasporangia 80–108(-130) μm in diameter and 3–5, narrow-clavate, 1-celled involucral branches 15–22 μm in diameter and L/D 8–11. Fascicles peripheral to a cluster (Fig. 153N) each produce also a clavate to reniform 1-celled involucral branch 160–250 μm in diameter and L/D 1.5–2, usually after tetrasporangia are shed, forming a composite palisade-like involucre about clusters.

**Type** from King George Sound, W. Aust. (Harvey); lectotype Harvey, Trav. set no. 41, in TCD.

**Distribution:** Houtman Abrolhos, W. Aust. (Huisman 1997) to Penneshaw, Kangaroo I., S. Australia.


**Selected specimens:** Tiparra Reef, S. Aust., on *Posidonia*, 5m deep (Shepherd 30.ix.1970; AD, A37310 and 24.x.1970; AD, A37715), and on *Amphibolis antarctica*, 5m deep (Shepherd 20.viii.1971; AD, A39470), Penneshaw, Kangaroo I., S. Aust., on *Plocamium cartilagineum*, on jetty, 6m deep (Lavers, 8.1.1997; AD, A66875).

*G. ovalis* belongs reproductively to the *G. monilis* complex and approximates *G. grandis* in cell size (Fig. 153D, F), but is characteristically epiphytic in relatively shallow bays. Plants are pale red in colour, small, with few, spreading branches, very large ovoid cells in the mid thallus, and moniliform filaments narrowing rapidly to small, globose, apical cells. Narrow-clavate sterile cells produced by tetrasporangial fascicles (notated by Harvey 1862, pl. 203) are unique to this species. Tetrasporangia, at least in Spencer Gulf specimens, are very large, about twice the dimensions of other members of the *G. monilis* complex.

Griffithsia

FI GS 153F, 154B, 155 I

Thallus (Fig. 154B) dark red, 8–14 cm high, branching lax, irregularly subdichotomous 3–5 times, ecorticate, distinctly moniliform. Attached by rhizoids; epilithic. Structure. Cells (Fig. 153F) near the thallus apex globose, 2–3 mm in diameter, without a short proximal neck, very large in mid thallus, ovoid, 3–4 mm in diameter and L/D 1.5–2, basal cells cylindrical, 0.8–1.4 mm in diameter and L/D 2.5–3; filaments strongly constricted between cells, gradually attenuate towards apices.

Reproduction. Gametophytes dioecious. Procarps unknown; hair-like, synchronic laterals associated with reproductive structures inconspicuous; hypogenous cell of carposporophyte producing 4–7, two-celled synchronic involucral branches, the lower cells small, terete, the terminal cells incurved, large, 400–450 μm in diameter and L/D 1.8–1.9, and often furcate apically. Spermatangia borne on whorls of numerous, minute, polychotomous fascicles from the upper ends of vegetative cells near the thallus apex, clustered in the constrictions between cells; involucre absent.

Tetrasporangia globose-lachrimiform, 50–60 μm in diameter and L/D 1–1.5, borne successively in clusters of 3–4 on whorls of numerous, minute, ovoid or urceolate pedicels, tetrahedraJ1y divided; fascicles internal to a cluster (Fig. 155 I, left) each bearing an ovoid sterile cell similar in size to tetrasporangia, those peripheral to a cluster (Fig. 155 I, right) each bearing inflated, incurved, clavate, 1-celled involucral branches, 50–60 μm in diameter and L/D 2–3.

Type from Port Phillip, Vic. (Wilhelm, in Herb. Kützing, L, 941, 61 ... 115).

Distribution: Waldegrave I., S. Aust. to Westernport Bay, Vic., and around Tasmania, at depths of (3–) 7–40 m.


Previously considered to be a large form of G. monilis by Baldock (1976, p. 517), G. grandis differs in its distribution and morphology (see Fig. 153E, F). G. grandis differs from G. ovalis which also has very large, ovoid cells, in having a lax branching pattern, dark red colour, and tetrasporangia about half the diameter of G. ovalis; it also occurs deeper than G. ovalis.


PLATE 1 fig. 4; FIGS 153E, 154D, 155A–H

Thallus (Fig. 154D) dark red, 1.5–4.5 (–8) cm high, branching spreading, several times subdichotomous, ecorticate, distinctly moniliform throughout. Attached by filamentous rhizoids from cells at the thallus base; epilithic or epiphytic. Structure. Cells prolonged at their bases into a short neck (Fig. 155C), near the thallus apex globose, 0.5–2 mm in diameter, in mid thallus globose to ovoid, 1.6–2.5 mm and L/D 1–1.3, basal cells ovoid, rarely cylindrical. Filaments strongly constricted between cells, attenuate towards the apices (Fig. 153E).

Reproduction. Gametophytes dioecious. Female axes subapical, of 3 small, discoid cells, displaced laterally or into an apparently terminal position by the continued growth of the vegetative axis, sometimes arising in opposite pairs on the same vegetative cell, flanked by caducous, hair-like synchronic laterals (Fig. 155A); procarp systems (Fig. 155D) subapical, each with a sterile lateral cell and a supporting cell bearing a sterile cell apically and 1–2 recurved carpogonial branches of 4 cells laterally; hypogenous cell (Fig. 155B) producing abaxially 2-celled synchronic involucral branches with swollen terminal cells (Fig. 155C);
post-fertilisation fusion cell columnar, bearing 1–3 gonimolobes terminally, most cells of which form globose-ovoid carposporangia, 27–45 μm in diameter. Spermatangia borne on whorls of numerous, minute, fascicles from the upper shoulders of vegetative cells near the thallus apex, clustered in the constrictions between cells, each fascicle initially a pedicel bearing 5 polychotomous branches (Fig. 155E) developing 2–8 further terete axial cells (Fig. 155F) each bearing whorls of 5 polychotomous clusters producing spermatia terminally; involucral cells absent, or present in var. cincta.

Tetrasporangia produced successively in clusters of 2–12 on whorls of numerous, minute, fascicles in similar positions to the spermatangial masses, globose or lachrimiform, 0.0–0.8 mm in diameter, tetrahedrally divided; fascicles internal to a cluster (Fig. 155G) consisting of single terete pedicels, those peripheral to a cluster (Fig. 155H) developing 1–3 further small axial cells, the basal cell displaced into a recumbent position by the production of a swollen reniform involucral cell, often apically furcate, 210–410 μm long and 130–180 μm in diameter.


**Distribution:** Rottnest I. and Fremantle, W. Aust., to Tasmania (Sonder 1881, p. 11) and N.S.W. (Millar & Kraft 1993, p. 40).

*G. monilis* is found in the lower eulittoral to 5m deep, and morphological variations occur with depth and degree of wave action which may make separation from *G. ovalis* and *G. grandis* difficult unless tetrasporangial plants are available.

Two varieties of *G. monilis* can be differentiated on reproductive features.

7a. **Griffithsia monilis** var. *monilis*  

**PLATE 1 fig. 4; FIGS 155A–C**  

**Thallus** (Pl. 1 fig. 4) 1.5–4.5 cm high, cells 1.2–2.5 mm in diameter.

**Reproduction.** Procarp (Fig. 155A) with a single carpogonial branch borne on the supporting cell; carposporophyte with 4–6 two-celled synchronic involucral branches, the lower cells small (Fig. 155B), urceolate, the terminal cells large (Fig. 155C), 210–409 μm in diameter and L/D 2–2.5, apically swollen, furcate or irregularly lobed. Spermatangial involucres absent.

Tetrasporangial features, as described above.


The type variety generally grows on rock from the lower eulittoral to 2m deep.


**FIGS 155D–H**

**Thallus** 2.5–4.5 cm high, cells globose, 1.5–3.2 mm in diameter.

**Reproduction.** Procarp (Fig. 155D) consistently with a pair of carpogonial branches on each supporting cell, cells of the fertile axis relatively large and discoid (50–70 μm in diameter); carposporophyte with 9–15 abaxial, two-celled synchronic involucral branches, the lower cells small, terete, the terminal cells large, 280–490 μm in diameter and L/D 2–3, apically swollen, often furcate. Spermatangial fascicles initially polychotomous (Fig. 155E), those peripheral to clusters (Fig. 155F) forming axes of 2–3 cells with large, clavate, apically furcate involucral cells 190–290 μm in diameter and L/D 1.3–7.

Tetrasporangial features (Fig. 155G, H) as described for the species.
Griffithsia

**Type** from Slipway reef, Robe, S. Aust., upper sublittoral, epiphytic on Cystophora (Womersley, 6.xi.1965); holotype and isotypes in AD, A29656.

**Distribution:** Kangaroo I and SE of S. Aust., but probably more widespread because diagnosis requires detailed examination of spermatangial clusters and carposporophytes.


This variety is invariably epiphytic on larger algae, in the upper sublittoral to 5 m deep.


**FIGS 154C, 156A**

**Thallus** (Fig. 154C) light to dark red, 8-14 cm high, irregularly branched with long axes bearing whorled laterals of limited growth, densely clothed below with anastomosing rhizoids. Attached by rhizoids; epilithic. **Structure.** Axial cells cylindrical, 350-410 \( \mu \)m in diameter and L/D 2.5-4.5, most bearing from their upper shoulders a whorl of 4 lateral subdichotomous tufts (Fig. 156A) produced sequentially and branched 1-3 times, occasionally bearing whorls of 4 laterals, the basal cells narrow-cylindrical, swollen distally, 180-210 \( \mu \)m in diameter and L/D 7-9; filament apices narrowing markedly, apical cells conical. Rhizoids robust, unbranched, arising from the lower parts of axial cells, intermingling with laterals and forming characteristic rope-like masses 7-12 mm in diameter.

**Reproduction.** Gametophytes unknown.

Tetrasporangia globose, 50-70 (-90) \( \mu \)m in diameter, produced successively in groups of 3-6 on fascicles consisting of 1 (-2) minute, terete cells developed in masses from the shoulders of inflated cells of long axes and from the subapical cells of many lateral branch tufts (Fig. 156A), tetrahedrally divided; apical cell above each mass of fascicles becoming ovoid, and producing a narrow filament of 1-2 cells that rarely divides subdichotomously; vegetative cell bearing the fascicles enlarging greatly, becoming pyriform, 530-700 \( \mu \)m in diameter and producing from its upper shoulders a whorl of 16-18, incurved, 1-celled branches 130-150 \( \mu \)m in diameter and L/D 2.5-5, enclosing the masses of fascicles in a pulisade-like involucre; vegetative filament above mature fascicles commonly lost, resulting in a cupulate structure.

**Type** from Hopetoun, W. Aust. (Gordon, 20.xi.1968); holotype in AD, A34133.

**Distribution:** Known only from the type locality and W of Flinders I., S. Aust., 32 m deep (Branden, 21.vi.1988; AD, A59308).

This species superficially resembles *Halurus*, a European member of the Griffithsiaeae, and *Anotrichium towiona* in the rope-like thallus base, irregularly branched main axes and whorled laterals. The masses of minute tetrasporangial fascicles in the constriction between vegetative cells and involucres consisting of whorls of 1-celled branches produced from the upper shoulders of vegetative cells bearing the fascicles clearly place *G. balara* in the *G. antarctica* group of Griffithsia.


**FIGS 154E, 156B-C**

**Thallus** (Fig. 154E) light red, complanately branched, 4-11 cm high, with 1-6 main axes bearing from the upper shoulder of each cell regularly alternate, distichous, flabellate laterals 2-5 times subdichotomous. Attached by rhizoids; epiphytic or epilithic. **Structure.** Cells cylindrical, near the thallus apex 200-490 \( \mu \)m in diameter and L/D 3.5-6, in mid thallus 400-900 \( \mu \)m in diameter and L/D 2.5-3.5, basally 750-1010 \( \mu \)m in diameter and L/D 2.0-2.5, with 1-3 decurrent branched rhizoids, without haptera, produced from the lower part of each axial cell, entwining with axes to form a rope like mass 2-3 mm in diameter in the lower thallus.
Reproduction. Gametophytes dioecious. Hair-like synchronic laterals associated with reproductive structures present but inconspicuous. Female axes 3-celled, subapical but displaced laterally by the continued growth of the vegetative axis; procarp systems subapical, each with a sterile lateral cell and a supporting cell with a terminal sterile cell and recurved 4-celled carpogonial branch laterally; hypogenous cell producing abaxially 9–270 µm in diameter and L/D 1–1.5, growth of vegetative lateral branches often inhibited by carposporophyte development (Fig. 156B). Sporangia on whorls of minute polychotomous fascicles, from the upper shoulders of pyriform subapical cells 660–800 µm in diameter and L/D 1–1.3, which produce separately 12–18 single-celled synchronic involucral branches of elongate incurved cells, 130–150 µm in diameter and L/D 3–5.5, that enclose the spermatangial masses in a palisade-like structure; vegetative apical cells above the masses swollen, ovoid with short proximal necks, 500–600 µm in diameter and L/D 1.3–1.6, sometimes producing single, small conical cells apically, often shed so that a cupulate structure remains.

G. elegans is often found in deep water, on larger algae. It belongs reproductively to the G. antarctica group, and smaller slender specimens may be confused with G. gunniana; however, the light red colour, and the complanate, regular and distichous branching are distinctive in G. elegans.

Type from Robe, S. Aust. (Baldock, 19.x.1964); holotype in AD, A27827.

Distribution: Elliston, S. Aust., to Portland, Vic. and SE Tasmania.


Thallus (Fig. 154F) medium to dark red-brown, branching essentially radial, tufted, 2.5–19 cm high, near the thallus apex subdichotomous, near the thallus base laterals sparse and spreading (“twiggy”); lower axes twisted together, with decurrent descending rhizoids, in larger plants forming a loosely woven, rope-like mass of filaments 2–10 mm in diameter. Attachment by rhizoids from the base; epiphytic, often on seagrass, or epilithic. Structure. Cells near the thallus apex cylindrical, 140–200 µm in diameter and L/D 2–4, in mid thallus cylindrical, 550–760 µm in diameter and L/D 3–4, axial cells in the lower thallus usually obscured by rhizoids.

Reproduction. Gametophytes dioecious. Female axes 3-celled, subapical, displaced laterally by the continued growth of the vegetative axis, flanked by a pair of hair-like synchronic
Griffithsia laterals; procarp systems (Fig. 156D) subapical, each with a sterile lateral cell and a supporting cell with a terminal sterile cell and recurved, 4-celled carpogonial branch laterally; hypogenous cell producing subdichotomously (Fig. 156E), the terminal cells large, incurred, elongate to reniform, 270–420 μm in diameter and L/D 2.3–2.6; subhypogenous cell becoming globose, 730–860 μm in diameter (Fig. 156F), adjacent vegetative branch forced to a lateral position by the expanding carposporophyte and similar in size to involucral cells; post-fertilisation fusion cell (Fig. 156E), bearing 1–3 gonimolobes terminally, most cells of which become ovoid carposporangia, 30–40 μm in diameter. Spermatangia borne on whorls of minute polychotomous fascicles from the upper shoulders of pyriform subapical cells 560–680 μm in diameter and L/D 1.2–1.6, which produce separately a whorl of 15–20 single-celled synchronous branches of elongate incurved cells, 130–170 μm in diameter and L/D 3–4, enclosing the spermatangial masses in a palisade-like involucre; vegetative apical cells above the clusters often lost so that a cupulate structure remains.

Tetrasporangia lachrimiform, 40–70 μm in diameter, produced successively in groups of 3–8 on minute, terete pedicels arising in whorls from the upper shoulders of pyriform subapical vegetative cells 660–820 μm in diameter (Fig. 156G), each bearing apically an obpyriform cell, a narrow filament of 1–4 cells often subdichotomous, and from the upper shoulder a whorl of 15–23 elongate, incurved, 1-celled, synchronous, involucral branches, 130–170 μm in diameter and L/D 3–4, enclosing the cluster; vegetative cells above the clusters often lost so that a cupulate structure remains.

Type from Georgetown, Tasmania (Gunn); holotype in Herb. Agardh, LD, 19793.

Distribution: Eyre Pen. to SE S. Aust., and around Tasmania.


G. gunniana agrees with the Griffithsia antarctica group in its tufted thallus, and slender filaments, and reproductively in carposporophytes with cupulate involucres borne on swollen vegetative cells. Spermatangial and tetrasporangial clusters in this group lie in the constrictions between pairs of swollen cells, the basal member of which produces also a palisade-like whorl of involucral cells independent of the fascicles.

Some specimens with sparse branching resemble sterile plants of G. ieses, but the texture of G. gunniana is softer, branching more tufted and filaments narrower than this species.

Species of uncertain status


Thallus light red, 1–2 cm high, of lax procumbent filaments and subdichotomous to subsecund erect branches 0.5–1 cm apart. Structure. Cells cylindrical 250–450 μm in diameter and L/D 3–5.5, apical cells obtuse; plants lacking whorls of hair-like synchronous laterals; branching from the distal ends of cells.

Reproduction. Fertile plants unknown for southern Australian plants.
Type from Hatidyo 1., Japan (Okamura 1930).

Distribution: Hainan, China; Japan; possibly Hawaii (Abbott 1946, p.442); eastern Australia.
In southern Australia, from Williamstown Victoria.

Selected specimen: Williamstown, Vic., 2.5-4 m deep (Kraft K10468 & Saunders, 6.ii.1995; AD, A67855).

The tangled, creeping filaments and sparse, erect axes give this species a distinctive habit resembling *Anotrichium tenue*, but it lacks the whorled, hair-like, synchronic laterals towards the filament apices and branches arise from distal ends of cells, not proximal ends as occurs in *A. tenue*. On the basis of tetraroporangiate plants, Cribb (1983, p. 92) provisionally recorded *G. subcylindrica* for Coffs Harbour, N.S.W., and the record of this species for Victoria based on sterile material must also be provisional.

Genus *ANOTRICHIUM* Nägeli 1861: 397

**Thallus** usually erect, tufted or with tufts arising from prostrate filaments (*A. planatum*), subdichotomous, adventitiously subsecund (*A. tenue*) or with whorls of short laterals (*A. towinna*), ecoricate or loosely clothed near the thallus base with decurrent, anastomosing rhizoids. Attached by rhizoids from the base or from branched haptera. **Structure.** Cells relatively small and elongate compared to *Griffithsia*, (40-)200-600 (-900) μm in diameter and L/D 1.7–10; filaments usually without constrictions between cells; synchronic hair-like laterals in whorls near the thallus apex, or grouped adjacent to female fertile axes; rhodoplasts discoid, scattered or in chains; cytoplasm with small crystalline inclusions.

**Reproduction.** Gametophytes dioecious. Female axes lateral, adaxial, 3-celled, the upper 2 cells short-cylindrical, the lowest (hypogenous) becoming large and pyriform and lifting the carpogonophyte from the constriction between vegetative cells into a prominent lateral position; procarp systems subapical, each consisting of a lateral, abaxial, sterile cell and adaxially a supporting cell bearing apically a sterile cell and a recurved, 4-celled carpogonial branch laterally; hypogenous cell bearing 1-celled, synchronic involucral branches in 1(-2) whorls consisting of elongate, incurved cells forming a cupulate involucre. Spermatangia in ovoid-pyramidal heads, each single and terminal on a large, adaxial, cylindrical-clavate pedicel near the thallus apex or single, subterminal, and adaxial from the upper ends of each clavate pedicel of several synchronic whorls near the thallus apex (*A. tenue* var. *thyrsigerum*).

Tetrasporangia borne singly on pedicels in similar positions and patterns to the spermatangial heads, involucre absent, with prominent hyaline sheaths, tetrahedrally divided.

**Type species:** *A. barbatum* Nägeli 1861: 397.

A genus of some 15 species, world wide in distribution, divided into two subgeneric groups by Baldock (1976, p.560) on the arrangement of spermatangial heads and tetrasporangia.

**KEY TO SPECIES OF ANOTRICHIUM**

1. Thallus a loose mat of creeping axial filaments and subsecund lateral branches produced irregularly from the lower ends of axial cells; hair-like synchronic laterals prominent, attenuate, in whorls of 8–16, initiated simultaneously from the upper shoulders of cells near the apices of branches. Spermatangial heads in whorls of 4–8 and tetrasporangia in whorls of 8–10 (-14), borne singly, subterminally and adaxially on clavate, synchronic pedicels from the upper shoulders of cells near the thallus apex which bear also hair-like synchronic laterals (*A. barbatum* group) ........................................... 1. *A. tenue* var. *thyrsigerum*

2. Thallus tufted, fastigate or spreading; branching subdichotomous from upper ends of cells, often prolific, or with complanate lateral branches from creeping filaments (*A. planatum*) or with short divergent laterals of limited growth in whorls of 3 (-4) (*A. towinna*);
hair-like synchronic laterals obscure, absent or readily shed, in groups of 1–3, adjacent to female structures. Spermatangial heads and tetrasporangia initiated successively in adaxial groups of 1–4, borne singly and terminally on pedicels (A. elongatum Group)............. 2

2. Main axes irregularly branched, with whorls of 3 (-4) divergent lateral branch tufts of restricted growth from most axial cells......................... 2. A. towinna
2. Main axes bearing single, subdichotomous, fastigiate or spreading lateral branches

3. Thallus tufted, cells small and slender, in mid thallus 44–92 μm in diameter and L/D 5.5–9. Reproductive structures diminutive; carposporophyte 150–400 μm across, spermatangial heads including pedicels 170–200 μm high, tetrasporangia 50–90 μm in diameter

3. A. subtile

3. Thallus tufted or with irregular main axes and spreading, fastigiate or corymbose lateral tufts; cells of thalli with pronounced axes 220–900 μm in diameter and L/D 3–6, otherwise cells in mid thallus 220–450 μm in diameter and L/D 2–6; carposporophytes 250–700 μm across, spermatangial heads including pedicels 350–450 μm high, tetrasporangia 60–105 μm in diameter

4. Main axes bearing regular, alternating, spreading lateral tufts (appearing flabellate when pressed) with immediate and pronounced narrowing of filaments from axes to laterals; filament apices mucronate. Tetrasporangia single (rarely in pairs), adaxial in subdichotomies of laterals. (Small and sparsely branched plants intergrade morphologically with A. elongatum.).................. 4. A. licmophorum
4. Main axes subdichotomously branched or bearing irregular subdistichous or corymbose lateral tufts, with gradual narrowing of filaments from axes to laterals; filament apices often obtuse. Tetrasporangia single at first, later usually in adaxial clusters of 3–8

5. Thallus coarse textured; cells near the thallus apex short-cylindrical, L/D 1.6–1.8, filament ends obtuse; sterile thalli subdichotomously branched. Lower axes twisted together and loosely clothed with decurrent rhizoids, forming a rope-like mass reaching 1 cm across. Tetrasporangia adaxial and subsecund on cells of terminal and lateral, spreading, corymbose branches of short cells. (Small plants with fine filaments and open (lax) branching intergrade morphologically with A. elongatum and can only be diagnosed if fertile.) ................................................................. 5. A. crinitum
5. Thallus soft textured; cells near the thallus apex elongate, L/D 6–8, filaments acuminate; branching open ( lax) with lateral tufts often well separated on main axes to regularly subdichotomous dense. Lower axes free, or loosely twisted together, clothed only sparsely with decurrent rhizoids. Tetrasporangia adaxial on most cells near the apex of subdichotomous terminal and lateral branch tufts of elongate cells. (Plants with prolific and regular lateral tufts intergrade with A. licmophorum.) ...................... 6. A. elongatum


Callithamnion thyrsigerum (Thwaites ex Harvey 1855a: 559; 1863, synop.: Iv.

Griffithsia tenuis sensu lato C. Agardh 1828: 131 (as ‘Griffitsia”). J.Agardh 1876:
Anotrichium

**GRIFFITHSIEAE**


**FIGS 157A, 158A-F**

*Thallus* (Fig. 157A) dark red, in dense or loose tufts, 1–5 cm high, with procumbent filaments producing erect, subsecond branches adventitiously from the lower ends of cells. Attachment by simple filamentous rhizoids opposite erect filaments (Fig. 158D) or alternate with them, and often ending in much-branched hapertia (Fig. 158B); on seagrasses and larger algae, epilithic or as a short turf mixed with sand. *Structure.* Cells near the thallus apex urceolate to short-cylindrical (Fig. 158A, C), 60–100 μm in diameter and L/D 0.8–0.9, in mid thallus elongate-cylindrical, 160–230 μm in diameter and L/D 2–5(9) and in the prostrate filaments cylindrical, 180–290 μm in diameter and L/D 1.5–2.5; synchronous hair-like laterals 8–16, arising as 1–2 whorls of papilllose protrusions (Fig. 158A) from sub-apical cells, and dividing 1–3 times di-poly-chotomously, greatly elongating and forming distinctive masses of extremely narrow branches (Fig. 158C) with basal cells 10–20 μm in diameter and L/D 12–14, persisting up to 7 axial cells from the apex, but eventually caducous.

*Reproduction.* Gametophytes dioecious. Female axes 3-celled, subapical, displaced laterally by the continued growth of the vegetative apical cell (Fig. 158A), not associated with synchronous hair-like laterals; procarp systems subapical, each with a sterile lateral cell abaxially and an adaxial supporting cell bearing a sterile cell apically and a recurved, 4-celled carpogonial branch laterally; hypogenous cell enlarging, becoming pyriform at time of fertilisation, and producing a whorl of 12-13 synchronic, single-celled involucral branches incurved about the developing gonimoblast (Fig 158B); post-fertilisation fusion cell columnar, bearing 1–3 gonimolobes terminally, most cells of which form globose carposporangia, 32–45 μm in diameter. Spermatangia borne in whorls of 4–8 pedicellate heads, produced synchronously from upper shoulders of cells near the thallus apex, within whorls of syncrctic, hair-like laterals (Fig. 158C) which are readily lost as the heads enlarge; each spermatangial head with a 2 (-4) celled fertile axis, and a basal cell elongating to become a clavate pedicel 88–120 μm in diameter and L/D 1.5–2, extending on its abaxial side so that the head is displaced to a slightly subterminal and adaxial position; mature heads globose-ovoid, or lobed if the axial cells elongate, 130–180 μm in diameter, produced from several polychotomous divisions of 4 periaxial cells on each of the axial cells.

Tetrasporangia (Fig. 158E, F) single on whorls of 8–10 (-14) clavate pedicels 75–123 μm in diameter and L/D 1.5–2, produced synchronously from the distal shoulders of cells towards the apex of axes, opposite 1–2 whorls of synchronous, hair-like laterals; globose, 65–105 μm in diameter, initially terminal on pedicels but, characteristically for this variety, displaced to a subterminal and adaxial position by the extension of the pedicel abaxially, tetrahedrally divided.

*Type of A. tenue* from Venice, Italy (Herb. Agardh, LD, 19891); lectotype of var. *thyrsigerum* from Rottnest I., W. Aust., (Herb Harvey, TCD, 533A); syntypes King George Sound (533B), Cape Riche (533 C ), Newcastle, N.S.W. (533M).

*Distribution.* Widely distributed in temperate and mixed temperate-tropic waters of southern Africa, the Indian Ocean, southern and eastern Australia, and Hawaii, in the lower eulittoral to upper sublittoral.

In southern Australia, Rottnest I., W. Aust. (Harvey) to Newport, N.S.W., apparently absent in the colder waters of Tasmania.

Anotrichium tenue is a distinctive species, unique in that branches arise from lower ends of cells, and whorls of synchronic, hair-like laterals are prominent near thallus apices. Baldock (1976, pp. 557-9) commented on the slightly subterminal and adaxial position of tetrasporangia (and spermatangial heads) on pedicels, in specimens from southern Australia assigned to A. tenue.

Boudouresque & Coppejans (1982, p.51) separated Mediterranean plants (as Griffithsia tenuis) from those of the Atlantic and Indo-Pacific, largely on the basis of 2–8 tetrasporangia per whorl, the terminal position of tetrasporangia on pedicels, and the 1–3 spermatangial heads which were lobed rather than globose-ovoid. On similar grounds Cormaci et al. (1994, p. 635) circumscribed A. tenue to include populations with up to 8 tetrasporangia per whorl, inserted terminally on pedicels, and reinstated A. secundum (Harvey ex J. Agardh) Furnari, for plants with 8 to 50 tetrasporangia per whorl inserted subterminally and adaxially on pedicels. However, Norris, & Aken (1985 p. 60) found in S. African specimens from Natal, a bridging of all important characteristics used by Boudouresque & Coppejans 1982, and concluded that

**Fig. 158.** *Anotrichium tenue* var. *thyrsigerum* (A–D, AD, A39034; E, F, AD, A26364). A. Procarp (left) and detail of the vegetative axis (right). B. Mature carposporophyte. C. Apex of a male plant, with a spermatangial head shown in section view. D. Detail of branching. E. Whorls of pedicellate tetrasporangia in various stages of development. F. Mature tetrasporangium. (All as in Baldock 1976, courtesy of Aust. J. Bot.)
only one taxon (Anotrichium tenue) was justified, and this appears to be the case for Australian specimens, although subsequently in Bucher & Norris (1995, p. 8) A. tenue has been confined to populations with terminal tetrasporangia.

Kim & Lee (1991 p. 19) considered the species to include three varieties: var. tenue, with Mediterranean-type tetrasporangial and spermatangial characteristics, but now known to be more widely distributed; var. secundum, with 30–40 tetrasporangia per whorl, subterminal on pedicels, up to 16 spermatangial heads per whorl, and vegetative cells with larger diameters; and var. thyrsigerum intermediate in morphology with 8–15 tetrasporangia per whorl, subterminal and adaxial on pedicels, 4–6 spermatangial heads per whorl and vegetative cells intermediate in diameter.

The range of characteristics found in Australian collections supports this concept of a single species with varieties.

Silva et al. (1996, pp. 376–7) have documented the considerable taxonomic tangles of the complex.

It appears that in Australia var. tenue is restricted to tropical regions, and var. thyrsigerum, is found throughout southern temperate regions excluding, possibly, Tasmania; var secundum has not been recorded. However, without microscopic preparations of tetrasporangial (or spermatangial) material, diagnoses cannot be validated.

2. Anotrichium towinna Baldock, sp.nov.

FIGS 157B, C, 159A–D

Thallus (Fig. 157B) light or dark red, 3–5 cm high, with several irregular main axes bearing whorls of 3 (-4) divergent lateral branch tufts of restricted growth from most axial cells. Attached by rhizoids from the thallus base; epiphytic. Structure. Axial cells elongate, 150–180 μm in diameter and L/D 3–10, branching (Fig. 159C) initially subdichotomous by oblique divisions of the subapical cell, rapidly adventitiously tri- or tetrachotomous with one of the branches developing into an indeterminate axis, the remaining branches forming short lateral tufts (Fig. 157C) branched trichotomously and divergently 5–6 times, basal cells 70–100 μm in diameter and L/D 5–8, apical and sub apical cells elongate, 68–80 μm in diameter and L/D 5–9, filaments ending obtusely or umbonately (Fig. 159B), apical cells often campanulate, 45–55 μm in diameter and notably narrower than subapical cells; branches bearing carposporophytes and tetrasporangia (Fig. 159B–D) less divergent. Rhodoplasts discoid, numerous, or elongate and net-like, with small refringent inclusions; large crystals sometimes present in the cytoplasm.

Reproduction. Female axes 3-celled, initially subterminal in lateral branch tufts (Fig. 159B) flanked by 1(-2) elongate, unbranched, caducous, colourless hair-like synchronous laterals; procarp systems (Fig. 159A) subapical, each with an abaxial, sterile lateral and adaxially a supporting cell bearing apically a sterile cell and a recurved, 4-celled carpogonial branch laterally; hypogenous cell enlarging, becoming pyriform, 80–210 μm in diameter and L/D 1–1.2 and producing from its upper shoulder a whorl of 10–12 incurved, reniform, 1-celled synchronic involucral cells 80–120 μm in diameter and L/D 1.8–2; fusion cell columnar, bearing 1–3 gonimolobes apically, most cells of which become ovoid-clavate carposporangia, 35–45 μm in diameter; vegetative growth inhibited by maturing carposporophytes which lie in axils near the ends of lateral tufts (Fig. 159C). Spermatangia unknown.

Tetrasporangia (Fig. 159D) single on solitary pedicels 40–45 μm in diameter, produced adaxially towards the apices of lateral tufts, initially in the position of a subdichotomous branch, but some later flanked by the development of 1(-3) further vegetative branches, thus appearing axillary; globose, 90–150 μm in diameter, tetrahedrally divided.

Thallus roseus usque sanguineus, 3–5 cm altus, cum axibus compluribus irregularibus principalibus basim rhizoldibus vestitis, ferens 3 (-4) fasciculos laterales ramosos trichtone et divergenter 5 vel 6 plo ex humero curusque cellularis axialis; epiphyticus in Posidonia. Structure. Cellulæ axiales 150–180 μm diametro et L/D 3–10; cellulæ apud apices fasciculorum lateralium 68–80 μm diametro et L/D 5–9, filæ obtuse aut umbonate terminantia.

Carposporophyta in axilibis ramorum in partibus superioribus fasciculorum lateralium verticillatorum, ramis vegetativis utrinque, globosa, 90–150 μm diametro, tetraedrice divisa.

Type from Saunders Beach, Kangaroo I., S. Aust. (Womersley, 29.ix.1964), holotype and isotype in AD, A28222.

Distribution: Coffin Bay and Kangaroo I., S. Australia.

Selected specimens: Coffin Bay, S. Aust., 3–4 m deep (Womersley, 4.xii.1975; AD, A46928) and in Posidonia bed, 2.5 m deep, (Womersley, 4.xii.1975; AD, A46939). American R. inlet, Kangaroo I., S. Aust., 2–4 m deep (Womersley, 22.vii.1963; AD, A26898).

Named for the Australian Aboriginal Kaurna word meaning “outstretched”, referring to the divergent branching of lateral tufts, obvious in pressed specimens.

Millar (1986, p. 87) described Baldockia verticillata Millar from Coffs Harbour, N.S.W., which is superficially similar to A. towinna in its adventitious sub-trichotomous branching. However, Baldockia also subsequently initiates 7 pigmented, robust synchronic branchlets from axial nodes, and also produces a unique sequence of female fertile axes, allying it to Halurus.

Calliclavula trifurcata Schneider from Grays Reef, Georgia USA (Searles & Schneider 1989, p. 732) produces whorls of 3 branchlets consisting of large, clavate cells branched subdichotomously; however, unlike the lateral tufts of restricted growth in A. towinna, these are indeterminate and are preceded by the development of subapical whorls of 2–4 slender, pigmented laterals, features which separate it from the genus Anotrichium.


Thallus (Fig. 157D) dark red, densely tufted, 2–9 cm high, filaments slender, subdichotomous with very fine terminal tufts, ecorticate throughout. Attached by basal rhizoids to jetty piles or pontoons, or epiphytic on seagrass. Structure. Cells near the thallus apex 18–30 μm in diameter and L/D 2–6, in mid thallus 44–92 μm in diameter and L/D 5.5–9, near thallus base 150–280 μm in diameter and L/D 4–5.

Reproduction. Gametophytes dioecious. Female axes (Fig. 160A) 3-celled, subapical, displaced laterally by the continued growth of the vegetative apical cell, flanked by 1–2 caducous, synchronic, hair-like laterals; procarp systems subapical, each with an abaxial, sterile, lateral cell, and adaxially a supporting cell bearing a sterile cell apically and a recurved, 4-celled carpogonial branch laterally; hypogenous cell enlarging at time of fertilisation, becoming ovoid–pyriform, 180–190 μm in diameter and L/D 1.5–2, and producing a whorl of 12–13 incurved, slender, 1-celled synchronic involucral branches, 75–114 μm in diameter and L/D 4–5 (Fig. 160B); fusion cell columnar, bearing 1–3 goniomolobes apically, most cells of which become small, ovoid carposporangia, 27–35 μm in diameter. Carposporophyte 150–400 μm across. Spermatangia in pyramidal heads (Fig. 157E) 75–100 μm in diameter and L/D 1.4–1.6, terminal on clavate pedicels 38–40 μm in diameter and L/D 1.4–1.6, produced singly and adaxially in upper thallus branches.

Tetrasporangia (Fig. 160C) single, terminal on cylindrical pedicels 26–29 μm in diameter and L/D 1–1.3 produced adaxially in groups of 1–3 from the upper shoulder of most cells near the thallus apex, globose, 50–90 μm in diameter, tetrahedrally divided.

Type from Semaphore, S. Aust., on jetty piles, upper sublittoral (Nielsen, 16.iii.1968); holotype in AD, A32281.
Fig. 159. Anotrichium towinna (A-C, AD, A28222; D, AD, A26898). A. Female axis, with single, hairlike, synchronic lateral. B. Lateral branch tuft with two female axes. C. Mature carposporophyte in a lateral branch tuft. D. Pedicellate tetrasporangia in a lateral branch tuft. (All by Baldock.)
**Anotrichium**

**Distribution:** Known from Gulf St Vincent, S. Aust., Port Phillip Bay, Vic., (Lewis 1983, p. 257) and Botany Bay, N.S.W.

**Selected specimens:** Port Adelaide, S. Aust., 2–10 cm deep on pontoon (Leupold, 12.iv.1984; AD, A55111). Botany Bay, N.S.W., on *Posidonia*, drift (Womersley, 20.v.1978; AD, A49371).

*A. subtile* occurs in calmer waters of bays, often on artificial substrates, and differs from other Australian species in the extremely slender filaments and small reproductive organs. Vegetative features are similar to *Griffithsia (Anotrichium) multiramosa* (Setchell & Gardner) Taylor (1939, p.14) from Baja California which is known only from tetrasporangial plants; however, the cells are smaller and branching less dense in *A. subtile.*


Callithamnion ligmaeophorum Harvey 1855a: 562.


Neomollospora ligmaeophorum (Harvey) Womersley 1950: 177.


**FIGS 160D–H, 161A, B**

*Thallus* (Fig. 161A) light red, 5–23 cm high, branching subdichotomous, main axes bearing regular, alternating, spreading lateral tufts (appearing flabellate when pressed) from each axial cell (Fig. 161B), clothed below with decurrent, anastomosing rhizoids. Attached by rhizoids bearing branched haptera (Fig. 160D); epiphytic. *Structure.* Cells of main axes 470–900 μm in diameter and L/D 3–4, basal cells of lateral tufts (Fig. 161B) significantly smaller, 220–320 μm in diameter and L/D 2.5–3.5, filament apices (Fig. 160H) mucronate, cells near the apex 25–50 μm in diameter and L/D 5–8.

*Reproduction.* Gametophytes dioecious. Female axes (Fig. 160E), 3-celled, subapical, displaced laterally by the continued growth of the vegetative axes, flanked by a pair of synchronic hair-like laterals; procarp systems subapical, each with a sterile lateral cell abaxially and an adaxial supporting cell bearing a sterile cell apically and a curved, 4-celled carposporoidal branch laterally; hypogenous cell enlarging, becoming pyriform, 200–370 μm in diameter and L/D 1.3–1.5, producing from its upper shoulder a whorl of 12–13, incurved, 1-celled synchronic involucral branches, 70–90 μm in diameter and L/D 6–7; fusion cell T-shaped to columnar bearing 1–3 gonimolobes terminally (Fig. 160F), most cells of which become globose-ovoid carposporangia, 35–45 μm in diameter. Carposporophyte 450–700 μm across. Spermatangia solitary, borne in heads (Fig. 160G) 130–225 μm in diameter and L/D 1–1.5, on clavate pedicels 80–120 μm in diameter and L/D 1.4–1.7, adaxial from cells towards the ends of lateral tufts; each spermatangial head initially globose, with 3 axial cells each bearing 4–5 periaxial cells dividing polychotomously several times, terminal cells budding off 1–2 sporoceci, heads becoming pyramidal and lobed as the axial cells elongate. Tetrasporangia (Fig. 160H) terminal on cylindrical pedicels 30–35 μm in diameter and L/D about 1, produced adaxially, singly or occasionally in pairs from the shoulders of cells near the apices of lateral branch tufts, occasionally on decurrent rhizoids (Fig. 160D), globose, 60–90 μm in diameter, tetrahedrally divided.


**Distribution:** Garden I., W. Aust. to Westernport, Victoria.

Small plants of A. licmophorum, consisting of a few subdichotomous lateral tufts are virtually indistinguishable from spicate forms of A. elongatum unless tetrasporangia (solitary in A. licmophorum and in clusters of 3–7 in A. elongatum) are present. Although other reproductive features are identical, the spreading lateral tufts with immediate and pronounced narrowing of filaments from axes to laterals, which regularly alternate along the axes in A. licmophorum distinguish larger plants of this species from A. elongatum.

Griffithsia crinita Kützing 1862: 7, pl. 21a–c.
Griffithsia setacea sensu Harvey 1844: 450. Tisdall 1898: 502. (NON C. Agardh 1817: xxviii.)
Griffithsia setacea var. tasmanica Kützing 1849: 660.
Griffithsia setacea var. filiformis Harvey 1855b: 258.
Callithamnion griffithsioides sensu Harvey 1859b: 336; 1860: pl. 160. (NON Sonder 1855: 512.)
Corynospora griffithsioides sensu Kylin 1956: 583.

FIGS 161C, 163A–C
Thallus (Fig. 161C) in dense tufts 5–17(-20) cm high, coarse in texture, when sterile light red, subdichotomous and fastigiate, when fertile, dark red, tufted, with tetrasporangial filaments ending in condensed, corymbose branches (Fig. 163C); basal filaments twisted together and entwined with dense, recurved, anastomosing rhizoids from the lower ends of cells, forming a rope-like mass 6–10 mm across. Attached by rhizoids; epilithic. Structure. Apical cells conical to cylindrical, 20–22 μm in diameter, subapical cells cylindrical, 100–130 μm in diameter and L/D 1.6–1.8; in mid thallus cells robust, 320–450 μm in diameter and L/D 3.5–5, axial cells obscured by rhizoids near the thallus base.

Reproduction. Gametophytes dioecious. Female axes 3-celled, subapical, displaced laterally by the continued growth of the vegetative axes, flanked by a pair of caducous, synchronic, hair-like laterals; procarp systems subapical, each with a sterile lateral cell abaxially and an adaxial supporting cell bearing a sterile cell apically, and a recurved, 4-celled carposporogonial branch laterally; hydropic cell enlarging, becoming pyriform, 200–230 μm in diameter and L/D 1.3–1.7, producing from its upper shoulders a whorl of 12–13 one-celled synchronic involucral branches incurved about the developing gonimoblast; fusion cell columnar bearing 1–3 gonimolobes terminally, most cells of which become angular-globose carposporangia, 25–35 μm in diameter; growth of adjacent vegetative filaments is slow so that mature carposporophytes lie 5–10 cells below the thallus apex and vegetative branches are curved over them (Fig. 163A). Carposporophytes 350–600 μm across. Spermatangia borne in heads (Fig. 163B) 180–280 μm in diameter and L/D 1.5–2.3, on clavate pedicels 70–120 μm in diameter and L/D 1.5–1.8, singly and adaxially from the upper ends of most cells of terminal, condensed, branch tufts; each head with 3 elongate axial cells each bearing 4–5 periaxial cells dividing phylactomously several times, the ultimate cells producing spermatia apically; adjacent vegetative branches initially inflexed, enclosing the developing heads, later reflexed, spreading and corymbose.
Tetrasporangia single, terminal on short pedicels 35–37 μm in diameter and L/D 1.2–1.3, produced adaxially in groups of 1 (-3) from most cells of terminal, condensed branch tufts which are initially inflexed, later reflexed forming distinct corymbose branch systems (Fig. 163C), globose, 95–105 μm in diameter, tetrahedrally divided.

**Type** from Tasmania (*Gunn*); lectotype in Herb. Klitzing, L, 941, 61 ... 119.


Anotrichium

AD, A39394) and 8 m deep (Watson, 28.vi.1974; AD, A45439). D'Entrecasteaux Channel, Tas., 10 m deep (Shepherd, 18.ii.1972; AD, A41698). Palmerston, New Zealand, drift (Parsons, 10.i.1981; AD, A53290).

A. crinitum is readily distinguished when tetrasporangial by the fertile corymbose branches. Sterile plants, however, resemble Griffithsia teges, although filaments are usually narrower in A. crinitum. Plants with slender filaments intergrade with A. elongatum, although filaments tend to be more robust with obtuse apices and conical not cylindrical apical cells in A. crinitum.


*Callithamnion elongatum* Harvey 1859b: 336; 1863: synop. iii.


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**Anotrichium**


**Corynospora arenata** (Harvey) Kylin 1956: 583. May 1965: 364.

- **Thallus** variable, soft in texture (PI. 2 fig. 1) light red to dark red, subdiehotomous with dense (Fig. 162C, D) or lax branching (Fig. 162A) or with lateral tufts arising irregularly (Fig. 163B) or somewhat regularly from main axes (Fig. 163C), 2-30 cm high, filaments twisted together or loosely entwined with decurrent rhizoids. Attached by basal rhizoids; epilithic or epiphytic mainly on seagrasses.

- **Structure.** Cells cylindrical, variable in size, near the thallus apex 48-60 μm in diameter and L/D 6-8, in mid thallus 220-250 μm in diameter and L/D 3-6, near the thallus base 260-300 μm in diameter and L/D 2-5; filaments gradually attenuate towards apices.

- **Reproduction.** Gametophytes dioecious. Female axes (Fig. 163D) 3-celled, subapical, displaced laterally by continued growth of the vegetative cell, flanked by 2 caducous synchronic, hair-like laterals; procarp systems (Fig. 163E) subapical, each with an abaxial sterile cell and an adaxial supporting cell bearing a sterile cell apically and a recurved, 4-celled carposporial branch laterally; hypogenous cell enlarging, becoming pyriform (Fig. 163F), 160-240 μm in diameter and L/D 1-2 and producing 1 (-2) whorls of 6-11, elongate, one-celled synchronic involucral branches 55-95 μm in diameter and L/D 4-6, incurved about the developing gonimoblast (Fig. 163G); fusion cell columnar, bearing 1-3 gonimoblasts terminally, most cells of which become globose carposporangia, 20-40 μm in diameter. Carposporophyte 250-460 μm across. Spermatangia borne in solitary heads, initially ovoid, becoming cylindrical, 180-250 μm in diameter and L/D 1.8-2, on clavate pedicels 70-90 μm in diameter and L/D 1.5-1.8, single and adaxial from the upper ends of many cells near the thallus apex; each head with 3 elongate axial cells each bearing 4-6 periaxial cells dividing polychotomously several times, the ultimate cells producing spermatia apically.

- **Distribution:** Recherche Archipelago, W. Aust. to Western Port, Vic. and around Tasmania.

A common species from the lower eulittoral to 38m deep, with very variable vegetative features and morphological intermediates with Anotrichium licmophorum and A. crinitum.


- **Slender form (PL. 2 fig. 1; Fig. 162D):** branching dense, with many soft, fine, sub dichotomous filaments. This superficially resembles Callihamnium longinode Harvey (1855a, p. 53) from Warnambool, Vic. (Watts), however, the type of that species is sterile, and the cells have L/D values of up to 20.
Tribe PTILOTEAE Cramer 1863: 106

by H.B.S. Womersley

Thallus erect, usually pinnate, complanately and distichously branched, laterals alternate or opposite, branches compressed. Structure. Apices with oblique cross walls, subapical cells cutting off cells alternately or oppositely, if opposite then developing equally or one (alternately) more so than the other; cortication usually commencing close to apices, pseudoparenchymatous, becoming several cells thick, outer cells small, compact and isodiametric, with the axial filament remaining as a large central cell. Cells uninucleate or multinucleate.

Life history triphasic, with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes dioecious. Procarps borne on ecorticate laterals close to apices, with 2–4 periaxial cells, one (the supporting cell) bearing a 4-celled carpogonial branch; auxiliary cell developing a foot cell and upper gonimoblast cell producing 1–3 successive rounded gonimolobes, the carposporophyte becoming surrounded by involucral branchlets from the sterile procarp cells or from below the procarps. Spermatangia in dense clusters on the pinnules or covering them on all sides. Tetrasporangia sessile or pedicellate on the ultimate ecorticate branchlets, or on 1–3 celled pedicels arising on the outer cortical cells of laterals; parasporangia present in some taxa, clustered, terminal on branchlets.

Type genus: Ptilota C. Agardh 1817, pp. xix, 39, nom. cons.

The tribe includes some 8 genera, characterised by the complanate, distichous and alternate or opposite branching, with apical cells dividing usually obliquely, dense cortication commencing close to the ecorticate apices and with compact, short, outer cells, carposporophytes with involucral filaments from the sterile procarp cells or from lower segments, and tetrasporangia borne on ecorticate filaments.
All Australian species need detailed study as to whether they satisfactorily agree with concepts of the tribe.

**KEY TO GENERA OF PTILOTEAE**

1. Subapical cells producing laterals alternately on successive cells, cortication commencing 10–15 cells below the ecorticate, branched apices ........................................ EUPTILOTA

2. Subapical cells producing 2 or 4 opposite laterals but with one of each pair alternately better developed ................................................................. 2

2. Apices overtopped by ecorticate, curved, alternately branched, pinnate to bipinnate laterals ........................................................... “PTILOTA” hannafordii

2. Apices not overtopped by ecorticate laterals, cortication commencing very close to apices ................................................................. DIAPSE

**Genus EUPTILOTA** Kützing 1847: 36

*Thallus* erect, pinnate, complanately and densely branched for 4 or 5 orders, laterals alternate, densely corticated from close to apices, branches slightly compressed; holdfast rhizoidal, usually conical. *Structure*. Apical axial filament with oblique alternating cross walls, cutting off alternate, distichous laterals which themselves branch almost immediately or later, with cortication commencing close to apices or 10–15 cells below terminal cells of ecorticate apices, becoming dense, pseudoparenchymatous and obscuring the axial cells, outer cells small and isodiametric; older branches with rhizoidal filaments around the axial cells. Cells uninucleate.

*Reproduction*. Gametophytes dioecious. Carpogonial branches 4-celled, borne on a supporting cell on subapical cells of ecorticate laterals, probably with other sterile periaxial cells. Carposporophytes at the apex of short lateral branches, with a gonimolobe surrounded by an involucre of tapering branchlets. Spermatangia in dense clusters on cells of pinnules. Tetrasporangia borne on short 1–3-celled pedicels on the outer cortex of the laterals, or laterally or terminally on the pinnules, sessile, tetrahedrally divided.

*Type species*: *E. formosissima* (Montagne)Kützing 1847: 36.

A genus of perhaps 4 species, the type and *E. mooreana* Lindauer (1949, p. 391) from New Zealand, *E. articulata* from southern Australia (and Japan and India?) and *E. fergusoni* Cotton and *E. pappeana* Kützing (see Silva et al. 1996, p. 409.) from the northern and western Indian Pacific Ocean respectively. Detailed comparisons of *E. articulata* with the type species are needed. The differences in apical structure and tetrasporangia arrangement may indicate that *E. articulata* should be placed in a separate genus.


**PLATE 2 fig. 2; FIGS 141E, 164, 165**

*Thallus* (Pl. 2 fig. 2; Figs 164A, 165A) erect, medium to dark red, 5–25 cm high, pinnate, complanately and densely branched for 4 or 5 orders, laterals alternate, becoming densely corticated except close to apices, axes and laterals slightly compressed, 0.5–2 mm broad. Ultimate largely eocortic ate branchlets alternately distichous, 200–500 μm long, pinnules 70–100 μm long. Holdfast densely rhizoidal, 2–10 mm across; epilithic. **Structure.** Apical filaments (Figs 164D, 165B) alternately branched, with oblique alternating cross walls, apical cells 20–25 μm in diameter and L/D 0.6–1, axial cells enlarging to 400–600 μm in diameter in lower thallus; cortication commencing usually within 10–15 cells of apices (Figs 164D, 165B), originating from basal cells of laterals, soon becoming dense and largely obscuring the axial cells (Fig. 164E), outer cells small, isodiametric to irregular and angular, 10–15 μm across; older axes (Fig. 164B,C) with a multilayered cortex around 3–4 large central cells, with rhizoidal filaments of long cells between the axial cells and inner, larger, cortical cells. Cells uninucleate; rhodoplasts discoid.

**Reproduction.** Gametophytes dioecious. Carposporophytes (Fig. 141E) borne on a supporting cell on subapical cells of eocorticate laterals, opposite a branch with often 2 or 3 in close succession, probably with 1 or 2 other sterile periaxial cells; post-fertilization stages unknown. Carposporophytes (Fig. 165C) situated at the apex of short lateral branches, with a single gonimolobe 300–500 μm across of ovoid carposporangia 30–70 μm in diameter, surrounded by an involucre of simple, tapering, branchlets 300–450 μm and 8–12 cells long, mid cells 35–50 μm in diameter and L/D 0.7–1.2. Spermatangia (Fig. 165D) in dense clusters on terminal and lower cells of pinnules.

**Tetrasporangia** (Fig. 165E) borne laterally or terminally on the pinnules, sessile, subspherical to slightly ovoid, 70–100 μm in diameter, tetrahedrally divided.

**Type** from “Nov. Holl.” (from Webb, ex Herb. Labillardiere); in Herb. Agardh, LD, 20116.

**Distribution:** From Flat Rocks (S of Geraldton) and Houtman Abrolhos, W. Aust., to Cooffs Harbour and Lord Howe I., N.S.W. (Millar & Kraft 1993) and E Tasmania.


*E. articulata* is a common species on rough-water coasts throughout southern Australia, from shaded relatively shallow situations to deep water. It is a fairly variable species, especially in how soon cortication develops and becomes complete below the apices of axes and laterals, and the length of the unbranched ultimate pinnules (e.g. in A63410). The habit and general appearance varies dependent on age, rate of growth, and proliferations on older, partly denuded plants.

There is no recognisable difference between *E. coralloidea* and *E. articulata*.

*E. articulata* has been reported from Japan (Okamura 1921, p. 130, pl. 183 figs 1–9; Itono 1977, p. 41) and from India (eg. Umamaheswara Rao 1974, p. 65, figs 12–14), indicating that it is a widely distributed species.
Fig. 164. *Euptilota articulata* (A, D, A66653; B, C, AD, A56269; E, AD, A63961) A. Habit. B. Transverse section of young branch. C. Transverse section of older branch. D. Branch apex with alternate, distichous, branchlets and cortication. E. Older corticated branch.
**Genus Ptilota** C. Agardh 1817: xix, 39, nom. cons.

*Thallus* erect, complanately branched, with main axes bearing indeterminate laterals for 3 or 4 orders, with opposite branches but one of each pair strongly developed and the opposite one short; determinate branches with opposite, shorter, branchlets; branches becoming corticated by closely appressed filaments from close to apices and oval in section; holdfast discoid, rhizoidal. *Structure.* Apical cells of indeterminate branches dividing obliquely, with first alternate laterals and later a smaller opposite branch. Periaxial cells producing ascending and descending branched cortical filaments forming a cortex of small cells, with rhizoids developing around the axial cells. Cells uninucleate.

*Reproduction.* Gametophytes dioecious. Procarps subterminal on indeterminate branches, with the axial cell bearing 4 periaxial cells, one (the supporting cell) with a sterile group and a lateral 4-celled carpogonial branch; the apical cell, sterile group and the 3 vegetative periaxial cells all produce short filaments with terminal hair cells. Auxiliary cells developing post-fertilization a gonimoblast of 2–3 successive globose lobes, with a basal fusion cell. Involucral branchlets develop from periaxial cells of the next lower segment. Spermatangia borne in clusters around cells of uniseriate filaments.

Tetrasporangia occur terminally in clusters on ultimate uniseriate filaments, pyriform, tetrahedrally divided.

*Type species:* *P. gunneri* Silva, Maggs & Irvine in Maggs & Hommersand 1993: 38.

The above generic description of *Ptilota* is based on that of Maggs & Hommersand, and is provided to permit differences in *P. hannafordii* to be assessed.


*FIGS 141F, 166*

*Thallus* (Fig. 166A) erect, medium to dark red, 10–35 cm high, densely branched for 4 or 5 orders, with major laterals more or less complanately situated, apices with dense, eocorticte, branchlets, laterals becoming densely corticated some distance below the apices, axes and laterals terete, denuded below, 0.5–1.2 mm in diameter. Holdfast conical, rhizoidal, 3–8 mm across, bearing 1–3 axes; epithelial or epiphytic (on *Doxodasya*). *Structure.* Eocorticte tufts clothing and overtopping apices, apical cells 10–15 μm in diameter and L/D 0.8–1.5, divisions oblique, with subapical cells producing 4 lateral branchlets (Fig. 166B), opposite ones in plane of thallus branching developing further; branchlets curved, pinnate, becoming bipinnate, with mostly opposite (±4) pinnules but uniaxial or more developed on the convex side (Fig. 166B); branchlets 700–1200 μm and 10–18 cells long, lower cells 50–150 μm in diameter and L/D 1–1.5, pinnules 80–220 μm and 5–12 cells long, lower cells 25–50 μm in diameter and L/D 1.0–1.2. Cortex becoming several cells thick, pseudoparenchymatous, outer cells isodiametric, 20–30 μm across and bearing a tomentum of anticlinal filaments 50–400 μm and 3–12 cells long, simple or branched, terminal cell mucronate. Cells multinucleate; rhodoplasts discoid, in reticulate chains in larger cells.

*Reproduction.* Gametophytes dioecious. Procarps (Fig. 141F) borne on subapical cells with a supporting cell bearing a 4-celled carpogonial branch. Carposporophyte with 1–3 subspherical gonimolobes 200–600 μm across, with ovoid carposporangia 10–27 μm across, surrounded by eocorticte branchlets. Spermatangial organs (Fig. 166C) lanceolate, 35–55 (–90) μm in basal diameter and 90–140 (–250) μm long, with 8–14 axial cells cutting off numerous cells radially and outer spermatangia forming a dense surface layer. Tetrasporangia (Fig. 166D, E) on branched clusters of smaller cells on lower cells of pinnules, terminal and pedicellate, subspherical, 40–60 μm in diameter, tetrahedrally divided.
Fig. 166. *Ptilota hannafordii* (A, C, E, AD, A67343; B, AD, A27397; D, AD, A67114). A. Habit. B. Branch apex with young lateral branchlets and branchlets unilaterally branched. C. Spermatangial branches. D. Branch apex of tetrasporangial thallus. E. Branchlets with tetrasporangia on basal, branched systems.
Type from Lady Bay, Warrnambool, Vic. (Hannaford); lectotype in Herb. Harvey, TCD.

Distribution: Port Elliot, S. Aust., to Warrnambool, Vic., and SE Tasmania.


_P. hannafordii_ clearly does not belong to _Ptilota_, differing in apical development, arrangement of laterals, degree of cortication, and form of the spermatangial branchlets.

_P. hannafordii_ was doubtfully placed in _Ptilota_ by Harvey (1862, pl. 221) and is currently being studied in detail by Dr Gerry Kraft, who will be placing it as a new genus.

**Genus DIAPSE** Kylin 1856: 390

_Thallus_ erect, pinnate, complanately and distichously branched for 4 or 5 orders, laterals more or less opposite, densely corticated from close to apices by closely appressed filaments, branches compressed; holdfast conical, rhizoidal. _Structure_. Apical filaments with slightly oblique cross walls, oppositely branched with laterals on alternate sides developing further. Cortex developed from axial and lateral filaments, becoming several cells thick, outer cells isodiametric and small. Cells uninucleate.

_Life history_ triphasic with isomorphic gametophytes and tetrasporophytes.

_Reproduction_. Reproductive bodies borne on cells of short dense tufts on margins of branches, filaments of tufts ecorticate and alternately branched. Carpogonial branches situated on subapical cells of the tufts, 4-celled on a supporting cell. Carposporophytes terminal on short lateral branches, with compact, surrounding, stout, involucral filaments. Spermatangia unknown.

_Tetrasporangia_ lateral or terminal on cells of the tufts, subspherical to slightly ovoid, deccusately to tetrahedrally divided.

_Type species:_ _D. pilota_ (Hooker & Harvey)Kylin 1956: 390.

A monospecific genus characterised by the opposite laterals, alternately more strongly developed, and cortication from very close to the apices.

**Diapse pilota** (Hooker & Harvey) Kylin 1956: 390, fig. 307D.


**FIG. 167**

_Thallus_ (Fig. 167A) erect, dark red, 10–30 cm high, pinnately and complanately branched for 4 or 5 orders, laterals distichous, dense, more or less opposite, becoming densely corticated from very close to apices, all branches slightly compressed, main branches 1–2 mm broad, lesser branches 0.5–1 mm broad. Holdfast conical, rhizoidal. 2–10 mm across, usually bearing a single stipe; epilithic. _Structure_. Apical filaments (Fig. 167B) of axes and branches oppositely branched, with slightly oblique cross walls, apical cells 15–20 μm in diameter and L/D 0.7–1, enlarging slightly in subapical cells which cut off distichous laterals with alternate
ones developing further; axial filament enlarging to 80–120 μm in diameter with cells L/D 1.3–2. Cortex cut off from axial and lateral filaments from shortly below the apices, becoming 250–400 μm and several cells thick with rhizoidal filaments around the axial cells (Fig. 167C) and between inner cortical cells, outer cells more or less isodiametric and 6–10 μm across. Cells uninucleate; rhodoplasts discoid.

Reproduction. Reproductive bodies borne on cells of short dense tufts of filaments 220–500 μm long, on the margins of the branches; each tuft with an axial filament bearing alternate lateral branchlets; carpogonial branches situated 3–4 cells below apical cells of the tufts. Carposporophytes (Fig. 167D,E) terminal on short lateral branches, with compact globular involucres 200–380 μm across, gonimolobe(s) with ovoid carposporangia 15–20 μm across; involucral filaments (Fig. 167E) arising below the carposporophyte, simple or branched, curved, 30–40 μm in diameter, cells more or less isodiametric. Spermatangia unknown.

Tetrasporangia (Fig. 167F) borne laterally or terminally on cells of the tufts, subspherical to slightly ovoid, 35–50 μm across, decussately to tetrahedrally divided.

Type from Port Arthur, Tas.; lectotype in Herb. Hooker, BM.

Distribution: Robe, S. Aust., to Port Phillip Heads, Vic. (Harvey) and E Tasmania.


Harvey (1859, p. 331) changed his earlier Thamnocarpus ptilota to Ptilota jeannerettii presumably to honour the original collector, Dr Jeannerett.

Tribe RHODOCALLIDEAE Hommersand, Wilson & Kraft 1998:878

by H.B.S. Womersley

Thallus erect, pinnate and complanately branched with irregularly alternate indeterminate branches bearing short, close set, distichous, determinate branchlets. Apical cells dividing obliquely, with either 4 spirally developed periaxial cells (filaments), the first formed becoming alternately distichous determinate branchlets, the second and third formed becoming caducous, and the fourth contributing only to the cortex (Rhodocallis), or with 2 lateral and 2–4 transverse (on each side) filaments (Psilothallia), with the lateral ones forming alternate distichous determinate branchlets. Indeterminate branches becoming densely corticated, and with dense rhizoidal filaments (appearing pseudoparenchymatous) around the axial cells. Gland cells absent. Cells uninucleate.

Life history triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes dioecious. Procarps borne on periaxial filaments, with the periaxial cell acting as supporting cell with a 4-celled carpogonial branch. Auxiliary cell dividing to form a foot cell and gonimoblast initial usually producing several gonimolobes, with or without a rhizoidal involucre from the basal cell of the sterile branchlet on the fertile axial cell and an outer involucre of determinate branchlets or simple filaments. Spermatangia cut off from initials on the surface cortical cells.

Tetrasporangia derived directly from surface cortical cells of the determinate branchlets, or on branched filaments or in siliculose branchlets on the determinate branchlets.

Type genus: Rhodocallis Kützing 1847: 36.
The tribe includes a second genus, *Psilothallia* Schmitz, though details of its apical development await clarification.

The above description is based on that of Hommersand *et al.* (1998), modified to cover the characteristics of *Psilothallia* as far as they are known. The tribe Rhodocallideae was presaged by Wilson, Hommersand & Kraft (1996).

### KEY TO GENERA OF RHODOCALLIDEAE

1. Apices with 4 periaxial cells and filaments, formed spirally, determinate branchlets alternate on successive axial cells, with terminal and marginal spines. Tetrasporangia formed directly from surface cortical cells in sori...............................RHODOCALLIS

1. Apices with 6–10 periaxial filaments, two lateral and 2–4 transverse on each side; determinate branchlets alternate 2–4 axial cells apart, without spines. Tetrasporangia borne on branched filaments on edges of determinate branchlets or in siliculose branchlets adaxial on determinate branchlets ......................................................PSILOTHALLIA

### Genus RHODOCALLIS Kützing 1847: 36

*Thallus* erect, complanately much branched pinnately with irregular, alternate, indeterminate compressed branches bearing close set, alternate, short, distichous determinate branchlets. Apical cells dividing obliquely, producing 4 periaxial cells spirally and in alternating sequence, the first formed periaxial filaments becoming alternately distichous determinate branchlets from each axial cell, the second and third becoming caducous, and the fourth contributing only to the cortex. Indeterminate branches becoming heavily corticated, with an inner layer of dense rhizoidal filaments around the axial cells. Cells uninucleate.

**Reproduction.** Gametophytes dioecious. Procarps borne on the second and third periaxial filaments of dwarf indeterminate branches, the periaxial cell being the supporting cell, with a 4-celled carpogonial branch but without sterile cells. Auxiliary cell dividing to form a foot cell and gonimoblast initial giving 4–6 gonimolobes, with a rhizoidal involucre and an outer involucre of determinate branchlets. Spermatangia cut off from initials on the surface cortical cells.

Tetrasporangia derived directly from surface cortical cells of the determinate branchlets, tetrahedrally divided.

**Type** (and only) species: *R. elegans* Kützing 1847: 36.

The structure and development of *Rhodocallis* was investigated in detail by Hommersand *et al.* (1998), who showed that the apical development of 4 alternately produced periaxial cells is unique in the Ceramiaceae, and the formation of spermatangia and tetrasporangia directly from cortical cells is distinctive.


**FIG. 168**

*Thallus* (Fig. 168A) erect, medium to dark red and fading to carmine, 10–20 (–28) cm high, much branched complanately and pinnately with subdichotomous to irregular, terete to slightly compressed, main branches 400–800µm broad, bearing regularly and closely arranged, distichous, compressed, simple determinate branchlets (1–) 2–4 mm long (Fig. 168B), with slight, spinous or blunt, marginal serrations on their upper half (especially on the abaxial edge). Holdfast rhizoidal, 2–10 mm across; epilithic. **Structure.** Apical cells (Fig. 168C) 10–12 µm in diameter and L/D 0.8–1, dividing by oblique alternate walls, each axial cell
Fig. 168. *Rhodocallis elegans* (A, E, AD, A60405; B, AD, A35771; C, AD, A63837; D, AD, A64074; F, AD, A46284). A. Habit. B. Branch apex with distichous laterals from alternate axial cells. C. Apex with oblique divisions and alternate laterals. D. Transverse section of branch with extensive rhizoids around the axial filament. E. Branch with carposporophytes. F. Laterals with tetrasporangia borne on cortical cells.
cutting off an initial periaxial cell, followed 1–2 axial cells lower by 2 more periaxial cells, then a fourth periaxial cell several axial cells below, formed in alternating sequence. The second and third formed periaxial filaments become transverse and are caducous (leaving only basal tissue) within a few mm of the apices, leaving the first formed filaments to form alternate, distichous, determinate laterals which become compressed, curved towards the branch apices, and have an apical spine and spines on the abaxial edges. Axial cells increasing to 120–180 μm in diameter and L/D 2–4 in the indeterminate axes; all branches becoming corticated by compacted filaments of short cells, arising from basal cells of the determinate laterals, with indeterminate branches producing rhizoidal filaments around the axial cells (Fig. 168D); these rhizoidal filaments extend out between the cortical cells close to the holdfast to form a hirsute surface coating. Lateral branches originate by continued growth of the apical cells of the distichous branchlets, with transition to spiral development. Cells uninucleate; rhodoplasts discoid in small cells, ribbon like in larger inner cells.

Reproduction. Gametophytes dioecious. Carpogonial branchlets occur in short series on successive axial cells of dwarf indeterminate axes, on the second and third formed periaxial cells which become the supporting cells, bearing 4-celled carpogonial branches, without sterile cells. Post-fertilization the supporting cell cuts off laterally an auxiliary cell, which, after nucleus transfer via a connecting tube, divides to form a foot cell and a gonimoblast initial, developing 3–6 gonimolobes each 400–600 μm across of ovoid carposporangia 20–30 μm in diameter. Rhizoidal involucral filaments arise from the basal cell of the sterile branchlet on the fertile axial cell and form a dense envelope around the developing carposporophyte, with the gonimolobes extending beyond the envelope at maturity; the carposporophyte (Fig. 168E) is also surrounded by incurved determinate branchlets. Spermatangia occur on the distichous branchlets and near the apices of indeterminate branches, with initials arising directly from outer cortical cells.

Tetrasporangia (Fig. 168F) occur on distichous branchlets near the tips of indeterminate axes, around the branchlets or in linear sori along the adaxial edges, developed directly from surface cortical cells, subspherical, 40–50 μm in diameter, tetrahedrally divided.

Type from ‘Neuholland’ (Herb. Binder); in Herb. Kätzing, L., 941, 253...292.

Distribution: Isles of St Francis, S. Aust., to Port Phillip Heads, Vic., and eastern Tasmania.


R. elegans, described in detail by Hommersand et al. (1998), is a distinctive species found in deep water on rough-water coasts. There are superficial similarities with the type species of Euptilota, E. formosissima, from New Zealand, especially in general form and in the tetrasporangial sori, but seemingly they differ in apical development; the New Zealand species needs detailed study.

Genus PSILOTHALLIA Schmitz 1896: 6

Thallus erect, much branched complanately and pinnately with compressed indeterminate laterals bearing close set, alternate, terete to compressed, tapering determinate branchlets 1–4 mm long. Structure. Axial filaments cutting off 2 lateral, and 2–6 transverse periaxial
filaments on each side, the lateral filaments forming indeterminate laterals or determinate branchlets on alternate sides and 2–4 axial cells apart; older branches with extensive rhizoid development around the axial and inner cells; cortex compact, pseudoparenchymatous, with outer cells small and isodiametric. Cells uninucleate.


Telrasporangia borne on branched filaments outside the cortex, originating from the periauxial filaments, or in special siliculose branchlets borne adaxially on the determinate branchlets.

Type species: *P. striata* (Harvey)Schmitz 1896: 7.

A genus of 3 species, 2 from Australia and both in need of detailed study, and *P. dentata* (Okamura)Kylin (1956: 395) from Japan.

KEY TO SPECIES OF PSILOTHALLIA

1. Surface view of branches showing transverse striations corresponding to the larger axial cells; extensive rhizoid development around the axial cells; axial filaments producing alternate determinate branchlets every 2 (-3) axial cells; tetrasporangia on branched filaments on the adaxial (and abaxial) sides of branchlets ........................................ 1. *P. striata*

1. Surface view of branches not striated; rhizoid development around the axial cells present but not extensive; axial filaments producing alternate determinate branchlets every (2-)3 (-4) axial cells; tetrasporangia formed on filaments of densely branched, elongate, siliculose branchlets adaxial on determinate branchlets ........................................ 2. *P. siliculosa*


Ptilotata striata Harvey 1855a: 558; 1859a; pl. 71; 1863, synop.: xlix. J. Agardh 1876: 80. Sonder 1881: 11.

Plumaria striata (Harvey)Kuntze 1891: 911.

**FIG. 169**

Thallus (Fig. 169A) erect, dark red-brown, 10–18 cm high, pinnate, much branched complanately with indeterminate branches bearing alternate, distichous, close set, terete, determinate branchlets (Fig. 169F) 1.5–2.5 mm long, upper branches 0.4–1 mm broad, compressed, near the base 1–1.5 mm in diameter, terete and denuded; branches horizontally striate (Fig. 169F) corresponding to the axial cells. Holdfast conical, 2–4 mm across; epilithic. Structure. Apical filaments soon overtopped by periauxial filaments from below, axial cells increasing to 90–140 μm in diameter and L/D 1.5–2.5, cutting off (close to the apex) opposite periauxial filaments in the plane of branching of which alternate ones 2 (-3) axial cells apart develop into determinate branchlets, and 2–4 transverse periauxial cells (Fig. 169B) which produce whorls of 6–10 periauxial filaments which remain compact and form the more or less terete central part of the branches; in tetrasporangial plants these filaments extend through the cortex but become denuded, with whorls of only the larger basal cells visible in the cortex surface. The central part of branches becomes swollen by extensive rhizoid development (Fig. 169C) around the axial and inner cells, separating these cells from each other; cells of the cortex are small, compact, isodiametric, 2–3 μm across. Cells probably uninucleate; rhodoplasts discoid.

Reproduction. Carpogonial branches unknown. Carposporophytes (Fig. 169D,E) formed in dense, globular tufts of simple filaments 250–350 μm long and 10–14 μm in diameter, with cells L/D 0.8–1.4; gonimolobes rounded, 90–140 μm across, carposporangia ovoid, 10–15 μm in diameter. Spermatangia unknown.
Tetrasporangia on clustered, branched filaments (Fig. 169F,G) derived from the periaxial filaments on the adaxial (and abaxial) sides of determinate branchlets and external to the cortex, filaments 10–15 μm in diameter, cells L/D 1–1.3, tetrasporangia slightly ovoid, 20–25 μm in diameter, tetrahedrally divided.

**Type** from Rottnest I., W. Aust. (Harvey); lectotype Trav. Set 240, Herb. Harvey, TCD.

**Distribution:** Fremantle, W. Aust., to Cape Northumberland, S. Australia.

**Selected specimens:** Fremantle, W. Aust. (Harvey. Alg. Aust. Exsic. 477A; MEL, 26396); Point Peron, W. Aust., drift (Royce 486, 28.i.1950; AD, A15500). 11 km off Cape Northumberland, S. Aust., 48 m deep (Shepherd, 6.v.1975; AD, A46282).

Details of the apical development and reproduction of this rare species await detailed study.


**FIG. 170**

Thallus (Fig. 170A) erect, dark red-brown, 4–10 cm high, pinnate, much branched complanately with compressed indeterminate branches bearing alternate, close set, slightly compressed, tapering determinate branchlets 1–2 mm long, branches 0.6–1.2 mm broad, not striate. Holdfast small, rhizoidal; epiphytic, usually on *Nizymenia conferta* (*Stenocladia australis*). Structure. Apical cells (Fig. 170C) 10–20 μm in diameter and L/D about 1, cutting off periaxial cells from subapical cells (Fig. 170B,C) and becoming enclosed by developing determinate branchlets, axial cells increasing to 90–120 μm in diameter and L/D 1.5–2.5, with lateral filaments of determinate branchlets lying in the plane of branching, alternate every (2-) 3 (–4) axial cells, with 2 transverse periaxial cells (Fig. 170D) on each side of the branch; periaxial filaments not extending beyond the compact cortex. Central part of older branches becoming swollen by slight to considerable rhizoid development around the axial cells (Fig. 170D); surface cells of the cortex small, compact, isodiametric, 2–3 μm across. Cells uninucleate; rhodoplasts discoid, in chains in larger cells.

**Reproduction.** Carpogonial branches unknown. Carposporophytes (Fig. 170E) formed in dense globular tufts 300–600 μm across, with a short multicellular base and curved surface filaments 90–180 μm long and 10–12 μm in diameter, cells L/D 0.8–1.5; gonimolobes several in each tuft, rounded, 120–180 μm across, with ovoid carposporangia 8–14 μm in diameter. Spermatangia unknown.

Tetrasporangia produced in siliculose branchlets (Fig. 170F) adaxial on determinate branchlets, each branchlet with an axial row of 12–20 cells bearing lateral cell rows and a surface layer of short 8–14-celled filaments, among which occur the slightly ovoid terminal (on 1–3-celled pedicels) tetrasporangia, 25–28 μm in diameter, tetrahedrally divided.

**Type** from Rottnest I., W. Aust. (Harvey); lectotype Trav. Set 243, Herb. Harvey, TCD.

**Distribution:** Champion Bay, W. Aust., to Point Roadknight, Victoria.


*see Chiiovitti et al. 1995, p. 164.*
Fig. 170. *Psilotheallia siliculosa* (AD, A32960). A. Habit. B. Branch apex with developing pinnules. C. Branch apex. D. Transverse section of branch with 6 periauxial cells connected to axial filament, and slight rhizoid development. E. Branch with cystocarp on pinnules. F. Branch and pinnules with adaxial, siliculose, tetrasporangial organs.
Tribe SPYRIDIEAE Schmitz 1889: 451
by H.B.S. Womersley

Thallus erect, radially branched, with uniaxial branches and apical cells which cut off a row of short axial cells which develop into an indeterminate branch, from each cell of which one or more determinate branchlets (ramelli) develop laterally or in whorls. The ramelli are of limited growth, developing rapidly by apical divisions to 10–30 cells long and expanding by cell elongation to their mature length of generally 1–3 mm. The axial cells of indeterminate branches also cut off in alternating sequence a ring of periaxial cells, which form a band around the node between two axial cells. Each of these periaxial (nodal) cells cuts off two cells from its lower end, and these elongate and become pit-connected to the nodal cells of the next lower segment to give complete cortication, showing bands of shorter and broader nodal cells alternating with the bands of internodal cells, which are longer, narrower, and approximately twice as many as the nodal cells. Further outer cortication occurs some distance from the branch apices, from descending rhizoids developed from the nodal cells, and this obscures the regular pattern of nodal and internodal cell bands, especially in certain species (e.g. S. squalida). The cells of the determinate ramelli each cut off a ring of 6–8 cells from their upper end, and these develop into a nodal band 1–3 cells broad; gland cells absent. Cells uninucleate.

Life History triphasic with isomorphic gametophytes and tetrasporophytes.

Reproduction. Gametophytes dioecious. Procarps (3–6) produced on small lateral branchlets of restricted growth, with normally three periaxial cells in each fertile segment, one of which (the supporting cell) bears the carpogonial branch, and each periaxial forms an auxiliary cell; two (or rarely three) gonimoblasts are initiated and the mature carposporophyte is commonly bilobed. Carposporophytes become surrounded by pericarpic filaments developed from the segments above and below the one bearing the procarp, giving the appearance of a cystocarp with a well developed pericarp wall held together by a mucilaginous sheath and some lateral pit-connections; these filaments disintegrate fairly readily in preserved material. Spermatangia cover several cells in the lower part of the ramelli, usually excluding the basal cell. They are derived from filaments originating from the nodal cells, which grow over the two adjacent cells, then cut off spermatangial initials before forming the continuous surface layer of spermatangia. Tetrasporangia occur on the lower cells of the ramelli, sessile and mostly on the upper (adaxial) side, tetrahedrally divided.

The tribe contains the single genus Spyridia.

Genus SPYRIDIA Harvey in W.J. Hooker 1833: 259,336.

With the characteristics of the tribe.

Type species: S. filamentosa (Wulfen) Harvey 1833:336.

Womersley & Cartledge (1975) considered 4 species occur on southern Australian coasts, and this account is followed here.

KEY TO SPECIES OF SPYRIDIA

1. Ramelli robust, opposite and decussate, usually (70–) 100–150 μm in diameter with isodiametric cells and nodal bands 3–5 cells broad ........................................ 4. S. dasyoides
1. Ramelli slender, single or whorled but not opposite, less than 70 μm in diameter, usually with cells longer than broad, and nodal bands 1—3 cells broad ........................................ 2

2. Lesser branches stout (0.5–1 mm in diameter), markedly basally constricted, heavily corticated to their apices, bearing slender, irregularly branched ramelli ........................................................................ 3. S. squalida
2. Lesser branches slender (under 0.5 mm in diameter), not or only slightly basally constricted, cortication dense only on older branches, with ramelli single per segment or whorled ................................................................. 3

3. Ramelli one per segment, 35–65 μm in diameter, nodal bands 2–3 cells broad ................................................................................................................. 1. Spyridia filamentosa

3. Ramelli becoming whorls of 3–6 (-8), 15–40 μm in diameter. nodal bands I cell broad ................................................................................................................... 2. S. tasmanica


FIGS 171, 173A, B

Thallus (Fig. 171A) grey to grey-red, sometimes red-brown, 7–18 cm high, lax and soft, irregularly much branched on all sides with longer and shorter branches intermixed, with one to several axes. Holdfast originally discoid, soon becoming fibrous or stoloniferous and entangled; epilithic or epiphytic on various larger algae and seagrasses. Structure. Axes and larger branches corticated, terete; axes 0.5–1 (-1.3) mm in diameter, tapering to lesser branches 100–300 μm in diameter; laterals arising from periaxial cells or adventitiously from cortical cells. Segments usually clearly defined on branches (Fig. 171B), variable in length and proportions but usually L/D (0.2–) 0.5–1, with bands of shorter nodal cells and longer internodal cells alternating; nodes with 11–14 periaxial cells, each corresponding to two internodal cells except for the (usually) larger periaxial cell bearing the ramellus. Cortication usually commencing a few mm from the apices but very variable, consisting of rhizoidal cells lying between the internodal cells and gradually forming a continuous cortex 1 (-2) cells thick. Larger branches corticated, terete; axes 0.5–1 (-1.3) mm in diameter, tapering to lesser branches 100–300 μm in diameter; laterals arising from periaxial cells or adventitiously from cortical cells. Segments usually clearly defined on branches (Fig. 171B), variable in length and proportions but usually L/D (0.2–) 0.5–1, with bands of shorter nodal cells and longer internodal cells alternating; nodes with 11–14 periaxial cells, each corresponding to two internodal cells except for the (usually) larger periaxial cell bearing the ramellus. Cortication usually commencing a few mm from the apices but very variable, consisting of rhizoidal cells lying between the internodal cells and gradually forming a continuous cortex 1 (-2) cells thick. Ramelli (Figs 171B) single per segment, irregularly spirally arranged, 0.5–1.5 mm and 12–20 (-27) cells long, cylindrical or gently tapering apart from the terminal 2–3 very short cells (Fig. 173A) which taper abruptly to a mucronate cell, (35–) 40–55 (-65) μm thick with cells L/D (1.2–) 1.5–2.5 (-3); mucronate end cell often lost from older ramelli, ramelli with about 9 nodal cells, each usually cutting off 1 (-2) cells anteriorly, giving a nodal band (Fig. 173B) 2–3 cells broad. Cells uninucleate; rhodoplasts discoid to elongate, becoming ribbon like.

Reproduction. Gametophytes dioecious. Carposporophytes (Fig. 171C) short-stalked, usually bilobed, lobes globular, 300–700 μm across. Spermatangia covering the lower (except basal) several segments of ramelli (Fig. 171D), forming male organs 75–120 μm in diameter. Tetrasporangia (Fig. 171E) sessile, 1–3 per cell on lower cells of ramelli, mostly on the upper (adaxial) side, subspherical, 50–75 μm in diameter, tetrahedrally divided.

Type from the Adriatic Sea; in Vienna? (Maggs & Hommersand 1993, p. 136).
Spyridia

Fig. 171. Spyridia filamentea (A, AD, A41869; B, AD, A41175; C, AD, A41881; D, E, AD, A41815). A. Habit. B. Branch with branchlets and a young carposporophyte. C. A carposporophyte with 2 gonimolobes and sterile filaments. D. Male plant with spermatangial ramelli. E. Branches with ramelli bearing tetrasporangia. (A, B, D, E, as in Womersley & Cartledge 1975, courtesy of R. Soc. S. Aust.)
**Spyridia**

**Distribution:** Widely distributed in most temperate and tropical seas.

All around the Australian coast (including Tasmania) in conditions of moderate to slight water movement.

**Selected specimens:** Port Denison, W. Aust., on jetty, 0-5 m deep (Kraft, 14.xii.1971; AD, A41175).

Smooth 1., Isles of St Francis, S. Aust., on Amphibolis antarctica, 22 m deep (Shepherd, 29.iii.1980; AD, A52255). Elliston, S. Aust., upper sublittoral pools, inner reef (Womersley, 15.i.1951; AD, A15142). Billy Lights Point, Port Lincoln, S. Aust., on Posidonia australis, 12 m deep (Shepherd, 23.viii.1975; AD, A46568).


As discussed by Womersley & Cartledge (1975, p. 225), Spyridia filamentososa is recognised as a widely distributed species, having been recorded from most seas, and many authors (e.g. Harvey 1846, pl. 46; Feldmann-Mazoyer 1941, p. 348) refer to it as a very variable species. J. Agardh (1876, p. 268) in segregating two Australian species (S. biannulata and S. brevivarticulata) from S. filamentososa, referred to their similarity in habit with S. filamentososa and the large number of forms classed as this species. J. Agardh apparently regarded his two segregate species with some doubt, and a detailed study of extensive collections of Australian material does not provide any satisfactory way of segregating S. biannulata and S. brevivarticulata from S. filamentososa. These species and their synonymy were discussed by Womersley & Cartledge (1975, pp 225–227).


*S. filamentososa* var. *tasmanica* Kützing 1849: 666.

*S. filamentososa* var. *verticillata* Harvey 1844: 449.


**FIGS 172, 173C-G**

**Thallus** (Fig. 172A) grey-red to red-brown, usually 8–25 cm high, much branched irregularly alternately, branches terete, with one to a few main axes and prominent lateral branches, bearing lesser branches on all sides, with whorled ramelli. Holdfast small, discoid; epilithic or on Amphibolis. **Structure.** Axes 1–2.5 (-2) mm in diameter, lesser branches 200–400 μm in diameter, segments L/D (0.5-) 0.8–1.3 (Fig. 172B, E) with usually 12 periaxial cells, each producing two internodal cells; cortication by rhizoidal cells from the nodal cells, commencing within 1–2 cm of apices but becoming thick on axes and main branches. Ramelli 1 (-3) per node near apices, becoming whorled (Fig. 172B, E) with 3–6 (-8) per whorl with the addition of adventitious ramelli, arising from enlarged periaxial cells, forming an involucre similar to that in S. filamentososa. Carposporophytes (Figs 172B, C) terminal on a short branchlet bearing ramelli, 0.5–0.8 mm across. Spermatangia cover 2–6 cells (Fig.
Fig. 172. Spyridia tasmanica (A, AD, A20567; B-D, AD, A37622; E, AD, A41066). A. Habit. B. Corticated branch with whorled ramelli and 3 carposporophytes. C. Squashed carposporophyte with slender, sterile filaments and clavate carposporangia. D. Male thallus with spermatangial ramelli. E. Thallus with whorled ramelli bearing tetrasporangia. (A, D, E, as in Womersley & Cartledge 1975, courtesy of R. Soc. S. Aust.)
172D) to within 1–2 cells of base of ramelli, forming a cylindrical male organ 70–130 μm in diameter and L/D 1–6.

Tetrasporangia (Figs 172E) on 1–4 cells near the base of the ramelli, borne mostly on the upper (adaxial) side, subspherical, 60–100 (-120) μm in diameter, tetrahedrally divided.

Type from: Tasmania (probably Gunn, ex Hooker); holotype in L (941. 311...371).


S. tasmanica is a distinctive species with its whorled ramelli and single row of nodal cells. It occurs generally in relatively calm localities, often with considerable current, 2–35 m deep, occasionally in partly sheltered habitats and shaded rock pools on rough-water coasts.


FIGS 173H, I, 174

Thallus (Fig. 174A) grey-red to red-brown, when dried often appearing somewhat farinaceous, usually 10–30 cm high, robust, erect, irregularly and proliferously branched, with one to several axes, usually with long, much branched, laterals on all sides. All branches terete and corticated to their apices, axes and main branches linear, lesser branches (Fig. 174B) basally constricted and bearing densely arranged ramelli, especially on their upper parts, sometimes denuded below. Holdfast small, discoid; epithecic. Structure. Axes 1.5–2.5 mm in diameter, denuded below or with short, proliferous branches, tapering slightly to branches 1–1.5 mm in diameter and lesser branches 0.5–1 mm in diameter. Segments largely obscured by cortication (Fig. 174B), L/D 0.3–0.5, with 16 periaxial cells and about twice as many internodal cells; cortication commencing within a few axial cells of apices, pseudoparenchymatous, 2–3 cells thick on lesser branches, several cells thick on axes. Ramelli (Figs 173H, I, 174B) one per segment close to apices, originating from periaxial cells and also scattered, adventitious, densely covering the lesser branches, sometimes persisting onto larger branches; ramelli 0.5–1 (-1.5) mm and (10-) 14–20 (-24) cells long. Larger cells (20-) 30–40 (-45) μm in diameter and L/D (1-) 1.5–2 (-2.5). Ramelli with a single row of small nodal cells (Fig. 173H, I) derived from 5–6 periaxial cells each of which cuts off 2–3 outer cells in the same transverse plane. Cells uninucleate; rhodoplasts discoid, becoming elongate in larger inner cells.

Reproduction. Gametophytes dioecious. Female axes developing as short, adventitious branchlets which are fairly heavily corticated but less so than in vegetative branches. Alternate segments each bear a procarp, with the sterile segments bearing ramelli. Usually three periaxial cells occur in fertile segments, one (the supporting cell) producing a 4-celled carpopogonial branch. Two, or probably often 3, auxiliary cells are formed, leading to a carposporophyte with two or three lobes (Fig. 174 I), short stalked and 0.5–0.8 mm in diameter (Fig. 174C, D). The pericarp develops similarly to that in other species. Spermatangia cover the lower 2–6 cells (except basal cell) of ramelli, forming a male organ 50–80 μm in diameter.

Tetrasporangia borne on the lower several cells of the ramelli, largely on the upper (adaxial) side, 1 (-2) per cell, sessile, spherical to slightly ovoid, 40–60 μm in diameter, tetradehtrally to sub-cruciatey divided.

Type from “Nov. Holland. australisem”; lectotype in Herb. Agardh, LD, 51533.

Distribution: Geographe Bay, W. Aust. to Waratah Bay, Vic., usually in deep water (2–24 m deep).

*S. squalida* is a distinctive and robust species of *Spyridia*, having cortication to the apices and thus forming swollen, basally-constricted, lesser branches, bearing ramelli often densely scattered but usually soon denuded; the farinaceous appearance is also a common feature of older dried plants.

![Image of Spyridia squalida](image_url)
Spyridia

SPYRIDIEAE

S. wilsoni J. Agardh is typical S. squalida. The type of the former is from Pt Phillip Hds, Vic. (J.B. Wilson, 1887; LD, 51532), and the thallus is not compressed as stated by J. Agardh (1897) and May (1965).

S. valida Sonder (1881: 16) is a nomen nudum, based on a specimen in MEL (45195) from Geographe Bay, W. Aust. (Bunbury, 1875), accompanied by Sonder’s drawings. It is typical S. squalida.


**FIGS 173J, K, 175**

Thallus (Fig. 175A, B) dark red to red-brown, usually 10–20 cm high, erect, much branched irregularly to subdistichously with one to several axes; axes and larger branches heavily corticated, terete to angular and becoming four-sided with thickened cortical flanges in line with the 4 ranks (Fig. 175C) of ramelli, densely branched. Axes 1–2 (-2.5) mm in diameter, often denuded but sometimes with numerous, short, proliferous branches, tapering to 0.5–0.8 mm in diameter with lesser branches 0.2–0.5 mm in diameter; laterals arising from nodal cells. Holdfast discoid, soon becoming fibrous and stoloniferous; epilithic or epiphytic. Structure. Segments largely obscured by cortication, L/D 0.5–1, with 8 periaxial cells producing 16 internodal cells and the 8 cells soon with interposed rhizoidal cells giving both nodal and internodal rings of 16 cells (Fig. 175C); cortication commencing within a few segments of apices, of elongate cells and later appearing pseudoparenchymatous, a few cells thick on lesser branches, many (especially on flanges) cells thick on axes. Ramelli (Figs 173J, K, 175C) arising from an enlarged periaxial cell, in opposite and more or less decussate pairs (Fig. 175C) on successive segments (often displaced to two rows on each side in the plane of branching), (1-) 1.5–2 (-2.5) mm and (16-) 18–22 cells long, relatively uniform in diameter but tapering fairly abruptly to a point, (70-) 100–150 μm in basal diameter, cells L/D about 1 (-1.5). Ramelli with 16–20 nodal cells, each cutting off 1–2 cells (which often divide again) on both sides (anteriorly first), producing a nodal band (2-) 3–4 (-6) cells broad (Fig. 173K). Cells uninucleate; rhodoplasts discoid to elongate.

Reproduction. Gametophytes dioecious. Female axes with alternating sterile and procarpic segments, the latter with a 4-celled carpogonial branch on the supporting cell and usually two other periaxial cells. The mature carpogonophore (Fig. 175D) is short-stalked, irregularly globular to bilobed, 400–600 μm across, with two or three discrete lobes and the pericarp is relatively firm at its periphery. Spermatangia (Fig. 175E) cover the lower (except basal) several segments of young ramelli of adventitious branchlets lying between older ramelli, forming male organs 120–200 μm in diameter. Tetrasporangia (Fig. 175F) sessile, 1–3 per cell, mostly on the upper (adaxial) side of the ramelli, subspherical, 30–90 μm in diameter, tetrhedral divided.

Type from Holdfast Bay, S. Aust. (F.v.Mueller); holotype in MEL, 45128.


*S. dasyoides* usually occurs on rough-water coasts from low tide level to depths of 33 m. Deeper growing plants are usually more delicate than those growing in turbulent conditions. It is characterised by its robust, opposite and more or less decussate ramelli, with cells about as long as broad and nodal bands 3–5 cells broad, together with the largely distichous branching. Eight periaxial cells are formed in branches and soon become separated by rhizoidal cells, thus forming both nodal and internodal rings of usually 16 cells, the bands being about equal in length.

**Tribe CERAMIEAE (Dumortier) Schmitz 1889: 106**

*Thallus* usually erect, subdichotomous or laterally branched, axial cells with 3–10 periaxial cells from their upper ends, producing acropetal and usually basipetal rows of corticating cells which adhere closely to the axial cells and may produce an outer cortex also of small, more or less isodiametric cells.

*Life history* triphasic with isomorphic gametophytes and tetrasporophytes.

**Reproduction.** Gametophytes usually dioecious. Carposporial branches formed on periaxial cells near apices, 4-celled usually with a sterile group. Carposporophytes with 1 to several rounded gonimolobes, all cells forming carposporangia, naked or involucrate by branches from below. Spermatangia cut off from periaxial or the corticating cells. Tetrasporangia cut off from periaxial or corticating cells, usually decussately divided.

**Type genus:** *Ceramium* Roth 1797: 146.

A tribe with about 9 genera (Kylin 1956, pp. 368, 369), of which *Ceramium* Roth and *Centroceras* Kützing occur on southern Australian coasts. These genera are readily recognised vegetatively by the characteristic nodal development of periaxial and corticating cells.

**KEY TO GENERA OF CERAMIEAE**

1. Periaxial and cortical cells rounded, not forming straight rows of angular cells, with successive nodes at first or throughout separated, leaving ecoricate internodal bands; spermatangia cut off from corticating cells............................... **CERAMIAEUM**

1. Periaxial cortical cells rectilinear, forming straight longitudinal rows of angular cells, completely covering axial cells with no ecoricate bands; spermatangia on clusters originating from periaxial cells.................................................. **CENTROERAS**

**Genus CERAMIAUM** Roth 1797: 146, nom. cons.

*Thallus* prostrate or (usually) erect, complanately or irregularly much branched, or with simple erect branches, branching alternate to subdichotomous, adventitious in some species, apices straight or involute; branches terete or compressed with nodal cortication from periaxial cells; attachment by unicellular or multicellular rhizoids, usually with digitate pads.
Structure. Apical cells dividing obliquely, lateral branches arising by oblique division of subapical cell and developing as strongly (hence subdichotomous) or less strongly (hence alternate) as the parent axis. Subapical cells cutting off 3–10 periaxial cells in alternating sequence (dividing laterally to form pseudoperiaxial cells in some species), and producing chains of cells acropetally and usually basipetally, which adhere closely to the adjacent cells, leaving a clear space on the axial cell or closing this space largely or completely; some species forming an outer cortex of small cells; short spinous laterals from the cortical cells present in some species, hairs common, and some species forming gland cells in the cortex; axial cells usually much larger than periaxial or cortical cells, usually with a prominent central protoplasmic strand between the pit-connections. Cells uninucleate.

Reproduction. Gametophytes dioecious, rarely monoecious. Procarps formed on the first periaxial cell, often in a short row, with a sterile group and a 4-celled carpogonial branch; post-fertilization the auxiliary cell divides to a foot cell and gonimoblast initial producing one to several successive gonimolobes, all cells becoming carposporangia, with the foot cell, supporting residual cell and axial cell fusing; carposporophytes naked, often partly involucrate by lateral branches from below. Spermatangia formed in extensive sori on the nodal cortices, with initials cutting off 1–3 spermatangia. Tetrasporangia formed from the periaxial or cortical cells, naked or partly involucrate by short branchlets, usually tetrahedrally divided.


A widespread genus of many species, with 15 recorded for southern Australia by Womersley (1978). Other species also occur in this region but are inadequately known. These include one provisionally referred to as *C. wilsonii* in Womersley (1978, p. 206), known only from tetrasporangial specimens of J.B. Wilson from Port Phillip Heads and Western Port, Victoria (MEL, 45466, 45467), and also a minute species of the *C. codii* group from Twin Rocks, Head of the Great Australian Bight, S. Aust., growing on *Amphiroa anceps*, 20–22 m deep (Branden, 19.1.1991; AD, A61152). This sterile collection has prostrate filaments with simple, straight, erect branches, nodes with 5 periaxial cells and only acropetal [1(-2)] cortical cells, with filaments 35–45 μm in diameter and axial cells L/D (1-) 1.2–1.8.

**KEY TO SPECIES OF CERAMIUM**

1. Cortical cells near the apices, and in some species in older parts, bearing short, spinous or tapering filaments 1–7 cells long, with cells much narrower than the axial cells. ....... 2.

1. Cortical cells not bearing spinous or tapering filaments (excluding slender caducous hairs).

.......................................................... 4

2. Cortical band normally 2 cells long in all parts, with many of the cells bearing slender filaments 2–7 cells long as a double whorl at each node; terminal cells of filaments rounded or forming a hair ................................. 1. *C. shepherdii* 2. Cortical band more than two cells long, bearing acute spines at least near the branch apices, but not in whorls ............................................................ 3

3. Spines single at each node, abaxial, 3–6 cells long, relatively coarse; internodal space present throughout thallus; tetrasporangia partly to largely involucrate; usually epiphytic on *Codium fragile* or *Corallina* ................................. 2. *C. monacanthum* 3. Spines one to several per node near apices, to 4 cells long, relatively slender; cortical cells on older branches with numerous 1–3-celled spines; internodal space present on young branches, closing on older parts; tetrasporangia mostly abaxial, largely enveloped by small cells; usually epiphytic on seagrasses (*Posidonia*, sometimes *Amphibolis*) ............................ 3. *C. puberulum*

4. Cortication complete except possibly within a few axial cells of the apices; outer cortex present; tetrasporangia enveloped (or almost so) within the cortex ....... 5
4. Cortical bands short to relatively long, separated by a clear (though sometimes narrow) internodal space in at least the upper part of the thallus; outer cortex present or absent; tetrasporangia usually protruding, naked or involucrate ....... 6

5. Branching usually subdichotomous, without alternate flabellate laterals; cortical cells becoming elongate and dovetailing to give complete cortication within 6–8 axial cells from apices; rosettes of outer cortical cells present around periauxial cells; older inner cortical cells usually L/D 3–5, usually without distinct rosettes of outer cells; tetrasporangia formed first from periauxial cells, later formed from cortical cells near nodes and thus more irregularly scattered; usually occurring in sheltered water ............. 4. C. rubrum

5. Main axes bearing alternate, flabellate, lateral branch systems; cortical cells isodiametric, remaining ovoid to subspherical (L/D usually less than 2) often with well-defined rosettes of outer cells; young inner cortical cells smaller acropetally than basipetally, with this distinction often visible for many segments from apices; tetrasporangia usually in a well-defined ring at each node, mostly cut off from periauxial cells; epiphytic and usually occurring under strong water movement .................................................... 5. C. pusillum

6. Thallus relatively robust with the cortical bands becoming 8 or more cells long; branching alternate to irregularly lateral, often with proliferous branchlets, becoming 300 μm or more thick in older branches; internodal spaces present or closed on older branches; tetrasporangia becoming whorled, largely involucrate, formed in branchlets which often become stichidiose .......... 7

6. Thallus either moderately robust and usually strictly dichotomous, usually without laterals and over 200 μm thick below, or relatively slender (usually less than 200 μm thick) and more irregularly branched; cortical bands normally less than 8 cells long (except in older nodes of C. flaccidum), with internodal spaces present throughout thallus; tetrasporangia naked or involucrate ..................................... 9

7. Thallus complanately branched, alternately branched every (3-) 4–5 cells; internodal space narrow and lenticular in face view of branches, cortication closing in older parts; outer cortex usually absent or slight ........................................ 6. C. lenticulare

7. Thallus complanately or irregularly branched; internodal space uniform around the node, distinct at least in younger branches; outer cortex well developed on older branches .. 8

8. Thallus complanately branched above; periauxial cells (7-) 8; internodal space usually very narrow forming an annular ring, cortical cell divisions synchronous with the space closing completely on older branches; outer cortex present on older axes as rosettes around the periauxial cells and later from the inner cortical cells, mainly covering the central part of the nodal cortication ............ 7. C. excellens

8. Thallus irregularly branched (not complanate); periauxial cells usually 7–8; internodal space usually 0.5–1 times as long as cortical band, normally remaining as a narrow gap on older axes; cortical cell divisions at first synchronous, later extending irregularly; outer cortex present in branchlets, becoming extensive over periauxial and inner cortical cells ........................................ 8. C. tasmanicum

9. Thallus over 200 μm thick below, usually strictly dichotomous, fastigiate; tetrasporangia naked or very slightly involucrate ................................................................. 10

9. Thallus rarely over 200 μm thick, irregularly subdichotomous to laterally branched; tetrasporangia with a slight to extensive involucrate ........................................ 11

10. Periauxial cells 7–8 (–9), each cutting off two cells both acropetally and basipetally; gland cells usually present; outer cortex present on older parts; tetrasporangia naked, produced from periauxial or cortical cells at first as a ring around upper end of node, later scattered ........................................ 9. C. isogonum

10. Periauxial cells 6–7, each cutting off laterally two pseudoperiauxial cells thus forming a ring of 18–21 cells at the node, from which cortical cells develop acropetally
and basipetally; gland cells occasionally present; outer cortex absent; tetrasporangia slightly involucrate, produced from the true periaxial cells, at first abaxially and later around the node .................................................. 10. C. australie

11. Cortical cells developing acropetally only (rarely single basipetal cells) from the periaxial cells .......................................................... 12

11. Cortical cells developing acropetally and basipetally (rarely few in C. cliftonianum) from the periaxial cells ........................................................................................................... 13

12. Periaxial cells producing acropetally branched chains of 4–5 cortical cells, progressively smaller, forming a cupulate node; tetrasporangia becoming verticillate .................................................. 11. C. cupulatum

12. Periaxial cells each cutting off laterally a wedge-shaped pseudoperiaxial cell which largely interposes in the periaxial ring (then of 10–12 cells), each then cutting off 1 or 2 cells acropetally giving a node 2–3 cells long; basipetal cells rare; tetrasporangia abaxial ............................................................... 12. C. macilentum

13. Periaxial cells each cutting off two cells acropetally but only a single laterally elongate cell basipetally; the latter may cut off a further single cell, or 2 cells, and may itself divide laterally into 2–4 smaller cells; tetrasporangia whorled, largely involucrate; rhizoids unicellular .......................................................... 13. C. flaccidum

13. Periaxial cells each cutting off 2 (-3) isodiametric cells acropetally and usually basipetally; tetrasporangia opposite and largely involucrate, or unilateral and partly involucrate; rhizoids uniseriate-celled with multicellular pads ......................................................... 14

14. Thallus epiphytic on larger brown algae, with prostrate filaments attached by clumps of rhizoids, and erect complanate branches; branching alternate, normally every 3 cells; internodal spaces about as long (to twice) as cortical bands; tetrasporangia essentially opposite in plane of branching, largely involucrate .................................................................................................. 14. C. filiculum

14. Thallus epilithic, epiphytic or epizoic, irregularly branched, subcomplanate above, branched at intervals of 4 or more axial cells; internodal spaces usually becoming several times as long as cortical bands; tetrasporangia unilateral and abaxial, partly involucrate .................................................................................................. 15. C. cliftonianum


FIGS 176A–C, 177A, B

Thallus (Fig. 176A–C) grey-red to red, 2–12 mm high, erect filaments sparsely subdichotomous or lateral, basal filaments prostrate, attached by rhizoids from periaxial cells or their derivatives, 1–3 cells long and with multicellular pads; epiphytic on Amphibolis, Posidonia or on algae associated with these seagrasses. Structure. Branches 70-150 μm in diameter, tapering only slightly above, with relatively straight apices (Fig. 176B); axial cells usually L/D 0.7–2, with narrow nodal bands 2 cells long and internodal spaces 3–6 times as long as nodal bands (Fig. 176A–C). Periaxial cells usually 6 (Fig. 177A, B), each cutting off laterally one (occasionally 2, rarely none) pseudoperiaxial cell which lies in the periaxial ring (Fig. 177B), and each cell of this ring then cutting off acropetally a single cortical cell, thus forming a nodal band 2 cells long (Fig. 177A). Each direct derivative of the true periaxial cells producing a short tapering filament (55–100 μm long) of 3–6 (-7) cells (with a rounded apex) which projects outwardly and forward from the axis (Figs 176A–C, 177A, B); the true periaxial cells usually do not produce such a filament, though both they and the acropetal derivatives of the pseudoperiaxial cells may do so; slender terminal hairs often present on these filaments. Rhodoplasts discoid in cortical cells, linear in axial cells.

Reproduction. Gametophytes dioecious. Carposporophytes (Fig. 176A) globular, 120–180 (-200) μm across, with angular to ovoid carposporangia 30–40 μm across, subtended
by 1–3 short branchlets. Spermatangial masses (Fig. 176B) cut off from adaxial nodal cells, later developing all around the nodes.

Tetrasporangia (Figs 176C, 177A, B) cut off from enlarged periaxial cells, usually single per node and abaxial, often with further sporangia formed later from adjacent cells, protected by slightly greater development of nodal filaments (some basally dichotomous) than in sterile plants; tetrasporangia 50–70 µm in diameter, tetrahedrally to decussately divided.

**Type** from 4 km S of Redcliff Point, N Spencer Gulf, S.Aust., on Posidonia sinuosa, 10 m deep (Johnson, 10.1.1977); holotype in AD, A47850.


All collections (except MEL 45455, probably drift) have been associated with seagrass beds, between 2.5 and 12m deep, in areas of moderate water movement. At Redcliff Pt it occurs 2–10m deep on Posidonia, throughout the year but most commonly in summer and autumn (December–June) and least in spring.

*C. shepherdii* is well marked by the irregular double whorls of filaments at the nodes and the pattern of nodal development. In forming pseudoperiaxial cells it shows similarity to *C. australis*, which is otherwise quite distinct. The blunt apices of the filaments separate *C. shepherdii* from *C. monacanthum* and *C. puberulum* and from the numerous extra-Australian species with acute spines, none of which are similar in their nodal development.


**Figis 176D-G, 177C, D**

*Thallus* (Fig. 176D) dark red, mostly erect, 0.5–1.5 cm high, branches dense, subcomplanate near apices, usually becoming irregular below, alternate (to subdistichous), 3–8 axial cells apart. Attachment by tufts of rhizoids from the base of erect axes or from short horizontal filaments, rhizoids arising from periaxial cells, uniseriate, simple or sparingly branched (sometimes with a multicellular attachment pad on *Corallina*); usually epiphytic on *Codium fragile* and *Corallina*. Structure. Branches 200–550 µm in diameter below, tapering slightly to 100–150 µm near the involute apices. Axial cells more or less isodiametric, slightly shorter than broad in younger parts and slightly longer than broad in older parts, with internodal spaces throughout. Periaxial cells 7–8, each cutting off 2 (-3) smaller cortical cells acropetally and basipetally to form the nodal bands (Figs 176E, 177D) 4–6 cells long when young and bearing relatively coarse spines (Figs 176F, G, 177C); node extending by fairly synchronous growth (Fig. 176E) but short internodal spaces present throughout the thallus, usually with long internodes in basal filaments. Spines usually single at each node, occasionally less common, abaxial, with a multicellular base and 3–6 cells (30–100 µm) long (Fig. 176G, 177C), usually lost from older parts of thallus. Rhodoplasts discoid in cortical cells, linear in axial cells.

Reproduction. Gametophytes dioecious. Carposporophytes globular, 180–300 µm across, borne on upper branches and usually subtended by lateral branchlets, with angular carposporangia 20–35 µm across. Spermatangia (Fig. 176F) in dense patches covering the adaxial side of the nodal band, later spreading around the node.
Fig. 177. A, B, *Ceramium shepherdii* (AD, A47850). A. Part of a branch showing periaxial (stippled) and pseudoperiaxial cells, acropetal cortical cells, tapering filaments and tetrasporangia. B. Transverse section of node, showing 6 periaxial cells (stippled), pseudoperiaxial cells and their tapering filaments (dotted), and tapering filaments from acropetal cortical cells (clear). C, D, *Ceramium monaxanthum* (AD, A42260). C. Spine near branch apex. D. Nodal cortication showing cell lineages from periaxial cells. E, F, *Ceramium puberulum* (AD, A46416). E. Node near apex of branch with a primary spine. F. Older nodal cortication, with 2 primary spines and several hairs. (All as in Womersley 1978, courtesy of Aust. J. Mar. Freshw. Res.)
Tetrasporangia (Fig. 176C) cut off from periaxial cells, at first single and abaxial, with later sporangia arising near the first and sometimes extending around the node, partly to largely involucrate by the cortical cells, 35–60 μm in diameter, tetrahedrally divided.

Type from Georgetown, Tas. (Gunn), on Codium; holotype in Herb. Agardh, LD, 21162.

Distribution: Cape Willoughby, Kangaroo I. and Robe in S. Aust., to Bridgewater Bay, Vic., and around Tasmania.


C. moncanaeum is a distinctive species in south-eastern Australia, and most records are epiphytic on Codium fragile or Corallina, at a low eulittoral or uppermost sublittoral level. It differs from C. puberulum, the only other spinous southern Australian species, in having only a single, usually massive, spine at each node and in the internodal spaces remaining distinct throughout the thallus. The form of the rhizoids depends on the host: on Codium the rhizoids form a dense tuft, often branched but with simple ends, penetrating between the utricles, but multicellular pads are often formed on Corallina.

C. moncanaeum was recorded by Huisman & Walker (1990, p. 422) from Rottnest I. W. Aust., on the basis of a Tilden, South Pacific Plants Ser 2, No. 77 specimen. The specimen is epiphytic on Codium fragile and is almost certainly mislabelled since the host is also confined to SE Australia.


C. puberulum α crassior J. Agardh 1876: 102.

C. puberulum f. spinosissima Reinbold 1898: 51.


C. monile β crassior J. Agardh 1851: 132.

C. puberulum β monile J. Agardh 1876: 102.

Celeceras monile (Hooker & Harvey) Kützing 1849: 684; 1862: 29, pl. 95.

FIGS 177E, F, 178

Thallus (Fig. 178A) light red to dark red-brown, erect, 4–10 cm high, much branched irregularly, laterally to subdistichous, sometimes with proliferations from older axes. Attachment by numerous, branched, uniseriate-celled rhizoids originating from the periaxial cells for several segments above the base of the erect axis, descending within the cortex and forming a compact discoid holdfast; usually epiphytic on seagrasses (usually Posidonia but also on Amphibolis). Structure. Branches 0.5–1 mm in diameter near the base, mid parts 100–250 μm, upper parts 45–125 μm in diameter. Axial cells L/D 0.5–2 below, above L/D 1–4. Periaxial cells 7–8 each cutting off 2–3 smaller cortical cells both acropetally and basipetally (Fig. 177E, F) which further divide to form nodes (6–)8–12 cells long in upper parts with narrow to distinctively longer internodal spaces, with the nodal cortication extending on older parts to become continuous near the thallus base; many plants show moniliform lower branches due to constriction of axial cells between the nodal cortication. Outer cortex
(Fig. 177F) forming a more or less continuous layer of small cells overlying the larger elongate inner cortical cells. Spines (primary) one to several per node near apices (Fig. 177E, F), 30–40 (-60) μm and up to 4 cells long, usually relatively slender; primary spines usually soon lost but cortex of lower segments becoming covered with numerous short slender secondary spines (1–2 (-3) cells long (Fig. 178B) arising from the outer cortical cells; spines which arise near the apices always larger than lower later formed spines; numerous fine hairs up to 250 μm long arising from nodal cortical cells in some plants. Rhodoplasts discoid to elongate in smaller cells, becoming ribbon like in axial cells.

Reproduction. Gametophytes dioecious. Carposporophytes gloularis, 150–350 μm across, with ovoid carposporangia 30–55 μm in diameter, borne on upper branches and surrounded by several small, lateral, involucral branchlets. Spermatangia (Fig. 178C) in dense patches covering the nodal cells of upper branches.

Tetrasporangia (Fig. 178D, E) at first single per node, later several, cut off from one or more periaxial cells usually abaxially, 50–100 μm in diameter, tetrahedrally to decussately divided, prominent but usually becoming entirely enveloped by small involucral cells (some bearing spines); the several tetrasporangia within the involucre form prominent, often scattered, enlarged nodes along the branches (Fig. 178D), though less so in young, slender plants (Fig. 178E).

Type from W. Aust. No specimen located in MEL. Isotypes in TCD and LD (20753).

Distribution: Shark Bay, W. Aust. (Kendrick et al. 1990, p. 51), around southern Australia to Jervis Bay, N.S.W. (Miliar & Kraft 1993, p. 39), and northern Tasmania; one record in BM from Coles Bay, Oyster Bay, east coast of Tasmania (Perrin & Lucas, March 1934 on Zostera).


C. puberulum is a common epiphyte on Posidonia throughout its geographical range and is less frequently found on Amphibolis; it is rare on other hosts. It is characterised by the presence of several spines per segment near the apices and by the virtual covering of small spines on the cortical cells in older parts, though in occasional plants the small spines may be rare or scarcely apparent (probably through loss with age). Kützing’s figures (1862, pl. 95b, d) of the rounded tetrasporangial groups were incorrectly interpreted by Dixon (1960a, p. 347) as galls.

The proportions of nodal cortication to internodal space, and the relative size of the axial cells, may differ markedly in young branches, depending in part whether older parts are present, or new, often proliferous, young branches have developed from older parts. Young plants (less than 5 mm high) on Posidonia in N Spencer Gulf, between February and July, have elongate segments with long internodal spaces and only 1 to a few spines per node; later in the year the older parts enlarge and the cortex extends.

*Ceramium rubrum* var. *proliferum* J. Agardh 1876: 100. Sonder 1855: 514. 
*Ceramium rubrum* var. *pygmaeum* Sonder 1848: 167. 
*Ceramium flagelliferum* Kützing 1849: 686; 1863: 4; pl. 8e-g. Sonder 1853: 676. 
*C. nodulosum* (Lightfoot) Ducluzeau. Maggs & Hommersand 1993: 64.

**Ceramium CERAMIEAE** 391

**PLATE 2 fig. 3; FIGS 179, 182A**

*Thallus* (Pl. 2, fig. 3; Fig. 179A) medium to dark red, 5–15 (~25) cm high, branching frequent to relatively sparse, subdichotomous (especially near apices) or irregularly lateral, often with numerous small proliferous branchlets below; main branches sometimes slightly moniliform due to denser cell formation at the nodes and slightly swollen axial cells. Branches 0.5–1 mm in diameter below, 200–500 μm in diameter above, tapering only slightly until near the apices which are slightly involute to straight. Base usually single, erect, attached by a tuft of rhizoids originating from perialgal cells; epiphytic or epiphyllous on seagrasses or larger algae.

**Structure.** Axial cells L/D 0.5–1, becoming completely corticated (Figs 179B, C, 182A) close to the apices, with the terminal cells of both the acropetal and basipetal corticating filaments becoming angular and dovetailing together to obscure the join. Periangial cells 7 (~8), each cutting off usually two cells acropetally and basipetally, continuing as corticating filaments often with two divisions if space permits; these inner cortical cells enlarge and elongate to L/D 3–5 (Fig. 179C); in some plants short acropetal filaments from the perialgal cells projecting outside largely over the margins of the inner cells but not usually forming rosettes except over the rounded perialgal cells (Fig. 179C). Hairs from the outer cortical cells often present in young parts. Rhodoplasts discoid in small cells, ribbon like in axial cells.

**Reproduction.** Gametophytes dioecious. Carposporophytes (Fig. 179D) 200–450 μm across, closely surrounded by 2–5 (~8) short, curved, involucral branchlets, carposporangia ovoid, 20–30 μm in diameter. Spermatangia covering the surface of branches, arising first on the adaxial side.

Tetrasporangia (Fig. 179E) cut off at first from the perialgal cells or the immediate cortical derivatives and thus in rings of 10–15 sporangia along the branches, later from any inner cortical cell and thus scattered, variable in size (30–60 μm in diameter), spherical to ovoid, more or less crucially divided, protruding slightly to moderately within the cortex and surrounded (in face view) by a rosette of outer cortical cells.

**Type from Britain.** Neotype to be selected (see Silva et al. 1996, p. 403).

**Distribution:** A widely distributed species in temperate regions, especially in the northern Atlantic and probably present in most oceans.

Freemantle, W. Aust (MEL, 45384) to Wilsons Prom., Vic., and arround Tasmania. Usually confined to areas of calm to moderate water movement, and is probably more widespread around the Australian coast.


Conservation of the name _C. rubrum_ is advocated by Silva et al. (1996, p. 403).

Australian plants were referred to _C. rubrum_ by early authors (see above) and by Harvey on herbarium sheets as _C. rubrum australis_, but were separated as a distinct species, _C. flagelliferum_, by Kützing (1849), based on plants from Tasmania (V.D.L.; Hooker, type in L., 938, 303...214). J. Agardh (1894) later described this species as both _C. nobile_ and _C. subacartilaginum_. These names were discussed by Womersley (1978, p. 219).

While Australian specimens referred to _C. rubrum_ are relatively uniform, it is closely related to _C. pusillum_ Harvey, differing in being larger with dichotomous or irregular and often proliferous branching, by the nodal cortical bands uniting relatively close to the apices...
with the cells usually dovetailing together, by the inner cortical cells becoming elongate in older parts with the outer cortical cells varying from a largely complete cover to rows along the larger inner cells but not forming distinct rosettes (except often around the periaxial cells), by the tetrasporangia usually developing from any inner cortical cell as well as the periaxial cells and thus on older parts appearing scattered, and by being generally a species of calm to moderate (often deeper) water movement.

While no one of the above features clearly distinguishes *C. rubrum* from *C. pusillum*, overall assessment of them permits ready separation of nearly all specimens of these taxa.

*Ceramium divergens* J. Agardh (1894, p. 27) was described from New Zealand (Invercargill) and Tasmania. The Tasmanian record was repeated by Lucas (1909, p. 53; 1929a, p. 26) and Guiler (1952, p. 98). J. Agardh’s description was based largely on the New Zealand specimens, of which LD, 21108 is a suitable lectotype. The Tasmanian specimens are almost

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**Fig. 179.** *Ceramium rubrum* (A, AD, A46912; B-E, AD, A47024). **A.** Habit of female (left) and tetrasporangial (right) plants. **B.** Cortication of young branch. **C.** Cortication of older branch showing rosettes around periaxial cells and elongate inner cortical cells. **D.** Carposporophyte with involucral branches. **E.** Tetrasporangial branch. (All as in Womersley 1978, courtesy of Aust. J. Mar. Freshw. Res.)
certainly not C. divergens, which is completely corticated but with the older branches showing smaller cortical cells when the nodal cortication joins and with numerous short proliferous branchlets with divergent apices. Pending re-examination of the Tasmanian specimens of J. Agardh, they are provisionally referred to C. rubrum.


C. nobile sensu Womersley 1948: 60; 1950: 180 (NON J. Agardh 1894=Ceramium rubrum).

FIGS 180, 182B

Thallus (Fig. 180A) light to dark red, 1–5 (-10) cm high, with one to a few linear, straight to slightly flexuous branches usually with alternate, flabellate groups of laterals (Fig. 180A), sometimes more irregularly branched or with a few lower proliferous branchlets. Attachment by a tuft of multicellular, branched rhizoids, some descending between the cortex and lower axial cells; epiphytic on various algae. Branches 400–1000 µm in diameter below, 100–200 µm in diameter in younger branches, tapering gradually until near the apices which are usually fairly straight (Fig. 180B). Structure: Axial cells L/D 0.6–1 (shorter near apices), becoming completely corticated close to the apices apart from a narrow separation marked by smaller cells terminating the acropetal growth, compared to slightly larger cells terminating the basipetal growth of the younger segment (Figs 180B, 182B), this separation often visible for many segments from the apices, though the acropetal and basipetal cortical cells abut each other. Periaxial cells (7–) 8–9 (-10), each cutting off two cells acropetally and basipetally (Fig. 182B), these continuing as corticating filaments often with two divisions if space permits, the cells usually angular and isodiametric at first; terminal cells of the acropetal filaments sometimes projecting slightly; the inner cortical cells enlarge but remain subspherical to ovoid. Outer cortex of small cells present, commonly forming rosettes around many of the larger inner cortical cells as well as the periaxial cells (Fig. 180C). Rhodoplasts discoid in small cells, ribbon shaped and branched in larger cells.

Reproduction. Gametophytes dioecious. Carposporophytes (Fig. 180D) usually near branch apices, globular, 200–450 µm across with 2–4 (-6) short involucral branches, carposporangia ovoid, 25–30 µm in diameter. Spermatangia (Fig. 180E) covering several segments, especially in axils of upper branches, later spreading around the branch.

Tetrasporangia (Fig. 180F) derived from the periaxial cells, forming prominent whorls of 10–15 (often including immature ones), often with some cut off later from inner cortical cells, mostly decussately divided, ovoid, 20–50 µm in diameter. Paraspores not infrequently occur on C. pusillum.

Lectotype from Port Fairy, Vic. (Harvey); in Herb. Harvey, TCD (Alg. Aust. Exsicc. 474D).

Distribution: Yanchep, W. Aust., to Gabo I., Vic., and around Tasmania.

Fig. 180, *Ceramium pusillum* (A, AD, A41147; B-G, AD, 33116). A. Habit of large (lower) plant and small (upper) plants. B. Young branches showing internodal spaces near apices. C. Older branch showing smaller terminal acropetal cells abutting larger basipetal cells, ovoid to subspherical inner cortical cells and rosettes of outer cortical cells (especially around periaxial cells). D. Carposporophyte. E. Spermatangial sori on male plant. F. Tetrasporangia in whorls on young branches. (All as in Womersley 1978, courtesy of Aust. J. Mar. Freshw. Res.)
Ceramium

**CERAMIEAE**

C. pusillum appears to be always epiphytic, on various algae (rarely on Posidonia) under conditions of strong water movement, especially at the outer edge of rock platforms, in the sublittoral fringe or uppermost sublittoral. Deeper growing plants (to 34m in Investigator Strait) have more irregular branching but otherwise agree with C. pusillum. In contrast, C. rubrum in Australia is characteristic of calmer waters and may be epiphytic or epilithic.

In his original description, Harvey gave three localities—"Western Australia, G. Clifton, Port Fairy, W.H.H. Warrnambool, H. Watts", but following the description he cited "Harv. Alg. Exsicc. n. 474". Accordingly Harvey’s 474D in TCD from Port Fairy, Vic., is selected as lectotype of C. pusillum. A specimen from Harvey’s "Travelling Set", from Port Fairy and numbered 528, is in MEL (45330), labelled by Harvey "Ceramium (Microcladia) pusillum ms". This is regarded as an isotype. Harvey’s 467A in BM is probably C. pusillum, though Harvey referred to this number as C. rubrum.

Liquid preserved material of C. pusillum and C. rubrum can usually be readily identified, but dried material is often not so easily distinguished. The habit of C. pusillum, with alternately flabellate branch systems, and the habitat in strong water movement, permit field recognition. Microscopically, C. pusillum generally shows smaller terminal acropetal cells abutting larger terminal basipetal ones of the cortical filaments, even after the slight gap between the nodal cortication near the apices has closed. The subspherical to ovoid inner cortical cells with this respect.

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**Figs 181, 182C**

Thallus (Fig. 181A, B) light to dark red, 0.5–7 cm high, complanately branched, regularly alternate (usually at intervals of 4–5 cells) with one to several narrowly to broadly pyramidal branches from near the base, and small proliferous branchlets on the lower parts of robust specimens (Fig. 181A). Attachment by a tuft of uniseriate rhizoids from a single erect (or slightly prostrate) base; epilithic on solid substrates. Structure. Branches 300–500 (700) μm in diameter below, terete to slightly compressed, tapering to 75–150 μm in diameter near the apices which are usually more or less straight and taper abruptly (Fig. 181D, E) to the apical cell. Axial cells subspherical throughout (often slightly broader than long), becoming largely corticated near the apices apart from the usual presence of a lenticular internodal space (Figs 181C, 182C) on the surface (complanate view) of the branches, resulting from the cortication closing up on the sides but not the central part of each segment; the lenticular space is usually visible throughout the thallus except in oldest parts where it may close. The terminal acropetal cortical cells are usually smaller than the basipetal ones (Figs 181C, 182C) and tend to lie outside the adjacent basipetal cells when the cortication has largely or completely closed. Periaxial cells 6–7, each cutting off normally two cells (Fig. 182C) both acropetally and basipetally, which continue to produce 1 or 2 derivatives, to form nodes 5–7 cells long (Fig. 182C) in upper parts, 8–9 (or more) cells long in older parts; a slight outer cortex of small cells is cut off and this may become extensive in robust plants with some rosettes around the periaxial cells only, in C. rubrum. Prominent rings of tetrasporangia, with sporangia much less frequently formed from the inner cortical cells, are also more characteristic of C. pusillum than of C. rubrum, though both species are variable in this respect.


**Figs 181, 182C**

Thallus (Fig. 181A, B) light to dark red, 0.5–7 cm high, complanately branched, regularly alternate (usually at intervals of 4–5 cells) with one to several narrowly to broadly pyramidal branches from near the base, and small proliferous branchlets on the lower parts of robust specimens (Fig. 181A). Attachment by a tuft of uniseriate rhizoids from a single erect (or slightly prostrate) base; epilithic on solid substrates. Structure. Branches 300–500 (700) μm in diameter below, terete to slightly compressed, tapering to 75–150 μm in diameter near the apices which are usually more or less straight and taper abruptly (Fig. 181D, E) to the apical cell. Axial cells subspherical throughout (often slightly broader than long), becoming largely corticated near the apices apart from the usual presence of a lenticular internodal space (Figs 181C, 182C) on the surface (complanate view) of the branches, resulting from the cortication closing up on the sides but not the central part of each segment; the lenticular space is usually visible throughout the thallus except in oldest parts where it may close. The terminal acropetal cortical cells are usually smaller than the basipetal ones (Figs 181C, 182C) and tend to lie outside the adjacent basipetal cells when the cortication has largely or completely closed. Periaxial cells 6–7, each cutting off normally two cells (Fig. 182C) both acropetally and basipetally, which continue to produce 1 or 2 derivatives, to form nodes 5–7 cells long (Fig. 182C) in upper parts, 8–9 (or more) cells long in older parts; a slight outer cortex of small cells is cut off and this may become extensive in robust plants with some rosettes around the periaxial cells; inner cortical cells remain isodiametric to ovoid, sometimes elongating in old robust specimens. Rhodoplasts discoid to elongate in small cells, becoming ribbon like in axial cells.

Reproduction. Gametophytes dioecious. Carposporophytes (Fig. 181D) 150–350 μm across, subspherical, with 2–4 moderately stout branches forming an involucre; carposporangia ovoid to angular, 15–25 μm across. Spermatangia forming patches, especially on the sides of branches, later becoming largely confluent.

Tetrasporangia (Fig. 181E, F) in several successive segments near the ends of the branches or in short stichidiose proliferous laterals (Fig. 181F), formed first in the plane of branching
but soon becoming whorled, situated largely within the cortex or covered by involucral filaments of cells, subspherical to ovoid, 20–35 μm in diameter, decussately or tetrahedrally divided.

*Type* from Vivonne Bay, Kangaroo I., S. Aust., 1–5m deep on jetty pile (*Krafi*, 19.1.1974); holotype in AD, A45063.


**Fig. 182.** A. *Ceramium rubrum* (AD, A47024). Part of a branch 19–21 segments from apex, showing "dovetailing" of cortical cell filaments giving complete cortication. **B. Ceramium pusillum** (AD, A33116). Part of a branch 21–24 segments from apex, showing slight internodal spaces between nodal cortication. **C. Ceramium lentiscusare** (AD, A45063). Segments of a branch showing cortical cell lineages and lenticular internodal spaces. **D. Ceramium excellens** (AD, A38371). Nodal cortication showing cortical cell lineages and internodal space. **E. Ceramium tasmanicum** (AD, A42758). Young nodal cortication showing cell lineages. (All as in Womersley 1978, courtesy of Aust. J. Mar. Freshw. Res.)


PLATE 2 fig. 4; FIGS 182D, 183

Thallus (Pl. 2, fig. 4; Fig. 183A, B) medium to dark red, 5–20 (-30) cm high with a single or several erect axes (or occasionally a slight prostrate base) producing several long lateral branches, usually complanately branched (Fig. 183B) and regularly alternate in younger parts but below often more irregularly branched, often with small, proliferous, often fertile branchlets along the lower main branches. Attachment by a tuft of uniseriate-celled rhizoids; epilithic. Structure. Branches 0.5–1.5 mm in diameter below, decreasing gradually to 150–250 μm in diameter just below the relatively straight, markedly tapering apices; proliferous branchlets on older branches 120–180 μm in diameter, often basally constricted. Axial cells L/D about 1 above, extending to L/D 2 in older branches, becoming corticated except for a narrow, annular, internodal space (occasionally almost as long as the nodes in upper parts) present throughout the thallus (Figs 182D, 183C), but with the cortication usually closing completely on older branches and extending as the axial cells enlarge. Periaxial cells usually 8, each cutting off a regular pattern of 2 cells acropetally and 2 (rarely 3) basipetally (Fig. 182D), these continuing as corticating filaments usually each with two divisions, occasionally one; divisions normally synchronous, producing a straight edge to the cortication (except where axial cells have elongated relative to cortical development), with smaller terminal cells on the acropetal filaments than on the basipetal ones (Fig. 182D), ultimately often with further production of small cells closing the internodal space completely. Outer cortex produced from the periaxial cells (Figs 182D, 183C) and some of the larger inner cortical cells (which elongate to L/D up to 5), often with well developed rosettes over these cells, and on older parts a further cortical layer of small cells may be cut off, forming a distinctly thicker cortex over the central part of the nodal cortication; in some specimens, scattered small outer cortical cells become gland-like. Rhodoplasts discoid in very small cells, ribbon like and longitudinal in axial cells.

Reproduction. Gametophytes dioecious. Carposporophytes (Fig. 183D) near the ends of short lateral branchlets, globular, 200–400 μm across, with 2–4 (-5) short, relatively stout, involucral branches; carposporangia ovoid, 22–30 μm in diameter. Sporophyll patches covering several segments, largely in the axils of upper branches, sometimes surrounding small lateral branches.

Carposporangia (Fig. 183E) formed mainly in stichidiose branch ends or proliferous laterals which are basally constricted, derived from periaxial cells and forming a ring of 8–12 lying within and bulging the acropetal cortical filaments (Fig. 183E), thus producing a torulose
appearance to the branch; tetrasporangia subspherical to slightly ovoid, 30–50 μm in diameter, decussately divided.

*Lectotype* from Tamar R. mouth, Tasmania (*Oakden*); in Herb. Agardh, LD, 21757.

*Distribution:* Head of the Great Australian Bight, S. Aust., to Western Port, Vic., and around Tasmania. This appears to be usually a deep water species.


C. excellens is usually well characterised by its normally complanate form and the presence throughout much of the thallus of the clearly defined, narrow and straight edged, annular internodal space; this is usually longest nearer the apices, but is rarely more than one fifth as long as the nodal cortication (except in specimens with enlarged axial cells), and in the older branches the cortex often closes completely.

C. excellens is closely related to C. lenticulare, but differs in habit, greater dimensions, and in details of the nodal cortication, especially in the uniform presence of the narrow, annular internodal space compared to the lenticular internodal space in C. lenticulare. Whereas the axial cells of C. lenticulare remain isodiametric throughout, in larger branches of C. excellens they elongate to L/D about 2 and the cortex extends to maintain complete cover of these cells; the latter also develops a considerably greater outer cortex.

C. excellens is also closely related to C. tasmanicum, but differs in having complanate branching (at least in younger parts) and in more regular nodal cortication with the narrow, annular internodal space; C. excellens usually also has a thicker cortex and well defined rosettes in the central part of the nodal cortication. Some apparent intermediates between these two species do occur.


Thallus (Fig. 184A) dark red, 1–10 cm high, usually bushy and tufted with several erect axes from the base. Branching usually dense and irregular on all sides, the upper parts sub dichotomous in varying planes, usually (especially in plants from rough-water coasts) with frequent small proliferous branchlets from the lower nodes; older branches often torulose due to swollen nodes. Attachment by a tuft of branched, uniseriate-celled rhizoids with occasional multicellular pads, originating from the periaxial and larger cortical cells of the lower 1–5 axial cells; epilithic or epiphytic (mainly on Codium fragile). Structure. Branches (300-) 400–1000 µm in diameter below, 60–100 µm in diameter shortly below apices, tapering gradually (apart from the slender proliferous branchlets on broader older branches) to relatively slender, involute to moderately straight apices. Axial cells L/D 1–1.5 near apices with internodal spaces 0.3–1 times as long as the nodal cortication (Fig. 184E, F); cortication on older branches extending irregularly (Fig. 184B) but usually not closing completely. Periaxial cells (5-) 7–8, each cutting off 2–3 cells acropetally and basipetally (Fig. 182E), which each cut off a further 1–3 cells which continue to divide to form nodes 6–7 cells long near to the apices, usually slightly more developed acropetally than basipetally; cortex extending gradually (Fig. 184B) until in larger branches where extension is more rapid and irregular (usually more so acropetally), with elongate cells, the nodal margins varying from relatively straight (Fig. 184C) to most irregular, but usually maintaining an internodal space. Outer cortex of small cells formed in relatively young nodes (Fig. 184B, C), later covering the whole nodal cortex (except at the margins) as an irregular, loose (especially in prepared mounts and older nodes) layer of small, rounded, widely separated cells, without distinct rosettes except sometimes over the periaxial cells; long slender hairs are usually formed profusely from the terminal acropetal and outer cortical cells of young branches. Rhodoplasts discoid in cortical cells, ribbon shaped and more or less longitudinal in axial cells.

FIGS 182E, 184
Reproduction. Gametophytes dioecious. Carposporophytes (Fig. 184D) on upper branches, globular, 100–300 μm across, with 3–6 straight to slightly curved branchlets arising just below them; carposporangia ovoid, 25–35 μm in diameter. Spermatangia (Fig. 184E) covering the nodal cortex of young branchlets, commencing adaxially but soon spreading around the node.

Tetrasporangia (Fig. 184F) in whorls of 2–6, arising from the periaxial cells (or immediate cortical derivatives), largely involucrate within the cortex, cruciately divided, subspherical to ovoid, 30–45 μm in diameter.

Type from Tasmania (Gunn 1310, ex Hooker); holotype in L, 938, 303...216.

Distribution: W. Aust. (Harvey) and from Robe, S. Aust., to Western Port, Vic., and around Tasmania.


The branching and nodal cortication, and especially the extending cortex often with an irregular growing margin, are characteristic of C. tasmanicum. Slender and more loosely branched forms, usually from relatively calm water localities, may be superficially similar to C. cliftonianum, but are usually recognisable by the extending cortex on older axes and by the whorls of tetrasporangia if present.

C. tasmanicum is closely related to C. excellens as discussed under the latter species.


FIGS 185, 187A

Thallus (Fig. 185A, B) grey-red to red-brown, 0.5–3 (-6) cm high in rough-water forms, to 12 cm high under slight to moderate water movement, with one to several axes arising from prostrate basal parts. Branching regularly pseudodichotomous, rarely with a few proliferous laterals, branches in rough-water forms 400–700 μm in diameter below, tapering gradually to about 200 μm near the apices, in slight water movement 200–400 μm in diameter below, tapering to about 100 μm near the apices; apices usually involute. Attachment by numerous rhizoids which arise from the periaxial and inner cortical cells and consist of one to a few uniseriate cells and a digitate pad which becomes multicellular; epilithic or epiphytic on various algae or Posidonia. Structure. Axial cells L/D about 1 (-1.5) in rough-water forms, extending in lower parts of plants in slight water movement to L/D 1.2–3 (-4), with distinct internodal spaces throughout and regular, well defined, nodal cortical bands (Fig. 185D, E). Periaxial cells 7–8 (-9), each cutting off two cells acropetally and basipetally, these cutting off (1-) 2 further cells, which divide further in older parts to form nodal bands 5–7 cells long and usually broader than long (Fig. 185D); ultimate acropetal cortical cells generally smaller than basipetal ones, developed more or less synchronously, leaving a very short (especially in rough-water forms) and well defined internodal space (Fig. 185C–E) in the younger branches, this space...
in older parts becoming as long as the nodal band in rough-water forms and up to 4 times as long in forms in slight water movement. Outer cortex (Figs 185C, 187A) developed from the larger inner cortical cells and periaxial cells, with small cells which may appear as rosettes. Darkly staining gland cells (Fig. 185C) occur occasionally to profusely, sometimes absent, derived from the smaller outer cortical cells, scattered over the nodes. Rhodoplasts discoid to elongate in cortical cells, ribbon like in axial cells.

Reproduction. Gametophytes dioecious. Carposporophytes 150–350 μm across, with 2–4 short involucral branchlets; carposporangia ovoid, 20–30 μm in diameter. Spermatangia (Fig. 185D) cut off from outer cortical cells, covering the node on all sides.
Tetrasporangia (Figs 185E, 187A) prominent, external and completely naked, derived initially from the first acropetal cortical derivatives of the periaxial cells and thus forming an irregular ring around the upper edge of the nodal cortication, later from other cortical cells, decussately or tetrahedrally divided, subspherical, 50–80 μm in diameter.

**Type** from Garden I., W. Aust.; holotype in Herb. Harvey, TCD (Trav. set 286).

**Distribution**: Houman Abrolhos, W. Aust., to Bondi N.S.W. (and Lord Howe I.) (Millar & Kraft 1993, p.38) and the Great Barrier Reef. Qld (Price & Scott 1992, p.95); Tasmania?. On rough-water rock platforms just below low tide level (stouter forms) and also 2–4 (~8) m deep in conditions of slight to moderate water movement.


*C. isogonum* is usually distinctive, as a relatively stout species (especially on rough-water coasts) with regular subdichotomous branching. The usual presence of gland cells and prominent naked tetrasporangia, together with the well defined nodal cortical bands (both superficially and in cell detail) further characterise the species.

Weber van Bosse (1923, p. 329) recorded *C. isogonum* from Indonesia, but detailed study is needed to verify this record from well outside its Australian distribution.


**Gongroceras australis** (Sonder) Kützing 1849: 679. 

**Eiptusperma australis** (Sonder) Kuntze 1891: 893. 

**Apona australis** (Sonder) Kuntze 1898: 395.

**FIGS 186A–D, 187B, C**

*Thallus* (Fig. 186A) brown-red to dark red, 1–4 (~6) cm high, regularly subdichotomous in varied planes, without proliferous branchlets, with several erect branchlets arising from slight, prostrate, basal filaments. Attachment by uniseriate-celled rhizoids which may develop multicellular pads, arising from the periaxial (occasionally pseudoperiaxial) cells; epiphytic on seagrasses or red algae. **Structure**. Branches (160-) 200–300 μm in diameter below, decreasing gradually to 100–150 μm in diameter near the apices, then tapering more abruptly to the strongly involute apices. Axial cells isodiametric near apices, L/D (1-) 2–2.5 (~3) below, with regular, straight margined, bands of nodal cortication (Fig. 186B) mostly 80–120 μm long, separated by an intermodal space 0.2–1 times the nodal length above and 2–3 times in the lower parts. Periaxial cells 6–7, each cutting off laterally (within the periaxial cell ring) two slightly smaller pseudoperiaxial cells (Figs 186C, 187B, C), each of which cuts off one cell acropetally and basipetally, these then dividing to form one or two cells which usually divide again, forming nodal cortication (5-) 7 cells long (Figs 186C, 187B); the true periaxial cells cut off one cell acropetally and this cuts off one or two more, but no cells are cut off basipetally (Fig. 187B); first acropetal derivative of the periaxial cells commonly cutting off a large gland like cell (Fig. 186C); no outer cortex is formed. Rhodoplasts discolid in small cells becoming ribbon like in larger cells.

**Reproduction**. Carposporophytes and spermatangia unknown

Tetrasporangia (Fig. 186D) produced in irregular abaxial series, with up to 3 per node formed successively, spreading around the node, cut off acropetally from periaxial cells, slightly basally involute by cortical filaments with slightly longer cells than in sterile nodes;
Fig. 187. A. Ceramium isogotonum (AD, 37504). Nodal cortication and tetrasporangia. B, C. Ceramium australe (AD, 39252). B. Two nodes showing periaxial and pseudoperiaxial cells, and cortical cell lineages. C. Transverse section of node showing periaxial and pseudoperiaxial cells. D. Ceramium cupulatum (AD, A15430). Cupulate nodes with acropetal (only) development of cortical cells, the terminal cell often bearing a hair. E. Ceramium macilentum (AD, A41286). Nodes with involucrate tetrasporangia, periaxial and pseudoperiaxial cells, and acropetal (only) development of cortical cells. (All as in Womersley 1978, courtesy of Aust. J. Mar. Freshw. Res.)
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tetrasporangia subspherical to pyriform, irregularly horizontally divided into bispores (in plants observed), 55–75 µm in diameter.

Type from W. Aust. (Preiss); probably from near Perth; type not located in MEL; lectotype in LD, 20679, on Halipiton.

Distribution: Shark Bay, W. Aust., to Walkerville, Vic., and N Tasmania.


While superficially similar to C. isogonum, C. australis is distinctive in the pattern of nodal cortication. The lateral formation of pseudoperiaxial cells, which lie largely in the periaxial ring as seen in thallus section, thus giving a ring of 18 or 21 cells with the larger periaxial cells separated by two smaller pseudoperiaxial cells, is a pattern not seen in any other southern Australian species of Ceramium. Many of the first acropetal derivatives of the periaxial cells cut off a comparatively large and densely protoplasmic gland like cell.

The tetrasporangia as observed in the Tiparra specimens all appear to have only an irregularly horizontal division, though the sporangia appear mature; further observations on the sporangial division and release of spores are needed.


Thallus (Fig. 186E) red, 0.5–1 cm high, forming a dense cover on Halipiton, with extensive prostrate filaments. Erect filaments numerous, arising from most nodes of the prostrate filaments, simple or usually with several subdichotomous to lateral branches; nodes, especially in erect filaments, cupulate in form due to acropetal development only of cortical cells. Attachment by one to several clumped rhizoids arising from the periaxial cells on the underside of the prostrate filaments; rhizoids single or often densely grouped, usually unicellular plus the multicellular pad of one or a group of rhizoids; epiphytic on Halipiton. Structure. Branches 75–200 µm in diameter (at nodes), fairly uniform in diameter to just below the erect or involute, usually tapering, apices (Fig. 186F, I). Axial cells isodiametric near apices, elongating to L/D 2–4 below, with prominent nodal bands 35–80 µm long and internodal spaces about as long as the nodes near apices (Fig. 186F), elongating to 2–4 times as long below. Periaxial cells 6–8, each cutting off two cells acropetally (Fig. 187D) with continued divisions into one or two cells (progressively smaller) to give a node 4–5 cells long in upper parts, 6–7 cells long below; usually no basipetal cells are cut off by the periaxial cells (Figs 186F, 187D), and no outer cortical cells are formed, but in A 19591 some of the periaxial cells in older nodes cut off single cells laterally (partly in the periaxial ring) or just basipetally; slender hairs are produced by many of the terminal cortical cells of each node. Rhodoplasts discoid in small cells becoming ribbon like in larger cells.

Reproduction. Gametophytes dioecious. Carposporophytes (Fig. 186G) borne part way up the erect branches, surrounded by 3–7 slightly curved to straight laterals (often relatively long) which arise from periaxial cells of the axial cell bearing the carposporophyte; carposporophytes globular, 200–350 µm across, carposporangia subspherical to ovoid, 20–30 µm in diameter. Spermatangia (Fig. 186H) covering nodes of erect branches, produced from all cortical cells of a node.

Tetrasporangia (Fig. 186 I) at first unilateral but becoming verticillate on upper parts of erect branches, prominent, with several produced successively from each node from the
CERAMIEAE

Ceramium

periaxial cells, with the lower third to half of the tetrasporangia involucrate by cortical filaments; these filaments usually showing 2–3 more divisions than the other nodal cortical filaments, which are often only 3–4 cells long; tetrasporangia with prominent persistent sheaths, subspherical, 35–60 μm in diameter, decussately divided.

Type from D’Estrees Bay, Kangaroo I., S. Aust., on Halithilon roseum in pools at reef edge (Womersley, 24. viii. 1950); holotype AD, A15430, isotypes also under this number.

Distribution: Only known from the type locality; from Point Sinclair, S. Aust., lower eulittoral on crustose corallines (Womersley, 7. ii. 1954; AD, A19591); and from Port Phillip, Vic., on Corallina? (Mueller), type of C. repens Harvey (holotype in TCD).

C. repens Harvey was recorded from Diego Garcia, Mahé, by Reinbold (1907, p. 576), but it seems unlikely that this record applies to the southern Australian species. C. cupulatum is a distinctive species, characterised by its small size, epiphytic habit on Halithilon, and especially by the cupulate nodes produced by the spreading, acropetal development from the periaxial cells. The commonly clumped rhizoids are similar to those of C. filiculum.


Thallus (Fig. 188A) light red, a few millimetres to 6 cm high, erect or often in tangled masses. Branching subdichotomous to alternate (often every 5–8 cells above) and sometimes tending to be somewhat complanate above, sparse in lower parts, with few if any proliferous branchlets. Attachment by rhizoids of 1–3 uniseriate cells with a multicellular pad, arising usually singly from a periaxial cell of each note of prostrate filaments; on solid substrates, ascidians or epiphytic on various algae. Structure. Branches 70–130 (-150) μm in diameter below, tapering very slightly to 40–70 μm several cells below the (normally) involute apices. Axial cells L/D (0.5–) 1–1.5 near apices, elongating in larger specimens to L/D 4–6, with a narrow cortical nodal band 30–50 μm long (Fig. 188B). Periaxial cells usually 6, most of which divide obliquely to form a wedge-shaped pseudoperiaxial cell (Figs 187E, 188B) which interposes between the periaxial cells to form a ring of 0–12 cells; each of these cells usually cuts off one or two cells acropetally, and in older parts these may cut off a further 1–2 cells; the node is thus 2–3 cells long (Figs 187E, 188B); very occasional basipetal cells (Fig. 187E) may be cut off from the periaxial cells but this is rarely found over several nodes or from more than one periaxial cell in a node. Slender hairs commonly present on cortical cells near apices. Rhodoplasts discoid in corticating cells, ribbon-like and longitudinally arranged in axial cells.

Reproduction. Gametophytes dioecious. Carposporophytes (Fig. 188C) with 1–2 irregularly globular lobes, 100–200 μm across, subtended by 2–4 curved branchlets, carposporangia angular, 18–25 μm across. Spermatangia forming patches on the adaxial sides of nodes, later tending to spread around the node.

Tetrasporangia (Figs 187E, 188D) in prominent, abaxial, unilateral rows (very occasionally in adaxial rows or opposite), usually some distance below the apices, with 1–3 sporangia per node, derived from periaxial cells; tetrasporangia basally involucrate (to half the sporangium) by cortical filaments of a few cells, subspherical to ovoid, irregularly decussately to tetrahedrally divided, 40–75 μm in diameter, with a persistent sheath.

Type from Port Phillip, Vic. (Wilson); holotype in Herb. Agardh, LD, 20616.

Distribution: Port Denison, W. Aust., to Port Jackson, N.S.W. and Lord Howe I. (Millar & Kraft 1993, p. 39) and the Great Barrier Reef, Qld (Price & Scott 1992: 100, fig. 31.).

Selected specimens: Port Denison, W. Aust., epiphytic, on jetty piles, 0–5 m deep (Kraft, 14 xii. 1971; AD, A41179). Mt Dutton Bay, Coffin Bay, S. Aust., 5 m deep (Womersley, 1 xii. 1975; AD, A46808). Douglas
C. macilentum is a slender species which seems well marked by its nodal cortex with the interposed pseudoperiaxial cells and the virtual absence of any basipetal derivatives of the periaxial cells, thus giving a very narrow nodal ring of cells; the unilateral rows of partly involucrate sporangia are also characteristic. There is considerable variation, however, in branching, diameter of the filaments, and degree of extension of the axial cells.

C. macilentum appears to be moderately common in regions of slight water movement. The closest species in southern Australia is the slightly more robust C. cliftonianum, which differs in its much greater cortical development, without pseudoperiaxial cells; occasionally, however, specimens apparently intermediate between them may be found. In the presence of pseudoperiaxial cells, C. australe shows relationship with C. macilentum but differs significantly in the more regular and twinned arrangement of the pseudoperiaxial cells and a more developed cortex, as well as in dimensions and sporangial arrangement.


Thallus (Fig. 188E) light red to dark red-brown, slender, 0.5–5 (–10) cm high, with prostrate basal filaments producing several to numerous erect axes, branches alternate or occasionally subdichotomous, irregular to almost complanate above, usually with moderately short laterals near the apices and becoming denuded in lower parts where the red-brown nodes contrast with the colourless internodal regions; proliferous branchlets, slenderer than parent branches, often present. Attachment by unicellular rhizoids (including the digitate pads) arising from the periaxial cells of prostrate filaments; epiphytic or epilithic. Structure. Nodes usually broader than internodes (Fig. 188F, G), variable in thickness depending partly on degree of water movement; in strong water movement, 150–300 μm in nodal diameter below, tapering gradually to 75–100 μm near the apices; in slight water movement, 100–150 μm in nodal diameter below, decreasing to 40–80 μm near the apices; apices slightly to strongly involute. Axial cells isodiametric near apices, extending to L/D 4 (–6) below, with nodes 5–9 (–11) cells long and usually slightly broader acropetally than basipetally; internodal space shorter than nodes near apices, soon elongating to 3–6 (–10) times as long as node. Periaxial cells 6–7, each cutting off 2 cells acropetally which further cut off 1 or 2 cells to produce acropetal chains 3–4 cells long, successively smaller; basipetally, only a single, elongate derivative (Figs 188F, 190A–D) is cut off from each periaxial cell, and this derivative may then divide in various ways to form a second (rarely a third) elongate cell which remains intact (Fig. 190A) or to cut off two smaller cells (Fig. 188F), often from the corners, which may then each cut off one or two cells and this may be repeated; or the elongate first (or later) derivative may divide transversely (Figs 188F, 190B) into 2–4 small isodiamic cells, only one of which remains in pit-connection with the periaxial cell; thus a node 6–8 cells long is formed. A few outer
cortical cells (Fig. 190D) may be cut off from the first periaxial cell derivatives in older plants, but they usually lie almost within the cortical layer. In some plants, the terminal cortical cells (especially acropetal) and sometimes other cortical cells become gland-like (Fig. 190D). Slender hairs are commonly produced from the cortical cells near apices, and in some plants few to many abaxial, elongate-clavate hairs (Fig. 190B) are also produced (‘fimbriate’ forms). Rhodoplasts discoid in small cells, moniliform in larger cells.

Reproduction. Gametophytes dioecious. Carposporophytes globular, 200–350 μm across, with 3–6 slightly curved involucral branchlets, carposporangia angular-ovoid, 25–35 μm across. Spermatangia (Fig. 188G) covering the nodal cells of young branches.

Tetrasporangia (Fig. 188H) usually in whorls of (2–) 4–7, produced acropetally from the periaxial cells, with a prominent cupulate involucre largely covering the sporangia, formed by cell enlargement rather than further divisions of the acropetal cortical filaments; sporangia subspherical, 35–90 μm in diameter, dicesatessely divided.

Type from Kilkee, Co. Clare, Ireland (Harvey); lectotype and isotype in L. 940, 265...55; isotypes also in BM and TCD.

Distribution: Probably cosmopolitan in cold temperate to tropical seas. Along the whole southern Australian and Tasmanian coasts, extending north along western and eastern Australia. Common near low tide level and in wave-washed pools, on rock or epiphytic (especially on Haliphtylon).


C. flaccidum and its synonyms were discussed by Womersley (1978). It is a variable species in size and robustness, as well as in the presence of ‘fimbriate’ hairs and gland cells. It is characterized by being relatively slender with alternate lateral branching, with the cells and internodal spaces relatively short above but elongating markedly below where few lateral branches remain; in living plants the short, pigmented nodes contrast with the long colourless internodes.

The most striking features however are the uniform formation of only one cell basipetally from each periaxial cell, compared to two cells acropetally, and the unicellular rhizoids and pads in contrast to the uniseriate-celled and multicellular pads of other southern Australian species. Further divisions of this single basipetal derivative do, however, vary considerably, even in the one plant. In slender species (of calm habitats), the single first derivative may cut off a second single elongate cell, and this even a third, remaining in this state. It is common however for the first single derivative to cut off (often from its corners) two cells, which then divide into one or commonly two more cells. Also, the first single elongate derivative commonly divides transversely, so that it appears that 2, 3 or even 4 cells correspond basipetally to one periaxial cell. A consequence of continuing production of pairs of cells acropetally in the node, and a single basipetal cell at least initially, is that the acropetal part of the node commonly broadens compared to the slightly narrower basipetal part, and (especially in stained and mounted specimens where the cells contract slightly) the basipetal cortication becomes separated by a narrow ‘line’ or space from the periaxial cells and acropetal cortication; this is only occasionally visible in living specimens.

**FIGS 189A–E, 190E, F**

*Thallus* (Fig. 189A) medium to dark red, 0.3–1 (-1.5) cm high, at first with a single erect base attached by rhizoids descending from the lower segments, and later with prostrate filaments. Branching essentially complanate (Fig. 189A), alternate and 3 (-5) cells apart, forming flabellate groups of laterals, usually without proliferations. Attachment by relatively large holdfasts (Fig. 189B) formed of numerous, usually tightly clumped, rhizoids originating from all the cortical cells on the underside of a node, and with the ends of the peripheral rhizoids splayed out and becoming multicellular; epiphytic on cartilaginous brown (and occasionally red) algae. *Structure*. Branches terete, 100–300 μm in diameter below, with the laterals 80–150 μm in diameter near their bases, tapering to 50–70 μm shortly below the straight to slightly involute apices (Fig. 189C–E). Axial cells L/D about 1 (-1.5) throughout the thallus, with internodal spaces 0.5–1 (-2) times as long as nodal bands in mature parts, shorter near the apices. Peri axial cells 6, each cutting off usually 2 cells acropetally and 2 (-3) cells basipetally (Fig. 190E, F); the basipetal cells usually cut off only 1 (rarely 2) more cell so that basipetal chains in older parts are only 2 (-3) cells long; acropetally, the derivatives cut off (1-) 2 (-3) cells which divide similarly twice in mid parts of the thallus and up to 4 times in older parts, with some cells being cut off in the reverse direction; the node is thus 5–6 cells long (30–70 μm) in mid parts of the thallus, and may be up to 9 cells long (80–150 μm) in older parts (Fig. 190F); the nodes have relatively straight margins and the acropetal development is always greater than the basipetal. No real outer cortex is formed, but rhizoidal cortication of the axial cells occurs near the thallus base. Fine, slender hairs occur in actively growing plants. Rhodoplasts discoid in small cells, ribbon like in larger cells.

*Reproduction*. Gametophytes dioecious. Carposporophytes (Fig. 189C) occur on upper branches, glo bular, 150–300 μm across, with 3–6 relatively robust, usually slightly curved, involucral branches; carposporangia ovoid-angular, 15–30 μm across. Spermatangia (Fig. 189D) covering the nodal cortex of upper branches and often reaching the apices, surrounding the branchlet or sometimes mainly adaxial.

Tetrasporangia (Fig. 189E) in lateral branches, opposite in the plane of branching with the fertile branchlet ovoid in section, arising acropetally from the opposite periaxial cells (often with a later formed sporangium), largely involucrate within the cortical filaments (which may be 1–2 cells longer than in vegetative parts), subspherical to ovoid, 30–50 μm across, decussately divided.

*Type* from Port Noarlunga, S. Aust., in low eulittoral pools on offshore reef, on basal leaves of *Sargassum lacerafolium* (Womersley, 13.iii.1977); holotype in AD, A47978 (isotypes also). “*Marine Algae of southern Australia*” No. 182.


Fig. 190. A–D. Ceramium flaccidum (A, B, AD; A43757; C, D, AD; A42759). A. Nodes of a young branch with single basipetal periaxial derivatives. B. Older nodes with most basipetal derivatives divided; a single clavate hair present. C. Node of more robust form showing cortical lineages and one acropetal gland cell. D. Node on older branch with slight outer cortex and several gland cells. E, F. Ceramium filiculum (AD; A32635). E. Node of young branch. F. Node of older mature branch. G, H. Ceramium cliftonianum (G, AD; A30860; H, AD; A34110). G. Cortex of node of robust plant, with regular basipetal cells. H. Nodal cortex of slender plant with 2 basipetal cells. (All as in Womersley 1978, courtesy of Aust. J. Mar. Freshw. Res.)
C. filicula was discussed by Womersley (1978, p. 240). It is a distinctive species, characterised by the striking holdfast of usually densely clumped rhizoids, the regular, alternate and complanate branching usually 3 cells apart, with short axial cells throughout, by the rather regular nodal cortex with short internodal spaces, and by the opposite, involucrate tetrasporangia. It is apparently always epiphytic on larger, usually cartilaginous, brown and occasionally red algae.

Apona cliftoniana (J. Agardh)Kuntze 1898: 395.
Gongroceras ramulosum (Hooker & Harvey)Kützing 1849: 678; 1862: 25, pl. 81a–d.
C. nodosum sensu Hooker & Harvey 1847: 410 (see Harvey 1859b: 330).

FIGS 189F–J, 190G, H
Thallus (Fig. 189F) light to dark red, forming erect, often much branched or entangled tufts from 3 mm to 10 (-15) cm high, with prostrate branches; branching in actively growing erect parts subcomplanate with fairly regular laterals usually 3–6 cells apart with broad axes, but often more irregular and sparse, commonly with older branches bearing proliferous laterals which are often markedly slenderer. Attachment by uniseriate rhizoids with pads becoming multicellular, 1–3 rhizoids arising from the periaxial cells at each node; epilithic or on other firm substrates (e.g. tunicates) or epiphytic. Structure. Branches 100–300 (-400) μm in diameter below, tapering gradually or more abruptly to (25–) 50–75 (-100) μm in diameter below the tapering apices, which are straight or occasionally slightly involute or divergent. Axial cells L/D about 1 near the apices (Fig. 189H, I), elongating to 2–3 (-4) below, with clear internodal spaces throughout. Periaxial cells usually 6, each first cutting off 2 cells acropetally and usually soon after 2 cells basipetally (Fig. 190G, H); acropetal cortical cells usually each cutting off 1 or 2 smaller cells, giving a node 4 cells and 30–50 μm long in the upper parts (Fig. 190G); on older, lower, branches further acropetal cells, and sometimes basipetal ones, may be cut off, giving a node 5–6 (-9) cells and 75–125 μm long, with the acropetal development always greater (and usually with smaller cells) than the basipetal; internodal space 0.5–1 times the nodal length in upper parts, and 1–3 (-4) times as long in lower parts of the thallus. On lower branches, occasional small cortical cells may be cut off in the reverse direction, and in some robust specimens a slight outer cortex may develop on the oldest parts; slender hairs commonly present on cortical cells near branch apices. Rhodoplasts discoid in smaller cells, ribbon-like and longitudinal in axial cells.
Reproduction. Gametophytes dioecious. Carposporophytes (Fig. 189G) on upper branches, globular, 150–250 (-300) μm across, with 1–4 slightly curved involucral branchlets, carposporangia ovoid-angular, 20–30 μm across. Spermatangia (Fig. 189H) covering cortical cells of upper nodes, sometimes largely restricted to the adaxial sides..
Tetrasporangia (Fig. 189 I) in unilateral, abaxial series, 1–3 per node, cut off from one (or 2) periaxial cells, involute over their lower half or less by branched acropetal cortical filaments 3–4 cells long from the periaxial cells, with the involucral cells lying in the outer part of the common gelatinous sheath with the tetrasporangia centrally situated; tetrasporangia subspherical to ovoid, 35–50 (-75) μm across, tetrahedrally (rarely decussately) divided.

Type from W. Aust. (Harvey); holotype in Herb. Agardh, LD. 20690.
**Ceramium**

**Distribution:** from Houtman Abrolhos, W. Aust. to Port Stephens, N.S.W. (Millar & Kraft 1993, p. 38), and around Tasmania.


*C. cliftonianum* is a moderately common species along southern Australia, from 1–35 m depth, occurring as tufts or often entangled masses of slender filaments, in moderate water movement. It is characterised by its dimensions, the nodal development, and the unilateral, half involucrate tetrasporangia. There is, however, considerable variation, especially in development of the basipetal cortical cells with occasional specimens having them only on the older branches.

The type material of *C. cliftonianum* is smaller but otherwise identical in dimensions, nodal development and tetrasporangia with that of *C. ramulosum* Hooker & Harvey from Tasmania (Gunn in BM). The latter species was distributed by Harvey as Alg. Aust. Exssicc. 469 I from Georgetown, Tas.

*C. cliftonianum* appears closely related to *C. diaphanum* (Lightfoot) Roth [C. tenuissimum (Roth) J. Agardh] in cortical appearance and in having unilateral, abaxial and involucrate tetrasporangia, but the latter usually has gland cells and comparisons of the cortical development are still needed.

*C. cliftonianum* also appears to be closely related in dimensions, nodal cortication and tetrasporangial arrangement to *C. cimbricum* Petersen in Rosenvinge 1924, p. 378 (C. fastigiatum Harvey) from Britain (see Maggs & Homersand 1993, p. 49). However *C. cliftonianum* rarely has the strongly fastigiate habit of the latter but is usually more irregular in its branching. Detailed study may show that *C. cliftonianum* is inseparable from one of these older species, but for the present it seems best to keep the Australian taxon separate.

*C. cliftonianum* also appears to be closely related in dimensions, nodal cortication and tetrasporangial arrangement to *C. tenuissimum* (Roth) J. Agardh in cortical appearance and in having unilateral, abaxial and involucrate tetrasporangia, but the latter usually has gland cells and comparisons of the cortical development are still needed.

*C. maclellanum* often occurs together with *C. cliftonianum* but the latter differs clearly in not having pseudoperiaxial cells and normally greater basipetal and acropetal cell development.

**Genus CENTROCERAS** Kützing 1841: 731

*Thallus* erect, tufted, of erect dichotomous and laterally branched filaments from a limited prostrate base, attached by rhizoids. Branches terete, with a ring of periaxial cells on the upper end of axial cells, each producing short acropetal cells and basipetally usually 2 regular rows of small corticating rectangular cells which extend as the axial cells elongate, thus completely covering the axial cells.

**Reproduction.** Gametophytes dioecious. Carposgonial branches borne on periaxial cells near branch apices, 4-celled. Carposporophytes with few rounded gonimolobes, surrounded by short involucral branches from below. Spermatangia terminal on branched filaments from periaxial cells, forming dense nodal sori.

Tetrasporangia produced from periaxial cells, becoming whorled at the nodes, with or without short involucral filaments, tetrachlorally divided.

**Lectotype species:** *C. clavulatum* (C. Agardh)Montagne 1846: 140.

A genus of about 9 species (Gallagher & Humm 1983, p. 266), well marked by the complete axial cortication by closely adjacent longitudinal rows of short cells.


Centroceras cryptocanthum (Kützing) Sonder 1848: 167.

Centroceras cinnabarinum (Kützing) Sonder 1848: 167.


See Silva et al. (1996, pp. 387–389) for the extensive synonymy and references for this species.

**FIG. 191**

Thallus (Fig. 191A) dark red-brown, usually densely tufted, 2–8 (-15) cm high, fastigate and usually even topped with straight, terete, largely sub dichotomous filaments 100–180 μm in diameter, completely corticated, with few adventitious laterals, apices involute with short abaxial spines. Attachment by rhizoids with multicellular pads, arising from slight prostrate filaments; epilithic or epiphytic on larger algae or sea-grasses. Structure. Apical cells shortly conical, 10–15 μm in basal diameter, enlarging rapidly to axial cells 40–90 μm in diameter and L/D (1–2)–3, with central longitudinal protoplasmic strands, and with 12–14 periaxial cells (Fig. 191B) formed in alternating sequence, these each cutting off 2 short cells acropetally and 2 (sideways and basipetally), rarely adjacent, corticating rows of small, rectangular cells (Fig. 191 E, G) 8–12 μm in diameter, tetrahedrally divided. Spines abaxial and unilateral near apices, sometimes opposite, originating from a periaxial cell, 1–3 (-4) cells and 20–45 μm long, usually lost from lower nodes. Elongate-clavate hairs frequent to absent. Branching sub dichotomous at apical cells or lateral from periaxial cells. Rhodoplasts discoid.

Reproduction. Gametophytes dioecious. Carpogonial branches on the first formed periaxial cells. Carposporophytes (Fig. 191D) with carposporangia ovoid, 25–45 μm across, carposporangia ovoid, 25–45 μm in diameter, with 2–5 involucral branches from below. Spermatangia in dense sori (Fig. 191E) around the nodes, borne on branched filaments from the periaxial cells (Fig. 191F).

Tetrasporangia (Fig. 191G) first abaxial but soon becoming whorled at the nodes, cut off from periaxial cells, without or with short involucral filaments, subspherical to pyriform, 40–70 μm in diameter, tetrahedrally divided.

**Type from Callao, Peru (Humboldt):** holotype in Herb. Agardh, LD (see Howe 1911, p. 509).

**Distribution:** Widely distributed on most tropical to temperate coasts.

Generally around Australia.

Fig. 191. Centroceras clavulatum (A, AD, A32095; B, C, AD, A63365; D–F, AD, A49285; G, AD, A32486).
A. Habit. B. Transverse section through node with 13 periaxial cells, cortical cells partly hidden. C. Transverse section between nodes, with 26 cortical cells. D. Branch with carposporophytes. E. Branch of male plant with nodal spermatangia. F. Longitudinal section of male branch showing origin of spermatangial clusters from periaxial cells. G. Branches with tetrasporangia.
Centroceras clavulatum is a common epilithic alga in the lower eulittoral zone and just below, forming dense, dark red-brown, tufts, and also occurs as smaller plants on a variety of larger algae (e.g. Hormosira) and robust sea-grasses.

Centroceras cinnabarinum was recorded by Harvey (1863, synop.: xlvii) from St Kilda, Port Phillip, Vic. (Watts), and reported by Lucas & Perrin (1947, p. 370) as a Ceramium. The Watts specimen (fragment in AD, A18561) appears to be typical Centroceras clavulatum but with spines generally absent.

The type of Callithamnion ramellosum Sonder (MEL, 573179) from W. Asut. (Preiss) is Centroceras clavulatum.

GENERAs OF UNCErTAIN POSITION
by H.B.S. Womersley

The following two genera cannot be placed satisfactorily. The first, Perischelia, while distinctive morphologically, is unknown reproductively; it agrees with the Ceramiaceae. The second, Episporium, has been placed in its own tribe (Episporieae) in the Ceramiaceae, but it is doubtful if it belongs to this family.

In both cases, the species are the only ones in the genus, so the specific description suffices for the genus.

There are also other undescribed taxa represented in AD by inadequate and usually non-reproductive specimens, which await description when better material is available.


FIGS 192, 193, A, B

Thallus (Fig. 192A) medium to dark red–brown, 5–20 (-30) cm high, much branched irregularly with extended axes or long branches, heavily corticated (Fig. 192B), upper branches bearing short glomeruliferous tufts (Fig. 193A) 1–2 mm long and across, on a short corticated stalk bearing branched monosiphonous filaments 1–2 mm long. Holdfast discoid, 2–5 mm across; epilithic. Structure. Axial cells enlarging rapidly from apices, becoming 200–800 µm in diameter and L/D (1.5-) 2-4 in mature branches, thick walled, corticated (Fig. 192B, D) from close to apices by compact rhizoidal filaments of inner elongate cells, surface cells (Fig. 192B) short, isodiametric, 2–3 µm across, forming a smooth, compact, surface layer. Axial cells clearly visible along the branches in dried specimens, with the end walls supporting the cortex slightly more than the side walls. Glomeruliferous tufts (Fig. 193A) on short, corticated, lateral branches, bearing several to many determinate, more or less alternately pinnate, branchlets (Fig. 192C) 0.5–1 mm long, with slender basal cells (Fig. 192E) 25–35 µm in diameter and L/D 1.5–3, mid rachis cells 40–85 µm in diameter and L/D 1–1.2, tapering only slightly in the pinnules to 30–50 µm in diameter and L/D 0.8–1.2 until the 1–3 terminal cells, with a small mucronate end cell. Rhodoplasts discoid.

Reproduction. Unknown.

Short-stalked globular bodies (Fig. 193A) 300–650 µm in diameter occur on the glomeruliferous laterals on most thalli, composed of a central mass (Fig. 192E) of short-celled filaments bearing compact radiating filaments with terminal, narrowly clavate, cells (Figs 192E, 193B) 3–5 µm in diameter and L/D 4–6. Function unknown.

Lectotype from Port Phillip Heads, Vic. (Wilson, Jan. 1882); in Herb. Agardh, LD, 20211. Isolectotype in MEL, 45157.

Distribution: Champion Bay, W. Aust., to Port Phillip Heads, Victoria.

Fig. 192. Perisselix glomulifera (A–C, E, AD, A60130; D, AD, A28635). A. Habit. B. Axis of large axial cells, small-celled cortication, and determinate lateral branchlets. C. Pinnate branchlets with alternate, distichous, pinnules. D. Transverse section of corticated branch. E. Squash of clavate organs at base of a glomeruliferous lateral branch.

Fig. 193. A, B. Perischelia glomulifera (AD, A60130). A. Branch with determinate branchlets and stalked globular organs. B. Squash of filaments from a globular organ. C–E. Episporium centroceratis (AD, A63366). C. Section of female thallus showing carpogonial branches with trichogynes. D. Squash of a male thallus with terminal spermangia. E. A young thallus showing the basal cell, branched filament, and terminal decussately divided tetrarosporangia.
Perischelia agrees morphologically with Ceramiaceae but cannot be placed in a tribe until reproductive plants are discovered. The nature of the globular organs is presently unknown.


**FIG 193C-E**

Thallus minute, hemispherical to globular, 300–500 μm across, supported on a relatively large basal cell, pale in colour; parasitic on Centroceras. Structure. Basal cells attached to host cells, elongate, becoming 20–35 μm in diameter at upper broader end and L/D 2–3, with several branches of cells from the upper end compacted to form the globular thallus; lower cells ovoid, 10–15 μm in diameter and L/D 1–1.5, decreasing to terminal cells 6–8 μm in diameter and L/D 2–3. Cells uninucleate; plastids absent.

Reproduction. Gametophytes monoecious or dioecious. Carpogonial branches (Fig. 193C) borne on outer filaments, 2 (-4) cells long, the carpogonium conical with a long trichogyne, the hypogynous cell elongate, with or without shorter lower cells. Carposporophytes (Pocock 1956; not seen in Wanna collection) hemispherical, slightly projecting on the thallus surface, with a relatively large fusion cell. Spermatangia (Fig. 193D) terminal on outer cells, ovoid, 2.5–3 (-4) μm in diameter.

Tetrasporangia (Fig. 193E) terminal on filaments, ovoid, 10–15 μm in diameter, cruciately or decussately divided.

Type from Dirk Hartog I., W. Aust. (Nauman); in B?.

Distribution: NW Australia, Lord Howe I, South Africa. In southern Australia, only known from Wanna, South Australia.


Episporium centroceratis is an inconspicuous species, as discussed by Pocock (1956, p. 14), and has only once been collected on southern Australian coasts. Schmitz (1889, p. 452), followed by Schmitz & Hauptfleisch (1897, p. 503) placed it in its own tribe, the Episporieae, in the Ceramiaceae, and Pocock (1956) tentatively accepted this, though some authors (e.g. G. Feldmann 1947) considered it more likely to belong to an order such as the Gigartinales.

While the structure and reproduction are reasonably well known from the account of Pocock, these are not easily interpreted in relation to other Ceramiaceae or earlier orders of Rhodophyta.

**Family Dasyaceae**

by M.J. Parsons and H.B.S. Womersley

Thallus erect, terete or compressed, much branched radially, bilaterally, or dorsiventrally, with sympodial apices producing axes with 4–11 pericentral cells and monosiphonous (or basally polysiphonous), branched, rhodoplastic, pseudolateral filaments (with laterally adherent basal walls to the upper cells of the branch subdichotomies) developed from the displaced apical cells of the sympodium; pseudolaterals free or forming a network; adventitious monosiphonous filaments present in some species; pericentral cells produced in a circular or alternating sequence, in some species dividing transversely; axes ecorticate or corticate by compact rhizoids. Holdfast rhizoidal, compact.

Life history triphasic with isomorphic gametophytes and tetrasporophytes; or apomeiotic.

Reproduction. Gametophytes dioecious. Procarps borne on lower pseudolateral cells, with 5 pericentral cells cut off in circular or alternating sequence, one being the supporting cell of
a 4-celled carpogonial branch, and with 2 groups of sterile cells which usually divide further after fertilization. Fertilized carpogonium producing 1 or 2 connecting cells, one fusing with the auxiliary cell, followed by the auxiliary cell, central segment cell, and other cells forming a fusion cell; gonimoblast filaments producing carposporangia in rows or terminally with further carposporangia developing from below. Cystocarps globular to urceolate; pericarp of adherent corticated filaments, ostiolate, with initials present or absent at fertilization. Spermatangia formed on branches of pseudolaterals, with 4-5 pericentral cells dividing to form a layer of initials which cut off spermatangia over the surface of the cylindrical to lanceoid male organs.

Tetrasporangia occur in simple stichidia (branched in Thuretia) borne on cells of the pseudolaterals, with 4-10 pericentral cells cut off in alternating sequence, with 2-4 pre- or post-sporangial cover cells and whorls of 4-6 subspherical sporangia, tetrahedrally divided.

The Dasyaceae include some 12 or 13 genera (de Jong et al. 1997, p. 422), of which only Dasya C. Agardh, Heterosiphonia Montagne, Thuretia Decaisne and Colacodasya Schmitz occur on southern Australian coasts. Of these 4 genera, the first 3 are richly represented in this region. Millar (1996) discusses the validity of several of the other genera.

Some authors (e.g. de Jong et al. 1997) include Halodictyon Zanardini in the Dasyaceae, but this genus lacks vegetative pericentral cells, growth is not sympodial, and the spermatangial branches and stichidia are not dasyaceous; it is more likely to be an unusual member of the Rhodomelaceae.

A feature of all Dasyaceae appears to be the adherence of the lower walls of the upper cells of the subdichotomies of the pseudolaterals, and in most species the sterile cells and adjacent pericentral cells of the procarp become darkly staining and may be nutritive in function.

**KEY TO GENERA OF DASYACEAE**

1. Thallus erect, monosiphonous filaments free, subdichotomous, not forming a network .......................................................................................................................................... 2

1. Thallus erect, terete or flat, with monosiphonous filaments united to form a network, or pulvinate to globose, 2–5 mm across, parasitic on Dasya clavigera ........................................ 3

2. Thallus radially branched, occasionally with somewhat bilateral branches; pseudolaterals usually on every segment (two segments apart in a few species); 5 (rarely 4) vegetative pericentral cells; procarp without surrounding pericarp initials; stichidia with whorls of 4–7 tetrasporangia and 3 (2–4) post-sporangial cover cells; ................................................................. DASYA

2. Thallus bilaterally branched; pseudolaterals borne alternately 2 or more axial segments apart; 4 or 7–13 pericentral cells; procarp with surrounding pericarp initials; stichidia with whorls of 4–9 tetrasporangia and 2 pre-sporangial cover cells, each dividing transversely .................. HETEROSIPHONIA

3. Monosiphonous filaments attached to form a network, thallus terete or compressed, with a central polysiphonous axis ................................................................. THURETHA

3. Thallus pulvinate to globose, 2–5 mm across, parasitic on Dasya ........................................ COLACODASYA

**Genus DASYA** C. Agardh 1824: 211, nom. cons.

Thallus erect, radially (occasionally more or less bilaterally) branched, sympodially developed; most species muclaginous. Sympodial axes terete, with 5 (rarely 4) pericentral cells cut off in a circular sequence and with each or every second segment bearing a pseudolateral. Axes ecoricate or corticate by rhizoidal filaments. Pseudolaterals monosiphonous, rhodoplastic, persistent, usually becoming branched subdichotomously and sometimes becoming polysiphonous at their base. Adventitious monosiphonous filaments may arise from the pericentral cells and/or the cortical cells in some species.
Lateral sympodial axes develop from basal cells of the pseudolaterals or adventitious monosiphonous filaments.

**Reproduction.** Gametophytes usually dioecious. Procarps occur spirally on successive segments of the sympodial axes or on 1–3 basal cells of pseudolaterals. The fertile segment bears five pericentral cells formed in a circular sequence, the third pericentral cell producing the procarp which consists of a 4 (rarely 3)-celled carpogonial branch and two groups of sterile cells originating from the supporting cell. No pericarp initials are present at fertilization. The fertilized carpogonium cuts off 1 or 2 connecting cells, one fusing with the auxiliary cell cut off from the supporting cell. A fusion cell is formed by the auxiliary cell fusing with the central cell of the fertile segment, and the supporting cell, adjacent pericentral cells and basal gonimoblast cells may also fuse with this fusion cell. Gonimoblasts monopodial, branched, with carposporangia maturing in chains or terminally. Cystocarps stalked or sessile, often with a prominent neck. Spermatangial branches formed from a branch of the monosiphonous portions of pseudolaterals or adventitious filaments, with four pericentral cells cut off in an alternating sequence, dividing several times to give spermatangial initials and outer spermatangia.

Tetrasporangia formed in stichidia on monosiphonous, rarely polysiphonous, parts of pseudolaterals or adventitious filaments, with 4–7 pericentral cells cut off in an alternating sequence, first dividing to give a tetrasporangium and a stalk cell. The stalk cell cuts off 2–4 post-sporangial cover cells which may divide again but never completely cover the tetrasporangium. Tetrasporangia tetradoically divided, 4–7 each segment.

**Type species:** *D. elegans* (Martens) C. Agardh. [= *D. baillouviana* (Gmelin) Montagne. See Dixon & Irvine 1970, p. 480].

A genus of more than 80 species, widely distributed in temperate and tropical seas, and particularly well represented on the coasts of southern Australia. *Dasya* differs from *Heterosiphonia* in having usually 5 (rarely 4) pericentral cells per vegetative segment and radial branching at the apices.

The generic key in de Jong *et al.* (1997, pp. 422, 423) covers several genera which are compared in their Table 1. While some groups of southern Australian *Dasya* species are relatively distinctive, it seems best to keep them all under *Dasya* in view of the variation in these characters. The groups involved are:

1. *D. villosa* — *D. extensa* complex, with abundant adventitious filaments arising from cortical cells. This group includes also the closely related *D. kraji* and *D. haldockii*, and the less closely related *D. haffiae* and *D. wilsonii* which have a rather different habit to the first 4 species, more similar to some species not bearing adventitious filaments.

2. *D. tenuis*, *D. capillaris* and *D. hookeri*, which have pseudolaterals (and lesser branches) borne mostly on every second segment rather than on each segment; however this is not consistent, and branching from every and from each third segment does occasionally occur. Branching 2 or more segments apart is a characteristic of *Heterosiphonia*, but the above *Dasya* species are radially rather than distichously branched.

3. *D. haffiae*, which is usually complanately and bilaterally branched, but this is a secondary development of a spirally branched apex where usually the first and second pseudolaterals become polysiphonous lateral branches and 3, 4 and 5 remain as monosiphonous pseudolaterals; occasionally all become polysiphonous and the thallus branching is irregular.

Several other species of *Dasya* than those described below occur on southern Australian coasts, but material is inadequate for their determination; specimens have been segregated in the AD herbarium.

Two other species (*D. elongata* and *D. frutescens*) occur on the west coast of Western Australia, extending north from Safety Bay; at present there is no satisfactory evidence that they occur in the southern Australian region, and any references to them in this region probably apply to other species (e.g. Reinbold 1899, p. 49).


These 2 species are closely related but appear to differ in habit, in terminal filaments of pseudolaterals (usually longer and slenderer in *D. frutescens*) and in stichidia of *D. elongata* having 5 tetrasporangia per whorl but *D. frutescens* only 4.

New, liquid preserved, collections of these species are needed to clarify their features.

**KEY TO SPECIES OF DASYA**

1. Adventitious monosiphonous filaments plentiful between the pseudolaterals........... 2
   1. Adventitious monosiphonous filaments absent (or rare) between the pseudolaterals.... 7

   2. Pseudolaterals and adventitious monosiphonous filaments soft, branching only basally and at narrow angles, always ending in a lax filament ....................... 3
   2. Pseudolaterals and adventitious monosiphonous filaments rigid, branches patent, usually ending with an acute apex (rarely with a lax filament) .................. 6

   3. Pseudolaterals and adventitious monosiphonous filaments gradually and evenly attenuate from their basal cells*; diameter of the basal cells usually less than twice that of the cell after the last subdichotomy ......................................................... 4
   3. Pseudolaterals and adventitious monosiphonous filaments distinctly attenuate from their basal cells; diameter of the basal cells usually more than twice that of the cell after the last subdichotomy ......................................................... 5

   4. Pseudolaterals and adventitious filaments usually with lower subdichotomies (1-) 2-3 (-5) cells apart, with no cell pairs (due to intercalary cell divisions) in the mature filaments; pericentral cells usually prominent in transverse sections of corticated axes with no or few internal rhizoids between them; cover cells in stichidia irregularly rectangular, palisade-like, sometimes subdividing ........................................................................................................ 1. *D. villosa*

   4. Pseudolaterals and adventitious filaments with no or few lower subdichotomies, (1-) 4-9 (-18) cells apart, with cell pairs (due to the intercalary cell divisions) occasional in the filaments; pericentral cells not conspicuous in transverse sections of corticated axes, or if apparent then usually with extensive rhizoid development between them; cover cells in stichidia irregular in shape, usually isodiametric ........................................................................................................... 2. *D. extensa*  

   5. Basal cells of monosiphonous filaments 45–65 μm in diameter; pairs of shorter cells occasionally present in ultimate branches of mature filaments, indicating recent intercalary cell divisions; spermatangial branches ovoid-ellipsoid with a terminal unbranched filament; (4-) 5 pericentral cells and tetrasporangia per segment in stichidia ............. 3. *D. kraftii*

   5. Basal cell of monosiphonous filaments (40-) 50–80 μm in diameter; no (or very rare) pairing of cells in mature filaments; spermatangial branches elongate-cylindrical; (5-) 6–7 pericentral cells and tetrasporangia per segment in stichidia .......... 4. *D. baldockii*  

   6. Frond more or less complanately branched, with percurrent axes and regular, subdistichous, branching of several orders; monosiphonous filaments radially arranged, subdichotomous, divaricate, curved, basal and lower cells 20–35 (-45) μm in diameter ......................................................... 5. *D. haffae*

   6. Frond with terete, irregular and distant branches, not complanate, without a percurrent axis and without short laterals; monosiphonous filaments simple to

* Either the basal cell of the totally emergent pseudolateral near apices, or the supra-basal cell immediately outside the cortication on corticated branches.
DASYACEAE

Dasya

(usually) 2–3 times subdichotomous, mostly 50–60 μm in diameter, ends subulate .......................................................... 6. D. wilsonii

7. Pseudolateral filaments coarse, simple or basally branched once or twice, curved, rigid, usually tapering to a point, (80-) 100–250 μm in diameter with cells L/D 1–3, longer in younger filaments ................................................................. 8

7. Pseudolateral filaments slender to moderately robust, basally branched several times, rigid to lax, 20–100 μm in diameter with cells L/D (0.75-) 2–8 ................................................. 9

8. Axes slender to moderate, lightly corticated near the apices with pericentral cells visible in side view for many segments from the apices, and with pseudolateral filaments along the branches; stichidia borne on monosiphonous pedicels .......... 7. D. ceramoides

8. Axes robust, heavily corticated, with pericentral cells visible in side view only close to the apices, and with dense clusters of pseudolateral filaments at ends of short laterals on otherwise bare branches; stichidia borne on polysiphonous pedicels ................................................................. 8. D. scopulifera

9. Axes and lateral branches heavily to moderately corticated, with the pericentral cells visible in side view in young laterals only near the apices ........................................ 10

9. Axes and lateral branches only lightly corticated, with the pericentral cells visible in side view in young and medium branches for very many (usually over 30) segments from the apices .............................................................. 17

10. Pseudolaterals divaricate, somewhat rigid, with many branches divergent at 45° or greater, branched throughout every 1–2 cells and without long, unbranched, tapering ends; pericentral cells usually remaining clearly visible in transverse section of older axes, with no or limited rhizoid development ...................... 11

10. Pseudolaterals usually lax, not divaricate, with branching mostly at distinctly less than 45° divergence and confined to the lower part of the pseudolateral which terminates in long, unbranched filaments, usually gently to distinctly tapering (except D. clavigera); pericentral cells remaining distinct or usually becoming separated and indistinguishable in size in transverse sections of older axes due to extensive rhizoid development .................................................. 12

11. Lateral branches occurring mostly two segments apart and tending to be subdistichously arranged; pseudolaterals moderately rigid, forming tufts at ends of branches, without an acute apex, filaments 40–50 (-60) μm in diameter near base of pseudolateral with cells L/D 3–5 .............................................................. 9. D. cliftonii

11. Lateral branches irregularly radial and often distantly arranged; pseudolaterals on each segment, clothing branches except in older parts, rigid, with (2-) 3–5 (-8) cells after last subdichotomy tapering to an acute apex, filaments (40-) 50–70 (-75) μm in diameter with cells L/D (1-) 2–2.5 ........................................ 10. D. divergens

12. Branched regions of mature pseudolateral filaments less than 45 μm in diameter .............................. 13

12. Branched regions of mature pseudolateral filaments more than (45-) 55 μm in diameter ................................................................. 15

13. Pseudolateral filaments very slender, 12–20 μm in diameter with cells L/D (2-) 3–4, becoming corticated at base of the pseudolateral; thallus much branched, dark brown .......................................................... 11. D. comata

13. Pseudolateral filaments (17-) 20–40 μm in diameter with cells L/D 2.5–8, not corticated at base of the pseudolateral; thallus with long branches bearing lateral tufts of pseudolaterals, medium to dark red ............................................. 14
14. Thallus with mainly long branches from near the subdichotomous base, fringed with short pseudolateral tufts; pseudolateral filaments 30–40 μm in diameter with cells L/D (2–) 2.5–3 where branched, L/D (2–) 3–4 near ends ....... 12. D. crinita

14. Thallus with long branches bearing numerous laterals with lax pseudolateral tufts near their ends; pseudolateral filaments (17-) 20–30 μm in diameter with cells L/D 2–4 where branched, L/D 6–8 near ends ................. 13. D. hapalathrix

15. Thallus robust, usually with short lateral branches on strongly developed axes; pseudolateral filaments usually slightly greater in diameter several cells above the base, then ending or tapering but not into a long, slender, hair; stichidia with 6 pericentral cells and sporangia per segment .......................................................... 14. D. clavigera

15. Thallus robust to moderately slender, usually with well developed lateral branches; pseudolateral filaments tapering from basal cells either gently or rapidly into long, slender, hair-like ends; stichidia with 4 or 5 pericentral cells and sporangia per segment .......................................................... 16

16. Thallus moderately slender, much and irregularly spirally branched with long laterals; pericentral cells remaining distinct in transverse section; mature pseudolaterals with basal cells 35–65 μm in diameter; stichidia with four pericentral cells and tetrasporeangia per segment .................................................. 15. D. quadrispora

16. Thallus robust with heavily corticated axes bearing laterals giving a narrowly to broadly conical outline; mature pseudolaterals with basal cells (50-) 95–130 μm in diameter; stichidia with five pericentral cells and sporangia per segment ............................................................................ 16. D. naccarioides

17. Pseudolaterals mostly on every segment of branches; stichidia with 5 pericentral cells and sporangia per segment .......................................................... 18

17. Pseudolateral filaments 45–65 μm in diameter near their base with cells L/D 3–4 throughout, tapering gently to a rounded terminal cell; stichidia often with terminal monosiphonous, simple or branched, prolongations; cystocarps with a corticated pericarp and subspherical carpogonia in chains ..................... 17. D. atactica

18. Pseudolateral filaments 20–30 (-40) μm in diameter near their base with cells L/D (3-) 4–10 (-14), gently tapering to slender, lax ends; stichidia without terminal, monosiphonous prolongations; cystocarps with a pericarp of lengthwise-elongate pericentral cells and only slight (or no) cortication and clavate to lacrimiform, terminal carpogonia .......................................................... 18. D. crescents

19. Branches ecorticate apart from cortical filaments lying between the pericentral cells near the thallus base; pseudolateral filaments with lower cells 20–40 μm in diameter; carpogonia terminal, clavate; stichidia with 6 pericentral cells and sporangia per segment ................................. 19. D. tenuis

19. Branches with moderate cortication, becoming complete on mid parts; pseudolateral filaments 15–40 or 50–80 μm in diameter in lower cells; carpogonophyte with small, subspherical to ovoid carpogonia in chains; pericarp corticated by small, irregular cells; stichidia with 4 pericentral cells and sporangia per segment ................................. 20

20. Pseudolateral lower cells (15-) 25–35 (-40) μm in diameter ...... 20. D. capillaris

20. Pseudolateral lower cells 35–90 (-110) μm in diameter ........................ 21. D. hookeri

DASYACEAE

Dasya


Endogena gracilarii J. Agardh 1897; 52, pl. 1 fig. 14.

It is probable that many references to Dasya villosa apply in part to Dasya extensa.

FIG. 194

Thallus (Fig. 194A) red-brown to very dark brown, occasionally light red, mucilaginous, 10–40 cm high, with 1–10 corticated axes 1–2 (–3) mm in diameter. Main axes irregularly radially branched with many lateral axes, lightly to densely corticated, bearing pigmented, basally branched, slender, monosiphonous, attenuate filaments, often denuded below. Holdfast discoid, 2–5 (–15) mm in diameter: epilithic and on solid substrates. Structure. Pericentral cells 5, cut off in circular sequence, at first lightly but below heavily corticated, remaining prominent (Fig. 194B) in transverse sections of the mature axis; in older axes, some of the inner cortical cells may enlarge to the same size as the pericentral cells and protrude between them, thus appearing to have 6 or 7 pericentral cells. and coarse rhizoids later develop between the central cell and the pericentral cells which develop very thick walls; occasionally a space occurs in the centre of the axis when the central cell breaks down. Pseudolaterals one on each segment, 1–6 (–8) mm long, attenuate, usually subdichotomous every (1) 2–3 (–5) cells near their base, with the distal end of these cells often of a slightly greater diameter than the proximal end, 3–6 (–7) subdichotomies on any filament giving 8–20 ultimate branches, supra-basal cells 30–60 μm in diameter and L/D 1–2; cells after the last subdichotomy 19–25 μm in diameter and L/D 2.5–9, cells of ultimate filament 12–25 μm in diameter and L/D (3–) 5–9. Adventitious monosiphonous filaments usually present, similar to pseudolaterals, arising from the cortical rhizoidal filaments and one, often two, from the basal cell of the pseudolateral; intercalary cell divisions absent. Lateral axes arising from the first branch of the one or two adventitious monosiphonous filaments arising on the basal cell of the pseudolateral, or later from the first branch of an adventitious monosiphonous filament. Rhodoplasts discoid, elongate and often reticulate in larger cells.

Reproduction. Gametophytes dioecious. Procarps borne spirally on successive segments of an adventitious polysiphonous axis, with 2 sterile group initials on the supporting cell but with a 3-celled rather than 4-celled carpogonial branch. Carposporophytes with a slight basal fusion cell and terminal clusters of apical and lateral clavate to lacrimiform carposporangia. Cystocarps (Fig. 194C, D) sessile, appearing terminal or nearly so on a corticated axis, globose, 630–880 μm in diameter with a short wide neck 0.2–0.4 as long as the diameter of the cystocarp; pericarp 3–4 cells thick, outer cortical cells irregular. Spermatangial branches (Fig. 194E) on the lower branches of the monosiphonous filaments, elongate, cylindrical or tapering, 200–850 μm long and 40–55 μm in diameter, 15–30 fertile segments long on a 1–3 celled monosiphonous stalk, with a (1–) 4–15-celled attenuate apical filament.

Tetrasporangial stichidia (Fig. 194F) on the lower branches of the monosiphonous filaments, lanceoid to cylindrical but usually swollen where the spores are mature, on a 1–3-celled monosiphonous stalk, 300–1200 μm and 10–25 fertile segments long, 100–190 μm in diameter, with 6 pericentral cells all of which become fertile. Each tetrasporangium with 3 (–4) undivided cover cells irregularly obloid in shape (Fig. 194F), palisade-like, (2–) 3–5 times taller than broad in surface view, covering more than half of the sporangium of the same segment and the segment below, occasionally cutting off a smaller cell at the base when mature.

Lectotype from Georgetown, Tas., Gunn 1263 (tetrasporangial), in Herb. Harvey, TCD (Parsons 1975, p. 568). Isolectotypes in TCD; Herb. Hooker, BM; MEL (Gunn’s book).

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

Fig. 194. *Dasya villosa* (A–D, F, AD, A32591; E, AD, A3377). A. Habit. B. Transverse section of axis. C. Branch with young cystocarp showing darkly staining sterile cells. D. Mature cystocarp. E. Spermatangial branches. F. Stichidia on pseudolaterals from a corticated branch, showing tetrarangia and cover cells.
Endogenia gracilaria J. Agardh (1897, p. 57, pl. 1 fig. 14; see also De Toni 1897, p. 352), from Port Elliot, S. Aust. (type in Herb. Agardh, LD, 29790) is a very denuded plant of D. villosa, with typical tetrasporangial structure and a few monosiphonous filaments and young stichidia.


Nematophora australis J. Agardh 1890a: 35, pl. 1 fig. 3. De Toni 1924:

FIGS 195, 196

Thallus (Fig. 195A) pale to dark red, occasionally brown-red, mucilaginous, 10–130 cm high, with 1–10 corticated erect axes 2–6 mm in diameter. Main axes irregularly branched with few to many long, linear, laterals, which may carry further lateral branches, densely clothed throughout with rhodoplastic, unbranched or basally branched, slender, attenuate monosiphonous filaments. Holdfast disoid, 3–6 cm in diameter or an expanded, tuberculate, sessile on an axis, or terminal but lateral on a corticated stalk up to 10–25 cm long, sometimes with extruding monosiphonous filaments, urceolate, 700–1600 µm in diameter, with a short neck less than 1/4 the diameter of the cystocarp in length; pericarp (Fig. 196F) 4–6 cells thick, outer cells small. Sporangial branches (Figs 195D, 196G) sessile or on a monosiphonous stalk 1–2 cells long, on the lower branches of monosiphonous filaments, lanceolate to cylindrical, occasionally branched and rarely with accessory sporangial branches, 350–650 µm long and 75–90 µm in diameter (Fig. 196H), with 10–25 fertile segments, terminating with a 1–5 celled filament.

Stichidia (Figs 195E, 196I) on a 1–3-celled monosiphonous stalk, on the lower branches of the monosiphonous filaments, rarely with accessory stichidia near their base, lanceolate to cylindrical, 300–1000 µm long and 90–130 µm in diameter, with 15–35 fertile segments of 5...
pericentral cells all of which become fertile. Each tetrasporangium with 2–3 cover cells (Fig. 196J, K), cuboidal to L/D 2, later becoming irregular in shape, often dividing into smaller cells covering less than half of the sporangium.

Fig. 195. Dasya extensa (A, B, D, AD, A8190; C, AD, A7017; E, AD, A67344). A. Habit. B. Young cystocarp with darkly staining cells and adventitious filaments. C. Mature cystocarp. D. Spermatangial branches. E. Stichidia.
**Dasya**

**DASYACEAE**

*Type* from Lefevre Pen., S. Aust. (Mueller 24, 16.xii.1847); lectotype in MEL, 1006628, tetrasporangial (see Parsons 1975, p. 569). Isolectotypes in MEL, 1005816, 1005817, 1005818, L 940,347...242.

**Distribution:** Dongara, W. Aust., to Walkerville, Vic., and the N coast of Tasmania.


The perennating base of *D. extensa* is closely appressed to the substrate, with large, rather rounded, cartilaginous tubercules (3–8 mm in diameter, 2–5 mm high) on its upper surface. An erect axis, often slightly constricted at its point of attachment, arises from the top of each tubercule. The constricted point of attachment of the axis to the tubercule is a point of weakness where the frond is more easily removed from the crustose base. Probably a new axis is formed from each tubercule the following season. Many of the more robust fronds of *D. extensa*, lacking a holdfast, were collected in the drift. These have a truncate base to the axis where they have been detached from the tuberculate perennial base. Further details on the morphology of *D. extensa* are given by Parsons (1975, pp. 571–578).

**Nematophora australis** J. Agardh (1890a, p. 35, pl. 1 fig. 3) from "Nov. Holl. (type in Herb. Agardh, L, 27573) is a denuded plant of *D. extensa*, with a typical transverse section, monosiphonous filaments and young stichidia.

3. *Dasya kraftii* Parsons & Womersley, sp. nov.


**FIG. 197**

*Thallus* (Fig. 197A) light to dark red-brown, soft and mucilaginous, 3–20 (45) cm high, with 1–2 corticated axes 1–2 mm in diameter. Main axes profusely and irregularly branched throughout, with lower laterals often as long as the main axes, moderately to heavily covered by basally branched, pigmented, attenuate, monosiphonous filaments. Holdfast small, discoid; epiphytic or on solid substrates. *Structure.* Pericentral cells 5, formed in circular order, not obvious in transverse sections of older axes (Fig. 197B), heavily corticated by rhizoidal filaments which occur both internally and externally to the pericentral cells. Pseudolaterals from every segment, 1–2 mm long, basally subdichotomous every 1–2 cells with 3–5 subdichotomies on any filament giving 10–20 ultimate branches, distinctly attenuate from their base to beyond the last subdichotomy and then scarcely attenuate in the ultimate unbranched filament. Adventitious monosiphonous filaments similar to young pseudolaterals, frequent, arising from the upper portion of pericentral cells 1, 3, and 4 (not the smaller 2 and 5), beginning about 12 segments from the apex, and also from later formed cortical cells. Basal cells of pseudolaterals and adventitious filaments 45–65 μm in diameter, L/D 0.7–1; cells after the last subdichotomy 22–23 μm in diameter, L/D 1–2 (-3); cells of ultimate...
filaments 12–22 μm in diameter, L/D (1-) 2–9. Intercalary cell divisions occasional in the ultimate branches. Lateral axes usually adventitious, arising from the basal cell of the first branch of a monosiphonous filament. Rhodoplasts disoid to elongate, reticulate in older cells.

Reproduction. Gametophytes dioecious. Procarps borne spirally on a polysiphonous, usually adventitious, axis. Carposporophytes with a moderate basal fusion cell and ovoid to clavate, apical and lateral carposporangia. Cystocarps (Fig. 197C) sessile on lateral axes, urecolate, 400–700 μm in diameter, with a neck (0.2-) 0.3–0.5 the diameter of the cystocarp in length; pericarp 3–4 cells thick, outer cells irregularly ovoid. Spermatangial branches (Fig. 197D) sessile or on a 1–2-celled monosiphonous stalk, on the lower branches of both pseudolaterals and adventitious monosiphonous filaments, prominent, ovoid to ellipsoid, 120–250 μm long and 75–100 μm in diameter, with 7–11 fertile segments and a 6–16-celled attenuate apical filament.

Stichidia (Fig. 197E) on a 1–2 (-3)-celled monosiphonous stalk, on the lower branches of both pseudolateral and adventitious monosiphonous filaments, cylindrical, 100–650 μm long and 100–150 μm in diameter, with 8–15 fertile segments of (4-) 5 pericentral cells (Fig. 197F) all of which become fertile. Each tetrasporangium with (2-) 3 cover cells (Fig. 197G) which are at first small, rather narrow and irregular in shape, scarcely covering the sporangium, later becoming elongate irregularly upwards and often dividing once.


Reproductio. Gametophyta dioecia. Procarpia in polysiphonous praesertim adventitio axe spiratim portata. Carposporophyta cum cellula moderata basali fusionis et ovoidea ad lacrimiformia, carposporangia apicalia et lateralia. Cystocarps sessilis in axibus lateralis, urecolata, 400–700 μm diametro cum collo (0.2-) 0.3–0.5 pro diametro cystocarpis longo; pericarpium 3–4 cellulas crassum, cellulae exteriores irregularum ovoidea. Rami spermatangiales sessiles aut in stipite monosiphon 1–2 cellati, prominentes, ovoidei ad ellipsoidalis 120–250 μm longi et 75–100 μm diametro, cum 7–11 segmentis fertilibus et filimento 6–16 celullato attenuato apicali. Stichidia in 1–2 (-3) cellula monosiphon stipite, cylindrica. 100–650 μm longa et 100–150 μm diametro cum 8–15 segmentis fertilibus (4-) 5 cellularum pericentralium quorum omnes fertiles crescent. Quodque tetrasporangium cum (2-) 3 cellulis tegentibus sporangium via subducentibus.

Holotype: Third Beach, Esperance, W. Aust., on fucoids at reef edge (Parsons, 21.xi.1968; AD, A33349; isotype CHR, 315367).

Erynome: named for Dr Gerald T. Kraft, University of Melbourne, for the contributions he has made to phycology, particularly the collection of uncommon species of *Dasya*.

*Dasya kraftii* has been often found with *D. baldockii*, and their general habit is very similar. They are however easily distinguished by the shape of their spermatangial branches and the occasional intercalary cell divisions in the monosiphonous filaments of the former. *D. kraftii* occurs on fucoids in the sublittoral fringe and in pools, or sublittoral on *Osmundaria prolifera* Lamouroux, on *Posidonia* sp. to 10 m deep and on wooden jetty piles 1–2 m deep; records of *D. kraftii* are from early spring to late summer, when plants are fertile.

4. *Dasya baldockii* Parsons & Womersley, sp. nov.


**FIG. 198**

*Thallus* (Fig. 198A) dark red-brown, soft and mucilaginous, 10–35 cm high, with 1–3 corticated axes 1–2.5 mm in diameter, much and irregularly branched, densely covered by basally branched, attenuate, monosiphonous filaments, but occasionally denuded at the base. Holdfast discoid; epilithic. Structure. Pericentral cells (Fig. 198B) 5, not obvious in transverse sections of the older axes, heavily corticated by rhizoidal filaments internally and externally to the pericentral cells; Pseudolaterals one per segment, 1–2 mm long, with 3–5 sub dichotomies every 2 (1–3) cells on any filament giving 10–20 ultimate branches, distinctly attenuate from the base to beyond the last sub dichotomy and then slightly attenuate as an ultimate unbranched filament. Adventitious monosiphonous filaments common, similar to young pseudolaterals, arising from the upper portion of pericentral cells 1 and 3, beginning at about 11 segments from the apex, and also from the later formed cortical cells; occasionally the adventitious filaments are arranged in apparent whorls. Intercalary cell divisions absent or rare. Basal cells of pseudolaterals and adventitious filaments (40–) 50–80 μm in diameter, L/D 0.5–1.5; cells after the last sub dichotomy 15–30 μm in diameter, L/D 3.5–8; cells of ultimate filament 10–20 μm in diameter, L/D 7–20. Lateral axes arising from the basal cell of the first branch of an adventitious monosiphonous filament. Rhodoplasts discoid to elongate.

Reproduction. Gametophytes dioecious. Procarps borne spirally on a polysiphonous, usually adventitious, axis. Carposporophytes with a basal fusion cell, much branched gonimoblast, and clavate to lacriiform carposporangia, formed apically and laterally in terminal clusters. Carposporangia (Fig. 198C) sessile on lateral axes, occasionally appearing almost terminal, urceolate, 950–1700 μm in diameter, with a distinct neck 0.2–0.4 (-0.5) the diameter of the cystocarp in length; pericarp 3–4 cells thick, outer cells irregularly placed. Spermatangial branches (Fig. 198D) sessile on a 1–2-celled monosiphonous stalk, on the lower branches of both pseudolaterals and adventitious monosiphonous filaments, elongate-cylindrical, 600–1000 μm long and 80–95 μm in diameter, with 15–25 fertile segments and a 4–9 celled apical filament.

Stichidia (Fig 198E) on the lower branches of both pseudolaterals and adventitious monosiphonous filaments, cylindrical, rarely branched once at the base, sessile or on a 1–2-celled monosiphonous stalk, 200–800 μm long and 110–150 μm in diameter, with 10–25 fertile segments each with (5–) 6–7 pericentral cells all of which become fertile. Each tetrasporangium with (2–) 3 cover cells (Fig. 198F) which are irregular to rectangular in shape and cover about half the sporangium, later becoming more elongate but rarely dividing.
Thallus moJlis et mucilaginus, 10-35 cm altus, 1-3 axibus corticatis 1-2.5 mm diametro, multum et irregulariter ramosus, dense tectus filamentis basin ramosis attenuatis monosiphonis, sed aliquando basi denudus. Hapteron discoideum, epilithicum. Structure. Cellulae pericentrales 5, non manifestae in sectionibus transversis axium veteriorum, corticatae dense per filamenta rhizoidalia interne et externe ad cellulas pericentrales., Pseudolaterales unus per segmentum, 1-2 mm longi, cum 3-5 subdichotomis separatis 2(1-3) cellulis in omni filimento 10-20 ramos ultimos producenti, distincte attenuati ex basi ad ultra subdichotomum extremum, deinde vix attenuati filamentum ultimum haud ramosum. Filamenta monosiphona adventitiia crebre, similia pseudolateralibus iuvenibus, orientia ex parte superiore cellarum pericentralium 1 et 3, initio in circa 11 segmentis ex apice, et etiam ex cellulis postea formati. Divisiones cellularum intercalares absentes aut rarae. Cellulae basales pseudolateralium et filamentorum adventitiorum (40-) 50-80 μm diametro, L/D 0.5–1.5; cellulae post subdichotomum extremum 15–30 μm diametro L/D 3.5–8; cellulae filamenti ulti 10–20 μm diametro, L/D 7–20. Axes laterales e cellula basali rami primi filamenti adventiti et monosiphoni.


Type from N side of Althorpe L., S. Aust., 9–12 m deep (Baldock, 4.i.1964). Holotype (tetrasporangial) and isotype (female) in AD, A27233.

Distribution: Rottnest L., W. Aust., to West L., S.Australia


Etymology: named for Mr Robert N. Baldock who has studied the Griffithsieae of southern Australia and who collected the type specimens of this species.

D. baldockii occurs in the sublittoral, on limestone or wooden jetty piles, 1–25 m deep, only known from late spring and early summer. It is closely related to D. kraftii, with which it sometimes occurs. The pseudolaterals and adventitious monosiphonous filaments of both species taper relatively distinctly from the basal cells to after the last subdichotomy. In D. kraftii however there are occasional intercalary divisions in the ultimate branches of these filaments, indicated by pairs of half-length cells and dividing cells. In D. baldockii the cells of the ultimate filaments continue to elongate as they increase in age and only rarely are half-length cells seen. The stichidia also differ, those of D. baldockii having 6–7 pericentral cells and tetrasporangia compared with 5 in D. kraftii. The cover cells are more prominent in D. baldockii and tend to be more obloid and palisade-like than those of D. kraftii, which are narrower and divide once or twice. The spermatantial branches are ovoid to ellipsoid in D. kraftii and long and cylindrical in D. baldockii. The cystocarps of D. baldockii are larger and consequently more prominent than those of D. kraftii.

**FIG. 199**

*Thallus* (Fig. 199A) pale crimson-red to dark red-brown, 15–30 cm high, usually with a single axis. Main axis corticated, 1–2 mm in diameter, regularly to irregularly distichously branched often from very close to the apex; lateral axes usually regularly distichously branched (Fig. 199B), occasionally radially, ultimately bearing spirally arranged, subdichotomous, monosiphonous pseudolaterals. Holdfast discoid, epilithic. **Structure.** Pericentral cells 5, developed in circular sequence, becoming obscured in transverse sections (Fig. 199C) of older axes by rizoidal cells which may become much enlarged. Pseudolaterals (Fig. 199B, F) one on each segment, 250–1100 μm long, patent and curved, tapering to an acute apex or rarely forming an attenuate filament, below subdichotomous every 2–3 cells with 3–5 subdichotomies giving 6–20 ultimate branches. Basal cell and lower cells 20–45 μm in diameter, L/D 1–2 (–2.5). Adventitious monosiphonous filaments scattered, arising from cortical cells, unbranched and acute, or subdichotomous resembling smaller pseudolaterals. Intercalary cell divisions absent. Lateral axes arise from the basal cell of the first branch of the pseudolateral, with adventitious lateral axes arising from surface cortical cells, scattered on older parts of the main axes. Rhodoplasts discoid, chained and reticulate even in smaller cells.

**Reproduction.** Gametophytes dioecious. Procarps spirally arranged on successive segments of lateral polysiphonous and adventitious axes. Carposporophytes with a basal fusion cell and ovoid to subspherical carposporangia, in apical and lateral rows of 2–3. Cystocarps (Fig. 199D) basally embedded in a corticated axis, urceolate, 0.3–0.5 of the cystocarp diameter in length, either straight or flared with the terminal filaments often extended and free; pericarp 3–4 cells thick, surface often with smaller, simple or subdichotomous, patent, adventitious, monosiphonous filaments. Spermatangial branches (Fig. 199E) sessile or on a 1–2-celled monosiphonous stalk, on the lower branches of the pseudolaterals or adventitious filaments, cylindrical, 170–400 μm long and 45–60 μm in diameter, with or without a short apical filament (1–3) 3 (–5) cells long, the apical cell being conical.

**Stichidia** (Fig. 199F) on a 1–2-celled monosiphonous stalk, on the lower branches of the pseudolaterals or adventitious filaments, cylindrical or occasionally ovoid, 80–110–200 (–410) μm long and 70–80 (–90) μm in diameter, with (2–) 3–12 (–20) fertile segments each with (–) 5 pericentral cells all of which usually become fertile, the basal segment of 4 pericentral cells with 1–2 (–3) becoming fertile. Each tetrasporangium with 2–3 cover cells, round to broader than high in surface view, which cover less than one quarter of the sporangium and are often moulded around the sporangium.

**Type** from Philip I., Vic. (Harvey, Alg. Aust. Exsicc. 222H); lectotype (HBSW) in TCD, isolecotypes MELU, 1006680, 1006659, 1006684.

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

Fig. 199. *Dasya haffiae* (A, D–F, AD, A34407; B, AD, A32945; C, AD, A33833). A. Habit. B. Branch with alternate, subdistichous laterals and pseudolaterals. C. Transverse section of a branch. D. Cystocarp showing gonimoblast and filaments on pericarp. E. Spermatangial branches. F. Stichidia on pseudolateral branches.
D. haffiae occurs sublittorally, down to 23 m, often on limestone; it appears to be present and fertile mainly in late spring and summer.

Harvey (1859b, p. 303), described Dasya haffiae from material collected at Georgetown, Tasmania by R. Gunn, from Western Port, Victoria by himself and from Table Cape, Tasmania by Miss Mackenzie. Harvey expressed some doubt, however, about the Table Cape specimens being the same as the others as he felt that they were "much injured and in part denuded of ramuli, and may possibly belong to a different ... species". A re-examination of the Table Cape specimen in TCD has shown that it represents a species of Micropeucea.

The specimen of D. haffiae illustrated by Kützing (1864, p. 24, pl. 68a, b) was collected by Harvey at Western Port, Victoria, and is in the Sonder Herbarium, MEL., 1006680. Harvey left two Western port specimens of Dasya haffiae from his Travelling Set No. 359 (MEL, 1006659, 1006684) with F. Mueller during his visit to Melbourne in 1854. These three MEL specimens are isolectotypes of D. haffiae.

Dasya meredithiae is based on material sent to J. Agardh from Orford, Tasmania by Mrs Meredith and from Swan Island, Bass Strait (L.D, 43935) by Miss Baudinet. From the three excellent Orford specimens in Herb. Agardh, L.D, 43936 is now selected as the lectotype of D. meredithiae, with L.D, 43936, 43937 as syntypes.

The distichous branching of the thallus of D. haffiae is unusual in Dasya. The apex of an axis is sympodial and pseudolaterals develop successively one to each segment in a 2/5 spiral; this is the usual pattern of Dasya. The thallus branching becomes distichous later when the first and second (or second and third) pseudolaterals of any series of five are the only ones which become differentiated into polysiphonous lateral axes. Pseudolaterals 3, 4 and 5 remain as monosiphonous, subdichotomous, patent pseudolaterals. Occasionally pseudolaterals 1, 2 and 3 all become polysiphonous and then the branching of the thallus appears irregular rather than bilateral. The monosiphonous pseudolaterals are very persistent, remaining on the corticated axes of most of the plant.


Pachydasya wilsonis (J. Agardh) J. Agardh 1890a: pl. 3 fig. 6.

FIG. 200

Thallus (Fig. 200A) red-brown, not adhering well to paper on drying, 10–25 cm high, irregularly radially branched, with patent laterals on one to several linear, corticated, axes, densely covered throughout with basally branched, upwardly curved, relatively rigid, patent, monosiphonous pseudolaterals and adventitious filaments. Main axes irregularly radially branched usually at intervals of 0.5–2 cm; laterals and lesser branches 1–2 mm in diameter. Holdfast conical, 2–10 mm across, with a loose rhizoidal surface; probably epilithic. Structure. Pericentral cells 5, not obvious in sections of older branches (Fig. 200B, C) due to enlarged cells of the rhizoidal cortication. Pseudolaterals (Fig. 200D) one per segment, 0.8–1.4 mm long, basally branched every 1–2 cells with 1–2 (-3) subdichotomies giving 4–6 ultimate simple branches several cells long; basal cells 40–50 μm in diameter and L/D 1–1.5, increasing to 55–60 μm in diameter and L/D 1.5–2, then tapering to a small, apically rounded, terminal cell. Adventitious monosiphonous filaments simple or branched, similar to the pseudolaterals, arising from the upper part of pericentral cells and later from cortical cells. Intercalary divisions not seen in monosiphonous filaments. Rhodoplasts discoid.

Reproduction. Gametophytes unknown.

Stichidia (Fig. 200E, F) borne on the lower branches of both the pseudolaterals and adventitious monosiphonous filaments, on a 1–2 (-4)-celled monosiphonous stalk, ovoid to lanceolate, 100–400 μm long and 50–140 (-150) μm in diameter with 5–20 fertile segments each with 5 pericentral cells and (3–) 5 sporangia per whorl; whole sterile segments occasionally present within the fertile part. Tetrasporangia 25–35 μm in diameter, each with (2–) 3 cover cells which remain short, exposing most of the sporangium.

Type from Portsea, Port Phillip Heads, Vic. (Wilson 33, 31.1,1883); lectotype (here selected), L.D, 43808. Syntypes: Western Port, Vic. (Wilson 57, 7.1,1885; L.D, 43809). South Channel, Port Phillip, Vic. (Wilson 33, 26.1,1884; L.D, 43810 and MEL., 1006692, 40 m deep).
Fig. 200. *Dasya wilsonis* (A, lectotype in LD, 43808; B-F, AD, A66983). A. Habit of lectotype. B. Transverse section of young branch. C. Transverse section of older axis. D. Two pseudolaterals. E. Part of a branch with pseudolaterals and adventitious filaments, one bearing a stichidium. F. Filament with small ovoid stichidium.
Dasya  

**Distribution:** Known only from Backstairs Passage, S. Aust., and Port Phillip Heads and Western Port, Victoria.  

**Known specimens:** 2 km E of Penneshaw (in Backstairs Passage), Kangaroo I., S. Aust., 19-22 m deep (Hone, 10.i.1997; AD, A66983). Port Phillip Heads, Vic., (Wilson, 28.i.1888; L, 965.91...509, 21.i.1886; L, 910.55...2589, and 1.i.1892; MEL). Port Phillip, Vic., south channel (Wilson, 25.i.1884; MEL, 1006691, 4.i.1884; MEL, 1006690, and 20.xii.1884; L, 965.91...466).  

*D. wilsonis* was known only from the above 1883-1892 specimens of Wilson’s in LD, L, M and MEL, one of which (MEL, 1006692) is recorded as from “20r” deep (40 m). Of the several Wilson specimens in LD, only one is annotated “stichidia in hac vidi”, and this is chosen as lectotype; others are considered syntypes. However, a further collection in 1997 from Backstairs passage, S. Aust., indicates that this is a deep water species where strong currents occur; however, only sparse tetrasporangial material is available, and study of further fertile material as well as the vegetative development and number of pericentral cells is needed.  


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*Trichothamnion ceramioides* (Harvey) Kiitzing 1849: 800.  


**FIGS 201, 202A-D**  

*Thallus* (Fig. 201A) dark brown to red, or pale rose-red, 10-30 (-40) cm high with 1-2 (-5) pyramidal main branches with corticated axes 1-1.5 (-2) mm in diameter. Main axes sympodial (Fig 202A), becoming irregularly radially branched (sometimes pseudolaterals subdistichus) with 2-10 (-15) well developed laterals arising at intervals of 2 mm to 1 (-2) cm, bearing basally branched, attenuate, large celled, pseudolaterals (Fig. 202B). Laterals corticated from close to apices (Fig. 202C), arising from the basal cell of the first branch of the pseudolateral. Adventitious laterals not formed. Holdfast discoid, 2-8 (-14) mm across; on solid substrates. **Structure.** Pericentral cells 5, remaining prominent (Fig. 202D) in sections at all ages, with slender rhizoidal filaments surrounding the individual pericentral cells and the central cell, later thickly covering the whole surface. Pseudolaterals one per segment, 1.5-3 (-4.6) mm long, simple or with 1-2 basal subdichotomies (Fig. 202B) giving (1-) 2-3 (-4) ultimate branches 8-10 cells long, cells relatively large, 80-230 μm in diameter and L/D 0.3-1 near the base, increasing to (120-) 160-300 μm in diameter and L/D 2-3 (-4) in mid filament, then tapering to 2-3 very small terminal cells in an acute apex, occasionally terminating in an attenuate, pale filament. Adventitious monosiphonous filaments absent. Rhodoplasts discoid to elongate, becoming chained.  

*Reproduction.* Gametophytes dioecious. Procarps borne spirally on successive segments of polysiphonous axes. Carposporophytes with a slight basal fusion cell and ovoid to subspherical carposporangia, in rows of 2-4. Cystocarps (Fig. 201B) sessile, terminal or nearly so on lateral branches, single or rarely paired, urceolate, 550-800 μm in diameter with a prominent neck 0.3-0.7 as long as the cystocarp diameter; pericarp 3-4 cells thick, outer cells relatively large and irregularly shaped. Spermatangial branches (Fig. 201C) in clusters of 2-6 near the base of the pseudolaterals, on monosiphonous stalks, cylindrical to slightly attenuate, 350-750 (-900) μm long and 40-70 (-80) μm in diameter, with 8-10 (-15) fertile segments and often a short, 1-2 (-3)-celled sterile apex.
Stichidia (Fig. 201D) in clusters of 2–5 near the base of pseudolaterals, on 3–6-celled monosiphonous stalks, cylindrical with slightly curved attenuate apices, 300–700 (-1000) μm long and 50–200 μm in diameter, with 10–25 fertile segments each with 6 pericentral cells all of which produce tetrasporangia. Tetrasporangia 25–45 μm in diameter, each with 3 (–4) cover cells (Fig. 201E) which lengthen to 1–1.5 diameters long and cover about 75% of the tetrasporangium.

Fig. 201. Dasya ceramioides (AD, A41509). A. Habit. B. Cystocarp and pseudolaterals. C. Spermatangial branches. D. Stichidia on pseudolaterals. E. Stichidia showing cover cells.
Type from Georgetown, Tas. (Gunn 1303 in part); holotype in BM.

Distribution: Port Denison, W. Aust., to Sealers Cove, Vic. and the N and E coasts of Tasmania.


Dasya ceramioides is a deep-water or shade species, fertile in late spring and summer, distinguished from all other species except D. scopulifera by the large-celled pseudolaterals. It is less heavily corticated than D. scopulifera, the pseudolaterals are branched once or twice

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**Fig. 202.** A–D. *Dasya ceramioides* (A, C, AD, A13526; B, D, AD, A30193). A. Sympodial apex. B. A mature basally furcate pseudolateral. C. Early cortication of an axis with secondarily subdistichous pseudolaterals. D. Transverse section of axis with prominent pericentral cells. (All as in Parsons 1975, courtesy of Aust. J. Bot.)
rather than 2-3 (-4) times and are only rarely basally polysiphonous, and the stichidia are borne on monosiphonous stalks rather than polysiphonous ones. The laterals of *D. scopulifera* remain short [5-15 (-30) mm long], whereas those of *D. ceramioides* are usually several cm long.

*D. ceramioides* is mainly an eastern species but probably extends to Port Denison, W. Aust., where it overlaps with the strictly western *D. scopulifera*. The Port Denison specimen is sterile but has the habit of *D. ceramioides*.

*Dasya pachyclada* Harvey (1863, synop.: xxiv) is based on a Clifton specimen from W. Aust. (type in TCD) and is very similar in habit to the above Port Denison specimen. Though sterile, it is probably a synonym of *D. ceramioides*.

A detailed account of the structure and stichidia, of *D. ceramioides* was given by Parsons (1975, p. 596).


**FIG. 203**

Thallus (Fig. 203A) dark red-brown, 20-40 cm high with a stout main axis and long laterals bearing short laterals 2-10 mm apart with tufted pseudolaterals. Main axis usually single, (1.5-) 2-4 mm in diameter, very heavily corticated, linear, occasionally slightly swollen between the short laterals, tapering slightly near the apex, smooth and denuded of pseudolaterals; long laterals similar to main axis. Short laterals simple or rarely branched, becoming tufted in older plants, usually 5-15 (-30) mm long, irregularly radially arranged, corticated but only 0.3-0.5 mm in diameter, terminating in compact tufts of incurved, large-celled, pseudolaterals. Holdfast conical, 4-10 mm across; probably usually epilithic. Structure. Pericentral cells 5, heavily corticated but usually remaining clear (by enlargement) in transverse sections (Fig. 203C), with rhizoidal filaments surrounding the pericentral cells and often obscuring them in the laterals. Pseudolaterals (Fig. 203B) one per segment, lost from older branches, 1-2 mm long, subdichotomously branched 2-3 (-4) times at each cell near their base with 1-2 (-4) basal segments becoming polysiphonous with up to 5 pericentral cells. Upper monosiphonous parts large celled, 90-230 μm in diameter with cells L/D 1.5-2.5 (-3), tapering to acute apices. Adventitious monosiphonous filaments absent. Rhodoplasts discoid.

Reproduction. Procarps spirally arranged on several successive polysiphonous segments. Cystocarps sessile on corticated laterals, globose and urceolate, 800-900 μm in diameter with a prominent corticated neck 0.5-1 as long as the cystocarp diameter. Spermatangial branches unknown.

Stichidia (Fig. 203D) in clusters at the base of pseudolaterals, on polysiphonous stalks (1-) 2-4 (-6) segments long with 5 pericentral cells plus small corticating cells, slightly curved, 250-500 μm long and 100-150 μm in diameter, with 5 pericentral cells all becoming fertile. Tetrasporangia 35-45 μm in diameter, each with three cover cells which cover 0.5-0.8 of the tetrasporangium.

**Type from Bunbury, W. Aust. (Clifton 64, 1855); lectotype in TCD (see below).**

**Distribution:** Port Denison to Bunbury, W. Aust.


While *Dasya scopulifera* is not known with certainty from the southern Australian region, the type locality is just north of Cape Naturaliste and the species would be expected to occur in the southern region.

*Dasya scopulifera* is apparently a rare, deep water, species known largely from drift specimens, few of which are fertile; the above description is based largely on the type, the
Cottesloe specimen of Burbidge, and Kraft 1128, 1129 from Port Denison. It is most closely related to *D. ceramioides*, from which it differs in habit, the thick, coarse, axes and long laterals fringed with short, terminally tufted, laterals, by having polysiphonous bases to the pseudolaterals and polysiphonous stalks to the stichidia.

Harvey (1863, pl. 271) illustrated two taxa; figures 1, 4 and 5 are of *D. scopulifera*, but 2 and 3 are of *Chiracanthia arborea* (which is present on the lectotype folder) and which (as

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Fig. 203. *Dasya scopulifera* (A, the lectotype in TCD; B, AD, A47063; C, D, AD, A56305, UWA, 218). A. Habit of the type. B. A tuft of pseudolaterals. C. Transverse section of a young branch. D. Stichidia with polysiphonous pedicels.
Harvey drew) has cystocarps without necks and with elongate carposporangia arising directly from the fusion cell (as typical for most Rhodomelaceae). The lectotype sheet bears a characteristic specimen of *D. scopulifera* similar to Harvey’s fig. 1, and a packet of fragments which have young stichidia. This sheet was annotated as TYPE by H.B.S.W. (in 1952), and is now considered to be the lectotype although Harvey stated that stichidia were unknown and his illustration of a cystocarp applies to *Chiracanthia*.

Other fine specimens from Red Bluff, Kalbarri, W. Aust., 6–9 m deep (*Kraft & Ricker, 15.xii.1980; MELU*) are 20–40 cm high and are typical in habit for *D. scopulifera*, with short laterals bearing pseudolaterals along their whole length of 2–4 cm, and thick axes and main laterals. Unfortunately these 6 specimens are all sterile, but it is possible that the known fertile plants of this species are second year plants and that those in their first year, while well grown, do not become fertile.


**FIG. 204**

*Thallus* (Fig. 204A) medium red to red-brown, soft, mucilaginous, (5-) 10–30 cm high, with one to a few relatively slender axes bearing alternate laterals radially to subdistichously (Fig. 204B), denuded below but with tufted filaments on branch ends. Main axes somewhat flexuous, 400–700 μm in diameter, bare, corticated, irregularly subdichotomous, with alternate laterals, more or less pyramidal in outline. Laterals with 2–3 orders of branches, more or less subdistichous and mostly two segments apart (some on each segment), alternately divaricate, arising from the first branch of a pseudolateral or adventitiously from the basal cell. Holdfast discoid, 1–3 mm across; epiphytic on *Amphiho/olis*. Structure. Pericentral cells 5, quickly corticated by rhizoidal filaments, leaving the pericentral cells visible in transverse section but becoming separated from each other by slender rhizoids, some of which later become as large as the pericentral cells; outer cortical cells irregularly placed, ovoid to elongate. Pseudolaterals arising from each 1 (-2) segments, lost from older parts, 1–2 mm long, divaricately and repeatedly branched every 1–2 cells, basal cells 45–65 μm in diameter and L/D 2–5, above gradually attenuate to an acute apex which is often lost. Adventitious monosiphonous filaments absent. Rhodoplasts discoid, becoming chained and reticulate.

Reproduction. Procarps not observed. Carposporophyte with a slight fusion cell and numerous darkly staining cells (Fig. 204C) of the lower pericarp and adjacent vegetative cells, gonimoblast much branched with short terminal chains of ovoid carposporangia 15–20 μm in diameter. Cystocarps (Fig. 204C,D) sessile on the base of short lateral branches, ovoid, with a slight to distinct neck, 300–600 μm in diameter. Pericarp with 10–14 erect filaments cutting off pericentral and cortical cells which become ovoid and irregularly placed. Spermatangial branches unknown.

Stichidia (Fig. 204E,F) borne as the ultimate branches of pseudolaterals on a single-celled monosiphonous stalk, 400–700 μm long and 100–200 μm in diameter, lanceoid, with about 6 fertile segments and 4 sporangia per segment, arranged in longitudinal rows, often ending in a simple or branched filament. Tetrasporangia 30–55 μm in diameter, each with 2–3 ovoid cover cells.

*Type* from Fremantle, W. Aust. (Clifton); lectotype (stichidal), here selected, in TCD.

**Distribution:** Cliff Head, W. Aust., to Sturt Bay, S. Australia.

Fig. 204. *Dasya cliftonii* (A, lectotype in TCD; B, C, E, F, AD, A59880; D, AD, A51235). A. Habit of lectotype. B. Branch with subdistichous laterals bearing pseudolaterals and cystocarps. C. Young cystocarp with darkly stained cells around the fusion cell and developing gonimoblast. D. Mature cystocarps with carposporophytes. E. Branch with stichidia. F. Stichodium with branched apical filament.
DASYACEAE

Dasya

D. cliftonii was based on a specimen “dredged in Fremantle Harbour by G. Clifton”, and such a specimen in TCD, accompanied by Harvey’s 1863 illustration, is selected as lectotype. Harvey also had specimens from Garden I., Rottnest I. and King George Sound, and a Rottnest I. specimen, though labelled ‘164’ (a Trav. set number) and labelled as ‘TYPE’ by H.B.S.W. in 1952, is now regarded as a syntype.

D. cliftonii is a distinctive species in its habit and the regularly alternate, radial to subdistichous branching mostly every two segments. However it is known from few specimens and only two cystocarpic collections are known (AD, A51235, A59880).

10. Dasya divergens Parsons & Womersley, sp. nov.


Wrangelia velutina sensu Womersley 1950: 181 in part.

FIG. 205

Thallus (Fig. 205A ) light grey-red to dark red, not mucilaginous and not adhering to paper on drying, 5–15 (-20) cm high, spreading, with 1–3 corticated axes 1–2 mm in diameter bearing irregular patent laterals densely covered (except near the base) with tufts of branched pseudolaterals. Main axes bearing, irregularly radially, laterals of various lengths at intervals of 1–5 mm; axes 0.2–1 mm in diameter, 0.5–3 cm long, more or less linear, moderately heavily corticated from close to their apices, arising from the basal cell of the first branch of the pseudolaterals. Holdfast discoid, loosely rhizoidal, 0.5–1.5 cm across; epilithic. Structure. Pericentral cells 5, always clear in section but corticated outwardly by slenderer rhizoids. The first pericentral is cut off 5–6 segments from the apex, and by the time the fifth pericentral cell is formed (on segments 8 or 9) a secondary pit-connection is established via a small cell from the whole lower end of the pericentral cell; later secondary pit-connections arise via cells cut off from near the end of a pericentral cell. The first corticating rhizoids form from pericentral cells 17–20 segments from the apices, and descend over the pericentral cells. Pseudolaterals one per segment, 1–1.5 mm long, with 5–12 subdichotomies every 1 (-2) cells from their base, of similar diameter until the ultimate branch of (2-) 3–5 (-8) cells which tapers to an acute point; branches divaricate, rigid, lying at right angles at each branching; basal cells 50–70 (-100) μm in diameter and L/D 0.5–1.5, mid cells (40-) 45–70 μm in diameter and L/D (1-)2–3 (-4). Adventitious monosiphonous filaments absent. Rhodoplasts discoid to elongate, becoming chained.

Reproduction. Gametophytes dioecious. Procarps borne successively and spirally on a polysiphonous lateral; the first sterile group initial is cut off from the fertile pericentral cell on the sixth segment, and by the ninth segment a mature procarp with a 4-celled carposporophyte branch and two sterile group initials is present; after fertilisation, the sterile group initials each divide once. The auxiliary cell fuses with the central cell of the fertile segment via a new connection, and produces three primary gonimoblast initials, then a monopodial gonimoblast often branching unilaterally. Carposporophyte with a slight basal fusion cell, carposporangia ovoid to subspherical, 15–22 μm in diameter, in rows of 3–4 (-5) often with 1 (-2) lateral sporangia on the basal one. Cystocarps sessile on laterals or on short polysiphonous stalks, globose, 700–1100 μm in diameter with a neck 0.2–0.5 as long as the cystocarp diameter; pericarp 3–4 cells thick with outer cells ovoid to elongate, irregularly placed. Spermatangial branches as ultimate branches of pseudolaterals, lanceoid, 90–170 μm long and 30–40 μm in diameter, with a 1–2 celled pedicel and sterile apex 3–5 cells long, and 6–10 axial cells cutting off initials and an outer layer of spermatangia.

Stichidia borne on the lower branches of pseudolaterals, on 1–3-celled monosiphonous stalks, cylindrical, 300–600 μm long and 120–150 μm in diameter, with (4-) 7–20 fertile segments each with (5-) 6 pericentral cells all of which become fertile, and with a short, mucronate, 2–3-celled apex. Tetrasporangia 25–35 μm in diameter, each with (2-) 3 cover cells, initially small but at maturity covering most of the sporangium.

Thallus non mucilaginus nec ad papyrum in sicco adhaerens, 5–15 (-20) cm altus, patens cum 1–3 axibus corticatis 1–2 mm diametro ferens laterales irregularis patentes densim tectos...
cum pseudolaterium ramosorum caespitibus. Axes principales ferentes, irregulatim et radiatim, laterales varie longos, 1–5 mm seorsum; axes 0.2–1 mm diametro, 0.5–3 cm longi, plus minusve lineares, moderatim graviter corticati, orientes e cellula basali rami primi pseudolateralium. Hapteron discoideum, laxe rhizoideale, 0.5–1.5 cm latum, epilithicum. Structure. Cellulae pericentrales 5, semper pellucidae in sectione sed corticatae extrinsecus

Fig. 205. Dasya divergens (A, B, AD, A53347; C, AD, A19306; D, AD, A67087; E, F, AD, A20100). A. Habit of holotype. B. Transverse section of branch. C. A cystocarp. D. Spermatangial branches. E. Pseudolaterals with young stichidia. F. Older stichidia.
per rhizoidea graciliora. Rhizoidea prima corticata e cellulis pericentralibus orienti 17–20 segmenta ex apicibus et super cellulas pericentrales descendientia. Pseudolaterales unus per segmentum, 1–1,5 mm longi, cum 5–12 subdichotomis in omnibus 1 (-2) cellulis e basi, diametro simili usque ad ramum ultimatum (2-) 3–5 (-8) cellularum ad punctum acutam angustatum; rami divaricati, rigidì, iacentes in angulis rectis in una quaque ramificatione; cellulae basales 50–70 (-100) μm diametro, et L/D 0.5–1.5, cellulae mediae (40) 45–70 μm diametro et L/D (1-) 2–3 (-4). Filamenta adventitia monosiphona carentia.

Reproductio. Gametophyta dioecia. Procarpia invicem et spiratim in laterale polysiphono portata; initium primae sterilis turmae e cellula fertili pericentrali in segmento sexto abscessum et apud segmentum novenum procarpium maturum cum ramo cellulari carpogoniali et 2 inilia 700–1100 μm diametro similis usque ad ramum ultimatum

Distribution: S. Ausl., drift from Robe, S. Aust., drift in bay (Parsons, 9.i.1982); holotype in AD, A53347, tetrasporangial. Isootype in CHR, 391866.

Selected specimens: 16 km E of Eucla, W. Aust. to Walkerville, Victoria

Type from Robe, S. Aust., drift in bay (Parsons, 9.i.1982); holotype in AD, A53347, tetrasporangial. Isootype in CHR, 391866.

Dasya comata Parsons & Womersley, sp. nov.

FIG. 206

Thallus (Fig. 206A) dark brown-red, mucilaginous, 5–15 cm high, spreading, usually with several axes. Main axes (Fig. 206B) bearing longer branches radially, sometimes subdichotomously, with short interspersed branches, heavily corticated to very close to branch tips, 1–1.5 mm in diameter. Ultimate branches tapering abruptly, bearing at the tips spirally arranged, subdichotomous, monosiphonous pseudolaterals which often have corticated basal cells. Lateral axes apparently arise from the basal cells of pseudolaterals. Holdfast discoid, 1–3 mm in diameter; on solid substrates. Structure. Pericentral cells 5, cut off very close to apices and rapidly corticated, with the pericentral cells becoming separated from the axial filament by rhizoids and relatively obscure (Fig. 206C), outer cortical cells isodiametric to slightly elongate, irregularly placed. Pseudolaterals one per segment, lost shortly below the
Dasya apices, 0.5–1.5 mm long, basally branched 3–5 times 2 or 3 cells apart, with adherent lower walls at subdichotomies, with long unbranched ends; lower cells 20–25 μm in diameter and L/D (1–) 1.5–2.5, tapering gradually to upper cells 7–10 μm in diameter and L/D 3–5 (-8). Occasional adventitious filaments occur, similar to pseudolaterals. Rhodoplasts discoid.

Reproduction. Gametophytes dioecious. Procarps not observed. Carposporophyte much branched, with terminal rows of ovoid carposporangia 15–20 μm in diameter. Cystocarps (Fig. 206D) sessile on short laterals, globular, 600–800 μm across; pericarp 3–5 cells thick, outer cells more or less isodiametric and 6–8 μm across and bearing adventitious branched filaments corticated basally. Spermatangial branches (Fig. 206E) as lower parts of ultimate branches of pseudolaterals, with long sterile terminal ends, 100–300 μm long and 40–55 μm in diameter. Tetrasporangial stichidia (Fig. 206F) (few seen) on lower branches of pseudolaterals, 100–180 μm long and 45–70 μm in diameter, short lanceoid, with a monosiphonous pedicel, each whorl with probably 5 sporangia 20–25 μm in diameter.


Type from Troubridge I., S. Aust., 23 m deep (Shepherd, 4.ii.1969); holotype in AD, A33831. Isotypes in AD, CHR, 315579.

Distribution: Waldegrave I., S. Aust., 23 m deep (Shepherd, 4.ii.1969); holotype in AD, A33831. Isotypes in AD, CHR, 315579.


D. comata is a name used by J. Agardh on specimens from Westernport, in LD and MEL, doubtless referring to the terminal tufts of pseudolaterals, but never published. The species is distinct in habit, with cortication commencing and becoming heavy very close to the apices.

12. Dasya crinita Parsons & Womersley, sp. nov.

FIG. 207

Thallus (Fig. 207A) red brown, slightly mucilaginous, 25–40 cm high, with 1–2 pale, heavily corticated axes 1–2 mm in diameter, irregularly branched. Main axes irregularly...
subdichotomous, not percurrent, bare below, branched at intervals of 1–4 cm above with very short laterals and tufts of basally subdichotomous pseudolaterals. Main laterals 200–400 µm in diameter, 1–20 cm long, arising from the first to fifth branch of the pseudolateral (with basipetal cortication of the lower pseudolateral cells then occurring) or adventitiously from the basal cell of the pseudolateral or adjacent cortical cells. Holdfast discoid, 1–3 mm across; probably epilithic. **Structure.** Pericentral cells 5, heavily corticated by slender rhizoids, at first clear in section (Fig. 207B) but later obscure (Fig. 207C) as rhizoids separate them from each other; cortication commences from short cells cut off basally from pericentral cells which recover their full length as the short cell is pushed outwards and develops into a rhizoid of relatively short cells, producing a small-celled outer surface. Basipetal cortication of lower cells of the pseudolaterals is also characteristic though rather variable. Pseudolaters one per segment, relatively firm (not lax), 1–3 mm long, below subdichotomous every (1-) 2–4 (-10) cortical cells at base of pseudolaterals. Rhodoplasts discoid.

**Reproduction.** Gametophytes monocoeus (?). Procarps borne spirally on a polysiphonous axis; with the first group of sterile cells dividing twice after fertilisation to produce 3 cells rather than the two usually produced in other species; carposporophytes with slight basal fusion cell and gonimoblast filament with apical and lateral clusters of 2–3 carposporangia, maturing terminally, clavate, 15–22 µm in diameter. Cystocarps terminal on corticated laterals, ovoid to globose, urceolate, 420–800 µm in diameter with a neck 0.3–0.7 as long as the cystocarp diameter; pericarp 4–5 cells thick, outer cells isodiametric to ovoid, 6–10 µm across, irregular in position. Spermatangial branches as the lower branches of the pseudolaterals, lanceoid to cylindrical, 170–250 µm long and 35–40 µm in diameter with 10–20 fertile segments, sessile or on a short monosiphonous stalk and with a 2-6 celled attenuate apical filament; 3 spermatangial branches were found on one abundantly procarpic-cystocarpic plant. Stichidia on the lower branches of the pseudolaterals, sessile or on a 1–2-celled monosiphonous stalk which often develops basipetal rhizoidal cortication back to the parent lateral, lanceoid to cylindrical and sometimes branched or with simple or branched apical filaments, 130–250 µm long and 65–90 µm in diameter, with 5–10 fertile segments each with 4 pericentral cells all becoming fertile. Tetrasporangia 30–40 µm in diameter, each with 3 cover cells, the outer two (occasionally the central one as well) cutting off further small cells upwards and downwards so that the mature sporangia become surrounded by and partly covered by a ring of small cells.

**Thallus** leviter mucilaginosus, 25–40 cm altus, cum 1–2 axibus pallidis, graviter corticatis 1–2 mm diametro, irregulariter ramosus. Axes principales irregulariter subdichotomi, infranudi, ramosi intervallis 1–4 cm supra cum lateribus brevissimis 1–3 cm longis, ferentes caespites pseudolateralium basaliiter subdichotomorum. Laterales principales 200–400 µm diametro, 1–20 cm longi, orientes e ramo primo ad quinto pseudolateralis (cum corticatone basipetali cellularum inferiorium pseudolateralium) aut adventitie e cellula basali cellularum pseudolateralium aut adiacientium corticatorum. Hapteron discoideum, 1–3 mm latum; probabiler epithecicum. **Structure.** Cellulae pericentrales 5, graviter corticatae, primo in sectione pelliculae sed deinde obscure, cum pagina exteriore minime cellulata. Pseudolaterales unus per segmentum, pro ratione firmi 1–3 mm longi, infra subdichotomi per (1-) 2–4 (-10) cellulas cum 3–8 subdichotomis producentes 30–40 ultimos ramos multas cellulas longos, cellulae basales 25–35 µm diametro et L/D 1–2, gradatim supra attenuatae; segmenta basalia saepe leviter corticata. Filamenta adventititia monosiphona rara, orientia e cellulis corticalibus basi pseudolateralium.

**Reproduction.** Gametophyta monoecia (?). Procarps portata spiratum in axe polysiphono; turma prima cellularum sterilium dividens bis post fecundationem producit 3 cellulas magis quam 2. Carposporophyta cum fusionis cellula levi basali et cum filamentis gonimoblastis cum fasciculis apicalibus et lateralis 2–3 carposporangiorum, terminaliter maturescentia, clavata, 15–22 µm diametro. Cystocarps terminalia in lateribus corticatis, ovoidea ad globosa, urceolata, 420–800 µm diametro, diametro, cum collo 0.3–0.7 longo quam cystocarpii diametro;
pericarpium 4–5 cellulas crassum, cellulae exteriores isodiametricae ad ovoideae, 6–10 μm latum. Rami spermatangiales sicut rami inferiores pseudolateralium, lanceoide ad cylindricas, 170–250 μm longi et 35–40 μm diametro, cum 10–20 segmentis fertilibus, sessilis aut in stipite brevi monosiphono et cum filamento 2–6 cellulato attenuato apicali; 3 rami spermatantiales in una planta procarpic cystocarpica. Sichidia sessilia aut in stipite 1–2 cellulato monosiphono saepe faciente corticationem recessim ad lateralem, lanceoide ad cylindricalia et interdum ramosa aut cum filamentis simplicibus aut ramosis apicibus, 130–250 μm longa et 65–90 μm diametro cum 5–10 segmentis fertilibus, unum quidque cum 4 cellulis pericentralibus omnes fecundescentes. Tetrasporangia 30–40 μm diametro, unum quidque cum 3 cellulis tegentibus, exteriores duae abscidentes cellulas ulteriores parvas sursum et deorsum ita sporangia matura cinctata et per cellularum parvarum annulum partim tecta.

**Type** from Tapley Shoal, Gulf St Vincent, S. Aust., 15 m deep outside shoal (Shepherd, 2.ii.1969); holotype in AD, A33513, tetrasporangial, isotype in CHR, 315398.

**Distribution:** Known from Eyre, W. Aust., Tapley Shoal and Vivonne Bay, Kangaroo I., S. Australia.


**Dasya crinita** is characterised by rapidly and heavily corticated axes which are often pale in colour in contrast to the very short laterals (1–2 mm long), covered with red tufts of pseudolaterals. The specific name *crinita* refers to these prominent tufts.


**FIG. 208**

**Thallus** (Fig. 208A,B) medium red-brown, 20 cm –1 (-2) m high, with strongly developed main axes 2–3 mm in diameter and long lateral branches radially developed and bearing third order branches 4–8 cm long, ultimate branches 5–20 mm long and 130–300 μm in axial diameter, with delicate pseudolateral tufts, most branches denuded below. Holdfast probably discoid, 1–3 mm across; epilithic. **Structure.** Apices sympodial, developing 5 pericentral cells with dense cortication obscuring the pericentral cells close to apices. Pseudolaterals (Fig. 208C,E) one per segment, 1–2 mm long, with 2–4 basal subdichotomies one cell apart and unbranched ends 0.5–1.5 mm and many cells long; lower cells 15–25 (-30) μm in diameter and L/D 1.5–2.5 (-4), upper cells 15–30 μm in diameter and L/D 3–8, tapering at the meristematic apex. Cortication by rhizoidal filaments separating the pericentral cells from themselves and the axial filaments but pericentral and large cells visible in most transverse sections. Rhodoplasts discoid to chained or ribbon like.

**Reproduction.** Gametophytes dioecious. Procarps not observed. Carposporophytes (Fig. 208D) much branched, with a basal fusion cell and terminal clavate carposporangia 18–30 μm in diameter. Cystocarps urceolate, 700–1000 μm in diameter, with a slight neck; pericarp with erect filaments cutting off 3 outer pericentral cells which develop slight outer cortication by elongate cells. Spermatangial branches (Fig. 208E) developed as lower branches of pseudolaterals, cylindrical, 200–700 μm long and 40–65 μm in diameter, with monosiphonous pedicels and short apical filaments, occasionally branched. Tetrasporangial stichidia (Fig. 208F) on lower cells of pseudolaterals, lanceoid, 150–350 μm long and 45–90 μm in diameter, with a monosiphonous pedicel and each segment with 5 (or 4) pericentral cells and tetrasporangia, with obloid and palisade like cover cells; tetrasporangia 25–55 μm in diameter.
Dasya

**Lectotype** from Point Rapid, Tamar Est., Tas. (Harvey, Alg. Aust. Exsiccat. 201 I); in Herb. Harvey, TCD. Isolectotypes in MEL, 1006638 and AD, A18293.

**Distribution.** Recorded by Harvey (1959a, pl. 85) also from Georgetown, Tas., and Port Phillip Heads, Victoria. Probably also from Tiparra Reef, S. Aust., 10–12 m deep (Shepherd, 16.iii.1985; AD, A56444).

*D. hapalathrix* is characterised by the dense cortication to close to the apices, and the form and dimensions of the pseudolateral filaments. The species is based on plants from Point Rapid in the Tamar Estuary (now Barrett’s Point, at the Batman Bridge), where strong currents flow through a narrow channel. Apart from nearby Georgetown, Harvey also recorded the species from Port Phillip Heads, Victoria. The fronds were stated to be “3–6 feet long”. It appears that *D. hapalathrix* has not been collected in the Tamar Estuary since Harvey, and is now unlikely to occur there due to shipping disturbance and pollution.

The Tiparra Reef, S. Aust., specimens are similar to the type in vegetative features, but the stichidia have consistently 4 tetrasporangia per whorl rather than 5, as in the type; measurements of reproductive structures are based largely on the Tiparra collection. It is highly desirable that *D. hapalathrix* should be re-collected near the type locality, with liquid-preserved material for detailed investigation.

References to *D. hapalathrix* from other localities (e.g. Reinbold from Lacepede Bay, S. Aust.) need verification.


**FIGS 209, 210**

*Thallus* (Fig. 209A,B) dark red-brown, occasionally paler, slightly mucilaginous, with 1–2 (-4) axes, pyramidal in form, (1-) 3–15 (-60) cm high, axes simple or rarely branched with robust laterals radially or occasionally bilaterally arranged and 2–10 (-25) cm long, densely covered with pseudolaterals but often basally denuded. Main axes heavily corticated, 1–2 (-3) mm in diameter, percurrent, branched at intervals of 0.5–2 cm. Laterals 2–10 (-20) cm long; axes 400–800 μm in diameter, moderately corticated from close to their apices, arising from the basal cell of the fourth branching of the young pseudolateral. Adventitious laterals common in older parts, arising from surface cortical cells near the base of normal laterals, singly or in clumps. Holdfast 2–10 mm across, with one to several erect axes; epilithic or often epiphytic on larger algae. **Structure.** Pericentral cells 5, becoming obscured in older axes (Fig. 210B) or laterals by profuse development of rhizoids. Pseudolaterals one per segment (Fig. 210A), spirally arranged, 1–1.5 (-2) mm long, the filaments increasing in diameter and length from the basal cell until a few cells after the last subdichotomy, then tapering to a slenderer filament which is often broken off but may have an acute apical cell; basal subdichotomies 3–7, every 1–2 (-3) cells, giving 25–40 ultimate branches; basal and lower cells 40–80 μm in diameter, L/D (0.5–) 1–2, mid and upper cells 55–100 μm in diameter and L/D 2–3 (-4). Adventitious monosiphonous filaments absent. Rhodoplasts discoid to elongate, becoming chained and reticulate.

**Reproduction.** Gametophytes dioecious. Procarps (Fig. 210C) alternating on the adaxial side of the second, third and fourth segments of the secondary sympodial axes on pseudolaterals. Carpogonial monosporophyte with a basal fusion cell, gonimoblast much branched, carposporangia ovoid to subspherical, 15–25 μm in diameter, borne singly or in rows of 2–4. Cystocarps (Fig. 209C) sessile on corticated laterals, urceolate, 800–1200 (-1400) μm in diameter, with a prominent corticate neck 0.2–0.5 as long as the cystocarp diameter; pericarp 4–5 cells thick, outer cells ovoid, irregularly placed. Spermatangial branches (Figs 209D, 210D,E) on the lower branches of the pseudolaterals, sessile or on a 1–2-celled monosiphonous stalk, 120–200 μm long and 40–45 (-50) μm in diameter with 7–10 fertile segments, terminated by a short, 1–5-celled, apical filament.
Stichidia (Figs 209E, 210F) on lower branches of the pseudolaterals, lanceoid to cylindrical, on a 1–2 (-3)-celled monosiphonous stalk and with a short apical filament, 200–400 (~450) μm long and 80–150 μm in diameter with usually 8–15 fertile segments each with 6 pericentral cells (Fig. 210G,H) all of which become fertile. Tetrasporangia 30–40 μm in

Fig. 209. Dasya clavigera (A, AD, A2845; B–E, AD, A64758). A. Holotype sheet (upper) with lower Vivonne Bay specimens. B. Habit. C. Young cystocarp with darkly stained fusion and vegetative cells. D. Sporophyllial branches. E. Stichidia. (A, as in Womersley 1946, courtesy of R. Soc. S. Aust.)
diameter each with 2–3 rather swollen cover cells covering 0.5–0.8 of the sporangium and dividing rarely.

**Type** from Pennington Bay, Kangaroo I., S. Aust., on eastern edge of main reef (*Womersley, 15.i.1946*); holotype in AD, A2845; isotypes in AD, MEL, NSW. Paratypes: S side of Ellen Point, Vivonne Bay, Kangaroo I., S. Aust., lower eulittoral (*Womersley, 23.v.1945*; AD, A2726; MEL, 1006636, and 31.xii.1945; AD, A2997; MEL, 1006637).

**Distribution:** Hopetoun, W. Aust. to Westernport Bay, Vic., and the east coast of Tasmania, epiphytic or epiphytic (mainly on larger brown algae) in the lower eulittoral or upper sublittoral on rough-water coasts, fertile throughout the year.


*D. clavigera* has been described in detail by *Parsons* (1975, p. 585, figs 7–9A, B, 40B). It and *D. naccarioides* are the only species which grow just above and below low tide level, on rough-water coasts, and it differs from *D. naccarioides* in the abrupt ending to most pseudolateral branches and in having 6 tetrasporangia per whorl instead of 5.

15. **Dasya quadrispora** *Parsons & Womersley, sp. nov.*

**FIGS 210 I, 211, 212**

**Thallus** (Fig. 211A) medium to dark red-brown, 10–30 cm high, slightly mucilaginous, with several much branched axes and laterals, pyramidal to spreading in outline, terminal pseudolateral tufts dense and fairly prominent, denuded below. Axes and branches spirally branched from each segment, 1–2 mm in diameter below; lateral branches 0.5–1 mm in diameter, lesser branches 1.5–5 mm long and basally 100–200 μm in diameter, mostly ecoricate. Holdfast discoid, 1–3 mm across; epilithic. **Structure.** Periclinal cells 5, becoming corticate from several segments below branch apices, first by filaments of elongate cells lying between the pericentral cells, densely corticated below with the pericentral cells without surrounding rhizoids and remaining clear in section (Fig. 211C). Lateral branches arising from the basal cells of pseudolaterals. Pseudolaterals (Fig. 211B) one per segment, spirally arranged, 0.5–1 mm long with 3–5 subdichotomies usually every 1 (2) cell below, upper filaments slender and unbranched; subdichotomies with joint walls basally adherent; basal and next cells 35–90 (130) μm in diameter and L/D (L) 1.5–2.5, usually tapering evenly and markedly to slender upper cells (often lost) 4–6 μm in diameter and L/D 8–15, ends rounded. Adventitious filaments absent; adventitious branches occasional. Rhodoplasts discoid to elongate, becoming ribbon like or in chains.

**Reproduction.** Gametophytes dioecious. Procarps not observed. Carposporophytes (Fig. 211D) with a prominent fusion cell and basal nutritive cells, gomonioblast much branched with terminal rows of ovoid carposporangia 15–25 μm in diameter. Cystocarps urceolate with a globose base 0.5–1.2 mm across and a neck 100–250 μm long, sessile on lesser branches; pericarp 3–4 cells thick, outer cells ovoid, irregular. Spermatangial branches (Fig. 211E) on mid cells of pseudolaterals, lanceoid to cylindrical, 120–250 μm long and 35–65 μm in diameter with 8–12 fertile segments, with a single pedicel and 1–2 apical cells.

Tetrasporangial stichidia (Fig. 211F) on lower cells of pseudolaterals, cylindrical and tapering above, on a 1–2-celled pedicel, 200–600 μm long and 80–140 μm in diameter, with 3–8 fertile segments each with 4 pericentral cells (Fig. 210 I) and subpherical tetrasporangia 30–50 μm in diameter, tetrahedrally divided, each with 3 ovoid cover cells.
Fig. 211. *Dasya quadrispora* (A, B, F, AD, A54559; C, D, AD, A57011; E, AD, A64821). A. Habit, type sheet. B. Branch with small lateral branches and pseudolaterals. C. Transverse section of branch. D. Carposporophyte with basal fusion cell and ovoid carposporangia. E. Spermangial branches. F. Stichidia.
Thallus 10–30 cm altus, leviter mucilaginus, cum aliquot axibus et lateribus ramosissimis, pyramidalis ad patens, turmae terminales et pseudolaterales densae et prominentes, infra denudatae. Axes et rami spiratim ramosi e quoque segmento, 1–2 mm diametro infra, rami laterales 0.5–1 mm diametro, rami minores 1.5–5 mm longi et basi 100–200 μm diametro, plerumque ecorticati. Hapteron discoideum, 1–3 mm latum; epilithicum.

Structura. Cellulae pericentrales 5 corticatae sub apices ramorum, dense corticatae infra cum

Fig. 212. Dasya naccarioides (AD, A53353). A. Habit. B. Transverse section of older branch. C. Cystocarp with carposporophyte. D. Spermatangial branches. E. Pseudolaterals with stichidia.
cellulis pericentralibus in sectione pellucidis remanentibus. Rami laterales e cellulis basalius pseudolateralium orientes. Pseudolaterales unus per segmentum spiratim dispositi, 0.5–1 mm longi, cum 3–5 subdichotomis plerunque in quaque (-2) cellula infra, filamenta superiora gracilla et sine ramis; celluale basales et proximae 35–90 μm diametro et L/D (1-) 1.5–2.5; plerunque acqualiter decrescentes et valde ad cellulas graciles superiores 4–6 μm diametro et L/D 8–15, apicibus rotundatis. Filamenta adventitia absentia; rami adventitiis aliquando.


Type from Bridport, N Tasmania (Womersley & Parsons, 6.xi.1982); type sheet (female, male and tetrasporangial) in AD, A54559 (holotype tetrasporangial), isotype sheet in CHR, 392851.

Distribution: Hopetoun, W. Aust., to N Tasmania.


D. quadrispora is named from the whorls of 4 tetrasporangia in the stichidia; it is probably closely related to the West Australian D. elongata Sonder (1845, p. 53), with which D. fruticescens Harvey (1853a, p. 542) is closely related. They are similar in lack of rhizoids in the axes and stichidia with 4 (or 5) tetrasporangia, but D. elongata differs in having pseudolaterals which taper evenly to relatively short upper and subterminal cells (20–30 μm in diameter and L/D 1–2).

AD, A44188, from a sheltered water habitat, has pseudolaterals with slenderer lower cells than plants from greater water movement, but otherwise agrees with D. quadrispora.


FIGS 212, 213

Thallus (Fig. 212A) light to medium to dark red with the axes paler than the branch tips, mucilaginous, with one to a few pyramidal and much branched robust axes 10–30 (-50) cm
high, terminal pseudolateral tufts prominent. Main axes simple or branched, heavily corticated, (1-2) 2–3 mm in diameter, percurrent, branched at intervals of 0.4–1 cm, denuded below. Laterals 2–20 cm long, decreasing in length above, 1–2 mm in diameter, themselves similarly branched but slenderer, arising from the basal cell of the fourth order of branching of a young pseudolateral. Holdfast discoid, 5–20 mm across; usually epilithic. Structure. Apices sympodial, pericentral cells 5, becoming obscured (Figs 212B, 213B) in older laterals and axes by profuse rhizoidal development and enlargement of their cells. Pseudolaterals (Fig. 213A) one per segment, spirally arranged, 2–3 mm long, with (3-) 5–7 subdichotomies every 1 (-2) cells from the base, giving usually 40–50 ultimate simple branches 7–12 cells long, tapering from the basal cells (50-) 80–130 μm in diameter and L/D 0.7–1.5 to the ultimate cells 10–25 μm in diameter and L/D 15–30. Adventitious monosiphonous filaments absent. Rhodoplasts discoid to elongate.

Reproduction. Gametophytes dioecious. Procarps (Fig. 212C) 1–3 borne alternately on the lower segments of the pseudolaterals (which then become polysiphonous). Carposporophyte (Fig. 212C) with a basal fusion cell (Fig. 213D) and carposporangia in rows of 2–4, obovoid-clavate to subspherical. Cystocarps (Fig. 212C) sessile on lateral corticated axes, urceolate to elongate.

Thallass. (Fig. 214A) medium red, 4–10 cm high, adhering to paper on drying, much branched with one to a few slender axes with well developed laterals, with terminal and
Fig. 213. Dasya naccarioides (AD. A31510). A. Mature pseudolateral, filaments on right showing base only. B. Transverse section of an older branch. C. Sympodial axis with a procarp. D. Young fusion cell and early gonimoblast. E. Sporogamal branches. F. Transverse section of a sporogamal branch. G. Stichidia. H. Apex of a stichidium with developing tetrasporangia. I. Longitudinal section of a stichidium. (All as in Parsons 1975, courtesy of Aust. J. Bot.)
lateral pseudolateral tufts, denuded below. Axes and lateral branches terete, 200–400 \( \mu \text{m} \) in diameter, moderately corticated (Fig. 214B) on lower parts by rhizoids, commencing many segments from apices and forming a light cover on upper branches, complete cover below; segments L/D 1–3. Attachment rhizoidal; epilithic or on mussels. Structure. Pericentral cells 5, remaining clear in transverse section without rhizoids between them. Pseudolaterals (Fig. 214C) on every segment, 1–1.5 mm long, slender, branches patent with 2–4 basal subdichotomies (1-2) (-3) cells apart, tapering from an isodiametric basal cell, lower cells 45–60 \( \mu \text{m} \) in diameter and L/D 1.5–2.5 to unbranched ends 8–14 (-20) cells long, subapical cells (15-) 20–30 \( \mu \text{m} \) in diameter and L/D 2.5–3.5; occasional pseudolateral branches (A56314) with moniliform ovoid cells 90–115 \( \mu \text{m} \) in diameter. Lateral branches arising on lower cells of pseudolaterals. Rhodoplasts discoid to slightly elongate.

Reproduction. Gametophytes probably dioecious. Procarps unknown. Carposporophytes much branched, with a slight basal fusion cell and terminal rows of ovoid to subspherical carposporangia 20-30 \( \mu \text{m} \) in diameter. Cystocarps (Fig. 214C) sessile on lesser branches, ovoid, 0.5–1 mm across, with a distinct and slightly flared neck; pericarp 2(-3) cells thick, with 12–15 erect filaments, outer pericentral cells becoming irregular and largely ecorticate. Spermatangial branches unknown.

Type from Port Phillip Heads, Vic. (Wilson); lectotype Wilson 61, in Herb. Agardh, LD, 44311.

Distribution: Only known from Port Phillip, Victoria.

Selected specimens: Gellibrand Light, Port Phillip, Vic., 6–8 m deep (Kraft 5698, 9.vii.1975; MELU and AD, A56314). Middle Park (Hobson Bay), Port Phillip, Vic., drift (Sinkora A378, 14.iii.1970; AD, A55580). Swan I., Port Phillip, Vic., 0–0.5 m deep on barge (Womersley, 8.iv.1959: AD, A22599).

1. Agardh distinguished \( \text{Dasya} \) atactica on the occasional stichidia which continue apical growth as a branched filament. While such stichidia are distinctive they are not frequent, and are occasionally seen in other species (see below, and also \( \text{Dasya} \) crescens and \( \text{Dasya} \) cliftonii). The length of branch segments and cystocarps with rows of subspherical carposporangia distinguish \( \text{Dasya} \) atactica from \( \text{Dasya} \) crescens.

\( \text{Dasya} \) atactica has been collected by Kraft and his students from Gellibrand light in all months of the year (1975, 1976), with the largest plants from May to February.

The following collections show apically proliferous stichidia even more strikingly than \( \text{Dasya} \) atactica. The thalli are similar but slightly slenderer, the pseudolaterals taper to very slender ends with long cells, and the stichidia (of which A56312 has numerous apically proliferous stichidia) have only 4 sporangia per whorl rather than 5. The carposporangia are ovoid, occurring in rows. These appear to be a distinct species from \( \text{Dasya} \) atactica, but this awaits confirmation.


18. \( \text{Dasya} \) crescens Parsons & Womersley, sp. nov. 

\( \text{D. capillaris} \) Harvey sensu Kützing 1864: 26, pl. 73.

**FIG. 215**

Thallus (Fig. 215A) medium red to dark brown, soft and lax, 5–20 cm high with one to a few slender axes, much branched radially, above with slender tufts of pseudolaterals, denuded
Fig. 214. *Dasya atactica* (AD, A56314). A. Habit. B. Branch with moderate cortication and laterals with slight cortication. C. Pseudolateral filaments and a cystocarp. D. Pseudolaterals with stichidia. E. Stichidia showing tetrasporangia and cover cells.
below. Axes and main laterals terete, 300–1200 μm in diameter, moderately corticated on lower parts by rhizoids, commencing many segments from apices with filaments first lying between the pericentral cells (Fig. 215B) and forming a light cover on upper branches, below cover complete and cell rows often slightly spiral; segments L/D 1–4 (–6). Holdfast discoid, rhizoidal, 1–3 mm across; epithiotic or on shells. **Structure.** Pericentral cells 5, remaining clear in transverse section without rhizoids between them. Pseudolaterals (Fig. 215C) on every segment, 1–3 mm long, slender, fastigiate, with 3–5 (–8) basal subdichotomies 1–2 cells apart, tapering gradually from an isodiametric basal cell, lower cells 27–36 μm in diameter (with broad sheaths) and L/D 2–3.5 extending to L/D 6–8, then to unbranched cells 6–12 cells long, subapical cells 6–8 μm in diameter and L/D 4–8 (–10). Lateral branches arising on basal cell of pseudolaterals. Rhodoplasts discoid to elongate, often chained.

**Reproduction.** Gametophytes dioecious. Procarps on a pericentral cell several segments below apices, with a carpogonial branch and 2 sterile groups, with adjacent axial and pericentral cells becoming darkly staining (Fig. 215C). Carposporophytes much branched, with a slight basal fusion cell and terminal clavate to lacrimiform carposporangia 18–30 μm in diameter, replaced from cells below. Cystocarps sessile (Fig. 215C) and lateral on axes which continue growth, broad based and becoming ovoid, 300–900 μm across, with a slight to distinct neck; pericarp with 18–22 erect filaments, ecorticate apart from cells cut off basal outer pericentral cells. Sporangia subordinated to lateral branches (Fig. 215D) elongate, cylindrical and tapering near their apices, 200–800 μm long and 20–45 μm in diameter, with 10–20 axial cells each cutting off several initials in an inner layer which produce an outer layer of spermatangia.

**Type** from Port Sorell, N Tasmania, drift (Womersley, 9.xi.1982); holotype and 3 isotypes in AD, A56245; isotype in CHR, 399521.
Distribution: N Spencer Gulf, S. Aust., to Port Phillip, Vic., and N and E Tasmania.


D. crescens is named for the continued axial growth after fertilisation, leaving the cystocarps in a sessile, lateral position.

D. crescens occurs mainly in sheltered waters. It is characterised by the slight cortication on upper branches, lack of rhizoids between the pericentral cells, pseudolaterals from every segment, cystocarps with terminal clavate to lachrimiform carposporangia and largely ecorticate pericarp, long, slender, spermatangial branches, and 5 tetrasporangia per whorl with obloid cover cells. One stichidium in the type collection had an apical, branched, filament.

Harvey’s Alg. Aust. Exsicc. 206 l, as D. capillaris (Illustrated by Kützing 1864, pl. 73) is D. crescens; it differs from the type of D. capillaris in having pseudolaterals on each segment rather than every 2 segments as in the type.

19. Dasya tenuis Parsons & Womersley, sp. nov.

FIG. 216

Thallus (Fig. 216A) dark red-brown, 3–10 cm high, profusely subdichotomously branched throughout with dense, slender, tufted, even-topped, upper branches, becoming denuded on lower axes. Attachment by rhizoids; epiphytic (on Halophila?). Structure. Apices sympodial. Pericentral cells 5. Branches 45–90 μm in diameter and L/D 2–3 (–4) shortly below apices, increasing to 200–450 μm in diameter and L/D 2–4 in lower parts, corticate apart from few longitudinal cortical filaments on oldest parts. Pseudolaterals (1–) 2 axial cells apart (Fig. 216E), 2–4 mm long, with 4–5 basal subdichotomies 2 cells apart and unbranched ends 15–20 cells long; basal cell isodiametric, lower cells 25–60 μm in diameter and L/D 2–4, tapering gradually to upper cells 10–15 μm in diameter and L/D 2 (–) 5–15. Lateral branches probably arising on basal cell of pseudolaterals. Rhodoplasts discoid to elongate, becoming chained.

Reproduction. Gametophytes probably dioecious. Procarps with a carpogonial branch and probably 2 sterile groups, axial and sterile pericentral cells becoming darkly staining (Fig. 216B). Carposporophytes much branched with terminal clavate to lachrimiform carposporangia (Fig. 216C) 15–20 μm in diameter. Cystocarps ovoid, 350–550 μm in diameter, with only a slight neck; pericarp of 15–20 erect filaments, each cell cutting off 2 pericentral cells outwardly, ecorticate apart from cortical cells on the bearing branch at the base of the cystocarp. Spermatangial branches (Fig. 216D) borne on lower branches of pseudolaterals, with 1–2 pedicels, 300–700 μm long and 45–90 μm in diameter, cylindrical and tapering terminally, with axial cells cutting off 1–2 layers of cells and then surface spermatangia.

Tetrasporangial stichidia (Fig. 216E,F) borne on lower cells of pseudolaterals, with a 1–2-celled pedicel, 500–1500 μm long and 100–220 μm in diameter, lanceoid, with 10–20 fertile segments, 6 pericentral cells and tetrasporangia per segment (sometimes 5 in basal segment), tetrasporangia subspherical, 35–65 μm in diameter, each with 3 obloid cover cells L/D 2–2.5, palisade like, covering only part of each sporangium.

Fig. 216. *Dasya testis* (AD, A42417). A. Habit, part of holotype sheet. B. Young cystocarp. C. Mature cystocarp, with clavate carposporangia. D. Spermatangial branches. E. Stichidia on pseudolaterals 2 cells apart on an ecorticate branch. F. Stichidium showing 6 tetrarosporangia per segment and palisade-like cover cells.


Type from American R. inlet, Kangaroo L., S. Aust., 2–3 m deep in channel opposite Muston (Kraft, 7.iv.1972); holotype and isotype in AD, A42417; isotype in CHR, 316104.

Distribution: Only known from American R. inlet, Kangaroo L., S. Australia.


Dasya tenuiss is named for the slender branches of the thallus; it is known from only few specimens from a single locality, but appears to be distinctive in having branching mostly 2 axial cells apart, in being largely eorticate, in having terminal clavate carposporangia, and in having whorls of 6 tetrasporangia in the stichidia.


Thallus (Fig. 217A) medium red, soft and lax, 7–25 cm high, with one to several slender axes, much branched laterally to subdichotomously, bearing above slender tufts of pseudolaterals, denuded below. Main axes terete, 200–800 (+1000) μm in diameter, eorticated in their lower parts by rhizoids which develop 20–40 segments below the apices, lying at first between the pericentral cells and later covering the whole surface of the axis, with both large and small cortical cells in surface view; axes occasionally slightly spirally twisted. Lateral branches situated 2 or more segments apart, arising from the basal cell of the first branch of the pseudolateral, 1–4.5 cm long, lightly eorticated only near their bases. Holdfast discoid, 1–5 mm across; on solid substrates. Structure. Pericentral cells 5, large and prominent, lightly eorticated below with the segments visible through the cortex for most of the axes, remaining clear in section but with some eorticating cells almost as large. Pseudolaterals (Fig. 217B) usually on every second segment, 1–4 mm long, subdichotomously branched below every 1–3 cells with ultimate simple branches 8–12 cells long; basal cells L/D 1–1.5, lower cells (15-) 25–35 (+40) μm in diameter and L/D (2–) 3–6 (+13), tapering to slender upper branches 6–12 μm in diameter and L/D 7–20. Lateral axes arising on the basal cell of the pseudolaterals.

Reproductive. Gametophytes dioecious. Procarps borne spirally on polysiphonous axes. Carposporophytes with a slight basal fusion cell, carposporangia in rows, slightly ovoid, 15–55 μm in diameter. Cystocarps sessile on lightly eorticated polysiphonous axes, urceolate,
Fig. 217. *Dasya capillaris* (AD, A44458). A. Habit. B. Axis with slight cortication and lateral with pseudolaterals 2 segments apart. C. Ruptured cystocarp with carposporophyte and ovoid carposporangia on right. D. Spermatangial branches. E. Stichidium with 4 tetrasporangia per segment.
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600–900 μm in diameter with a prominent neck about one quarter the cystocarp diameter in length. Spermatangial branches (Fig. 217D) replacing the ultimate branches of the pseudolaterals, sessile or on a 1 (-2)-celled monosiphonous stalk, cylindrical, 230–400 (-500) μm long and 25–40 μm in diameter, with 5–20 fertile segments and a sterile apical filament up to 6 cells long.

Stichidia (Fig. 217E) replacing the ultimate branches of pseudolaterals, on a 1 (-2)-celled monosiphonous stalk or occasionally sessile, cylindrical, 260–500 μm long and 70–110 μm in diameter with 5–20 fertile segments each with 4 pericentral cells and sporangia, terminated by 1–3 apical cells. Tetrasporangia 30–65 μm in diameter, each with 2 (-3) cover cells which are higher than broad and cover less than half of the tetrasporangium plus part of the sporangium of the segment below.

Type from Georgetown, Tas. (Gunn); lectotype (here selected) Gunn 1307; in Herb. Hooker, BM.

Distribution: N Spencer Gulf and Kingscote, Kangaroo I., S. Aust., and N Tasmania. Probably more widespread but most records doubtful due to species confusion.


Two descriptions of this species were published in 1847. Harvey’s description in “Nereis Australis” is clearly the original, based on a specimen in TCD, and the Hooker & Harvey description in “Algae Tasmanicae” repeats the Nereis description (omitting two words) and refers to “Harv. Ner. Aust. p. 60, t.19”. This original illustration of Harvey shows clearly the pseudolaterals 2 segments apart and their slender nature. Some specimens if not most of Harvey’s Alg. Aust. Exsicc. 206 I (as D. capillaris), from Georgetown, Tasmania (illustrated by Kützing 1864, p. 26, pl. 73), have pseudolaterals from each segment and terminal clavate carposporangia. These are D. crescens; also some specimens of 206 I are D. hookeri.

Due to confusion with D. crescens and D. hookeri, and possibly other species, many records of D. capillaris must be considered doubtful. Well prepared slides of fertile material are necessary for sure determination of species.

21. Dasya hookeri Parsons & Womersley, sp. nov.

FIG. 218

Thallus (Fig. 218A) medium to dark red to grey-red, 5–30 cm high, profusely branched with several axes and main branches bearing lesser branches with slender lateral pseudolateral tufts, becoming denuded below. Attachment probably by tufts of rhizoids; epiphytic on Amphibolis, Posidonia, Sargassum and other algae. Structure. Apices sympodial. Pericentral cells 5, remaining clear in transverse section and without surrounding rhizoids. Lesser branches (50-) 100–300 μm in diameter with segments L/D 0.8–1.2, becoming corticate from 10–20 segments below apices, cortication complete below and 2–5 cells thick where axes are 500–1000 μm in diameter with segments L/D 0.5–1. Pseudolaterals mostly 2 axial cells apart (Fig. 218B), 1–2 mm long with 2–5 (-7) lower subdichotomies usually 2 cells apart, with adherent joint lower walls and unbranched ends 6–12 cells long; basal cell short, lower cells 35–90 (-110) μm in diameter and L/D 2–7, tapering markedly but evenly to upper cells 8–12 μm in diameter and L/D 6–15. Lateral branches arising from basal cells of pseudolateralss. Rhodoplasts discoid to elongate, becoming chained in larger cells.

Reproduction. Gametophytes dioecious. Procarps not observed. Young carposporophytes with cells at base darkly staining, carposporophytes much branched, with a basal fusion cell, carposporangia in rows, ovoid, 12–20 μm in diameter. Cystocarps (Fig. 218C,D) ovoid, 0.4–1.2 mm in diameter with a slight neck, sessile on short lateral branches with the pericarp often enclosing the continuing branch. Pericarp (Fig. 218D) with 12–14 erect filaments, the cells cutting off outwardly irregularly shaped cells and occasional smaller corticating cells.
Fig. 218. *Dasya hookeri* (A, C-E, AD, A37692; B, AD, A41133). A. Habit, holotype sheet. B. Branch with pseudolaterals 2 segments apart. C. Young cystocarp. D. Mature cystocarp showing pericarp cortical cells. E. Stichidium with 4 tetrasporangia per segment.
Spermatangial branches borne as branches of pseudolaterals, sessile, 90–140 µm long and 30–45 µm in diameter, with 1–3 sterile apical cells.

Tetrasporangial stichidia (Fig. 218E) borne on lower cells of pseudolaterals, sessile, lanceoloid, (100–) 200–500 µm long and (50–) 90–140 µm in diameter, with 5–12 fertile segments each with 4 tetrasporangia, subspherical and 25–35 µm in diameter and 2 ovoid to obloid cover cells.

**Thallus** 5–30 cm altus, profuse ramosus cum aliquot axibus et ramis principalibus portentibus ramos minores cum caespitibus gracilibus lateralisibus pseudolateralibus, infra deinuneudescens. Hapteron probabiliter per caespites rhizoideos; epiphyticum in Amphibolis, Posidonia, Sargassum et alteris algis. **Structure.** Apices sympodiales. Rami minores 100–300 µm diametro cum segmentis L/D 0.8–1.2, corticati ex 10–20 segmentis infra apices, omnino corticali infra et 2–5 cellulae crassi apud axes 500–1000 µm diametro cum segmentis L/D 0.5–1. Cellulae pericentrales 5, pellucidae in sectione transversa manentes et sine rhizoideis cingentibus. Pseudolaterales plerumque ab 2 cellulis axialibus seorsum, 1–2 mm longi cum 2–5 (-7) subdichotomis plerumque 2 cellulis seorsum, cum apicibus sine ramis 6–12 cellula longis; cellula basalis brevis, cellulae inferiores 35–90 (-110) µm diametro et L/D 2–7, contractantes valide sed aqualiter ad cellulas superiores 8–12 µm diametro et L/D 6–15. Rami laterales orientes e cellulis basaliis pseudolateralium.

**Reproductio.** Gametophyta dioecia. Procarpia non visa. Carpoborsprophyta inuenia cum cellulis basi fuscantibus, carpoborphyta valde ramosa, cum cellula fusionis basali, carpoborpsoragna seriatim, ovoidea 12–20 µm diametro. Cystocaripa ovoidea, 0.4–1.2 mm diametro diametro cum parvo collo, sessilia in ramis brevibus lateralisibus cum pericarpio ramum continuum saepe intercludente; pericarpium cum 12–14 filamentos erectis, cellulæ abscindentes extrinseceus cellulas irregulariter formatas et interdum cellulas minores corticantes. Rami spermatangiales in ramis pseudolateralium portati, sessiles, 90–140 µm longi et 30–45 µm diametro, cum 1–3 cellulæ sterilibus apicalibus. Stichidia tetrasporangialia in cellulæ inferioribus pseudolateralium portata, sessilia, lanceolida, (100–) 200–500 µm longa et (50–) 90–140 µm diametro, cum 5–12 segmentis fertilibus quodque cum 4 tetrasporangis, subsphericæ et 25–35 µm diametro et cum 2 cellulis ovoideis ad obloidis tegentibus.

**Type** from off West Beach (Adelaide), S. Aust., on Amphibolis, 6 m deep (Shepherd, 13.x.1970); holotype sheet (female, tetrasporangial) in AD, A37692.

**Distribution:** Hopetoun, W. Aust., to Western Port, Vic. and Flinders Is., Bass Strait, and N and E Tasmania.


*Dasya hookeri* is named after J.D. Hooker who contributed significantly to knowledge of Tasmanian algae. It is closest to *D. capillaris*, differing in having much coarser (basally) pseudolaterals. It occurs in relatively sheltered waters and has often been confused with *D. capillaris* (e.g. Harvey specimens from Georgetown, Tas., as *D. capillaris*, include *D. hookeri* as well as *D. crescens*).
The following names are not otherwise referred to in this account of the Dasyaceae.

*Dasya adunca* J. Agardh (1890a, p. 112) from King George Sound, W. Aust., lectotype LD, 44372, is *Thaumatella disticha* (Falkenberg) Kylin (1956, p. 511), now *Thaumatella adunca* (J. Agardh) Parsons & Womersley, comb. nov.

*Dasya archeri* Harvey (1859b, p. 304) from Tasmania (W. Archer), lectotype in Herb. Harvey, TCD, also referred to as *Heterosiphonia archeri* (Harvey) De Toni (1903, p. 1219) belongs to the *Dasyclonium incisum* complex.

*Dasya bolbochaete* Harvey (1844, p. 434) from Georgetown, Tas., holotype Gunn 1264 in Herb. Hooker, BM, is *Doxodasya bolbochaete* (Harvey) Falkenberg (1901, p. 538).

*Dasya dictyuroides* J. Agardh (1890a, p. 111, pl. 3 fig. 5), holotype from Western Port, Vic. (Wilson 66, 7.i.1885; LD, 44358) is *Wilsonaea dictyuroides* (J. Agardh) Schmitz (1893, p. 231). It is characterised by transversely divided pericentral cells, by lower adherent walls at the subdichotomies of the monosiphonous rhodoplastic filaments, stichidia with whorls of 4 tetrasporangia, but doubtfully by sympodial apices. Detailed study of its relationships is needed.


*Dasya harveyi* Kützing (1864, p. 26, pl. 71 e,f), based on Harvey, Alg. Aust. Exsicc. 216A as *D. lallemandii* Harvey, holotype in Herb. Sonder, MEL, 608855, is a later homonym of *D. harveyi* Ashmead ex Harvey (1858, p. 127, pl. 50A), which when used by Schmitz (1893, p. 223) as *Lophocladia harveyi* is regarded as a new name.


*Dasya proxima* Harvey (1855a, p. 542), from King George Sound, W. Aust., holotype in Herb. Harvey, TCD (Trav. Set 336) is probably a species of *Micropeuce*.

*Dasya sarcocaulon* Harvey (1863, pl. 278), from Freemantle, W. Aust., lectotype Clifton 82 in Herb. Harvey, TCD, is *Micropeuce sarcocaulon* (Harvey) Kylin (1956, p. 511).

*Dasya spyridoides* Falkenberg (1901, p. 626) is based on a specimen of Wilson called *Spyridia biannulata*; the type has not been located. Falkenberg’s description refers to one tetrasporangium per segment and the species is likely to be one of the Lophothalieae, probably a *Micropeuce*.

*Dasya tenera* Harvey (1855a, p. 543), from Freemantle, W. Aust., lectotype in Herb. Harvey, TCD, is *Sarcotrichia tenera* (Harvey) Womersley & Shepley (1959, p. 209).


*Dasya verticillata* Harvey (1844, p. 434), from Georgetown, Tas., holotype Gunn 1306 in Herb, Harvey, TCD, is *Lophothalia verticillata* (Harvey) Kützing (1849, p. 797).
Genus HETEROSIPHONIA Montagne 1842: 4, nom. cons.

Thallus erect from a discoid holdfast or prostrate axes. Axes sympodially developed and alternately distichously branched, terete or occasionally compressed, ecorticate or corticated by compact rhizoidal filaments, with pseudolaterals and lateral branches arising 2–9 segments apart. Structure. Axes with 4 or 7–13 pericentral cells cut off in alternating sequence. Pseudolaterals monosiphonous or becoming basally polysiphonous, persistent, subdichotomous once to several times, with adherent lower walls at the subdichotomies; adventitious monosiphonous filaments may arise from cortical cells.

Reproduction. Gametophytes dioecious. Procarps occur on segments subtending the subdichotomies of the pseudolaterals, with a supporting cell bearing a 4-celled carpogonial branch and 2 groups of sterile cells, the supporting cell being the fifth and last formed pericentral cell of the fertile segment; the sterile pericentral cells divide before fertilization to form the pericarp initials. Post-fertilization, fusion between the carpogonium and auxiliary cell occurs via a connecting cell, and the fusion cell involves the auxiliary cell, residual supporting cell, adjacent pericentral cells and lower gonimoblast cells. Carposporangia occur in rows or terminally on the much branched gonimoblast. Cystocarps have an urceolate pericarp, with or without a prominent neck. Spermatangial branches occur as branches of the pseudolaterals, elongate lanceoid, with 4 or 5 pericentral cells cut off in alternating sequence, dividing to form an outer surface layer of spermatangia.

Tetrasporangial stichidia occur as branches of the pseudolaterals, sessile or with monosiphonous or polysiphonous stalks, with 4–9 pericentral cells formed in alternating sequence, dividing to produce 2 pre-sporangial cover cells and then a tetrasporangium; the cover cells divide once horizontally and cover the mature sporangium with 4–9 sporangia in each segment.

Type species: H. berkeleyi Montagne 1842: 4.

A genus of numerous species, widely distributed. Heterosiphonia differs from Dasya in having thalli always bilaterally (distichously) branched, 4 or 7–13 pericentral cells per segment, pseudolaterals borne 2 or more axial segments apart, pre-fertilization pericarp initials, and stichidia with whorls of 4–9 tetrasporangia and 2 pre-sporangial cover cells, each dividing transversely and covering the sporangium.

Certain species of Dasya show some of the above features, as discussed above.

As well as the southern Australian species described below, H. multiceps (Harvey) Falkenberg (1901, p. 654) occurs on the western coast of Australia.

KEY TO SPECIES OF HETEROSIPHONIA

1. Thallus ecorticate throughout ................................................................. 2
   1. Thallus corticate at least in the basal portions ............................................. 5

2. Internodes of (2-) 4–7 segments between pseudolaterals; pseudolaterals polysiphonous except at branch ends ............................... 1. H. microcladioides
   2. Internodes of 2 (-3) segments between the pseudolaterals; pseudolaterals monosiphonous except for basal polysiphonous segments ........................................... 3

3. Thallus with 4 pericentral cells ............................................................. 2. H. callithamnium
   3. Thallus with 7–11 pericentral cells .......................................................... 4

4. Thallus small, to 3 cm in length; axes 150–250 μm in diameter; 7–8 pericentral cells; epiphytic or epilithic ........................................... 3. H. australis
   4. Thallus larger, to 12 cm in length, axes (200-) 300–700 μm in diameter; 8–11 pericentral cells; usually epiphytic ........................................... 4. H. wrangelioieces

5. Pseudolaterals separated by 2 (-3) segments; basal corticated axes with short anticlinal filaments ............................................................ 6
5. Pseudolaterals separated by (3-) 4–7 segments; basal corticated axes without anticlinal filaments ................................................................. 7

6. Main axis of feather-like fronds corticate to apex; heavily corticated basal portion of axis with copious adventitious monosiphonous filaments ........ 5. H. muelleri
6. Main axis of feather-like fronds ecorlicate, arising from a corticate basal portion of the axis which has a light covering of adventitious filaments . 6. H. crassipes

7. Ultimate branches of pseudolaterals monosiphonous, subulate, more than 85 μm in diameter; (12-) 13 pericentral cells ........................................................... 7.
7. Ultimate branches of pseudolaterals monosiphonous, usually tapering to a fine filament, occasionally subulate, less than 85μm in diameter; 8–12 pericentral cells ............ 8

8. Pseudolaterals consisting of ecoricate polysiphonous and monosiphonous filaments borne on a corticate sympodial axis; no thickened perennating basal axis, older axes in transverse section showing large and conspicuous pericentral cells around the axial cell ................................................................. 8. H. gunniana
8. Pseudolaterals consisting of corticate polysiphonous segments and ecoricate monosiphonous filaments; polysiphonous segments completely corticated in older plants which also have a thick perennating basal axis; older axes in transverse section with a large axial cell and pericentral cells inconspicuous in the rhizoidal cortex ......................................................................................... 9. H. lawrenciana

   *Dasya microcladioides* J. Agardh 1890a: 83.
   *Dasyclada pellucida* sensu Harvey 1855a: 543; 1859b: 304; 1863, synop. xxiv. Sonder 1881: 36. (NON Harvey 1847: 67, pl. 27 lower left.)

**FIG. 219**

*Thallus* (Fig. 219A) medium to dark red-brown, tufted, 2–6 cm high, with several erect axes, ecoricate, more or less complanately branched, arising from prostrate axes. Attachment by rhizoids; epizooic or epiphytic on seagrass or algae. *Structure.* Apices of axes and lateral branches sympodial and distichous (Fig. 219B), developing 7–8 pericentral cells beginning 5–10 cells below the apices, mature segments 150–350 μm in diameter and L/D 0.4–1.2 (-2). Pseudolaterals (2-) 4–7 segments apart (Fig. 219B), 1.5–3 mm long, becoming polysiphonous below but with simple (occasionally branched) terminal filaments of 6–12 (-20) cells, lower segments 100–130 μm in diameter and L/D 0.5–0.8, tapering markedly to subapical cells 35–90 μm in diameter and L/D 0.5–1. Pseudolaterals with adaxial and distichous branches, usually with a secondary sympodial axis arising adaxially on the fourth (occasionally third) segment from their base, and with the primary branch of the pseudolateral extending in length and becoming hamate, cells 100–140 μm across and L/D 0.5–1. Attachment rhizoids arising from cells of pseudolaterals, with multicellular haptera. Rhodoplasts discoid, in chains in larger cells.

*Reproduction.* Gametophytes unknown, apart from Falkenberg’s (1901, p. 638) description of procarps as arising on the third segment below the fourth segment bearing the secondary lateral symposium.

Tetrasporangial stichidia (Fig. 219C–E) developing from a polysiphonous branch of the pseudolaterals, (350-) 500–1500 μm long and 100–180 μm in diameter, lanceoideal with a short polysiphonous pedicel and short blunt apex, occasionally continuing growth with a simple or branched filament (Fig. 219E); tetrasporangia 5 per segment, each with 2 pre-sporangial cover cells which divide horizontally giving 4 squat cells covering each sporangium.

**Lectotype** from Port Phillip Heads, Vic. (Wilson, 4,ii.1889); in Herb. Agardh, LD, 43617.

**Distribution:** King George Sound, W. Aust., to Gabo I., Vic., and around Tasmania.
Fig. 219. *Heterosiphonia micrneladioides* (A, AD, A32793; B, AD, A22600; C, D, AD, A43355; E, AD, A35264). A. Habit. B. Axis with polysiphonous pseudolaterals 3-5 segments apart. C. Branch with stichidia. D. A stichidium. E. Stichidium with branched apical filament.
Selected specimens: King George Sound, W. Aust. (Harvey, Trav. Set 308, as Dasya pellucida, in TCD).


Polyposis callithamnium Sonder 1845: 54; 1848: 180. Harvey 1847: 45.
Europogonium callithamnium (Sonder) Kützing 1849: 799.
Baillouiana callithamnium (Sonder) Kuntze 1891: 885.

FIG. 220

Thallus (Fig. 220A) medium to dark red-brown to grey-red, 1–3 cm high, with several, dense, erect axes from prostrate axes, erect axes with few lateral branches, bearing pseudolaterals dichotomously arranged (Fig. 220B) but branched largely in transverse planes. Attachment by rhizoids; epiphytic on Amphibolis, Sargassum, Haliptilon and other algae.

Structure. Apices of axes sympodially and distichously branched, developing 4 pericentral cells beginning 8–15 cells below apical cells, mature axial segments 130–180 µm in diameter and L/D 0.8–1.4. Pseudolaterals (Fig. 220B) 2 axial segments apart, 1–1.5 mm long, the basal 2 segments only becoming polysiphonous, the rest monosiphonous and branched 4–5 times mostly 2 cells apart at wide angles (usually >90°), lower monosiphonous cells 60–80 µm in diameter and L/D 0.8–1.4 (–2), tapering gradually to upper cells 25–40 µm in diameter and L/D 1–1.5, then to acute to mucronate terminal cells. Lateral branches probably arising on lower segments of pseudolaterals. Attachment rhizoids arising from lower cells of pseudolaterals, several cells long with multicellular haptera. Rhodoplasts disoid.

Reproduction. Gametophytes dioecious. Procarps unknown. Cystocarps (Fig. 220C) sessile on a polysiphonous branch, ovoid with a short neck, 350–700 µm in diameter; pericarp with erect filaments, each cell producing 3 pericentral cells which divide to form a layer of irregularly shaped cells; carposporophyte much branched, with a basal fusion cell and terminal rows of ovoid carposporangia 20–40 µm in diameter. Spermatangial branches (Fig. 220D) as ultimate branches of pseudolaterals, cylindrical, 100–250 µm long and 40–55 µm in diameter, with a 1–2-celled pedicel and 3–5-celled sterile tip. Tetrasporangial stichidia (Fig. 220E) 100–700 µm long and 100–150 µm in diameter, becoming fertile when very short, occurring as branches of pseudolaterals with a 2–3-celled pedicel and short sterile tip, with 4 tetrasporangia per segment each with 1 (–) 2 pre-sporangial cover cells each divided transversely; tetrasporangia 40–50 µm in diameter.

Type from W. Aust., on Haliptilon (Preiss); lectotype in HBG (plant second from left on type sheet); isolecotype in MEL, 1005969.

Distribution: Champion Bay, W. Aust., to Kangaroo L., S. Australia.


Fig. 220. *Heterosiphonia callithamnium* (A, AD, A37658; B, E, AD, A33362; C, D, AD, A33378). A. Habit. B. Axis with ecoricate pseudolaterals 2 segments apart. C. Cystocarp, sectional view. D. Spermatangial branches. E. Stichidia.


**FIGS 221, 222A-F**

Thallus (Fig. 221 A) dark red, tufted, with polysiphonous, corticate, erect axes 2–3 cm high and 150–250 µm in diameter, arising from prostrate axes. Attachment by rhizoids; epilithic or epiphytic. Structure. Apices of axes (Fig. 222A) sympodial and distichous, developing 7–8 pericentral cells beginning 6–8 segments below apical cells, cut off in alternating sequence. Pseudolaterals 2 segments apart, each with 1–3 subdichotomies (Fig. 222B), 300–1000 µm long, cells (15–) 20–65 µm in diameter and LID 0.8–1.5 (–2), tapering near the apices; basal segments may form 4–6 pericentral cells. Rhizoids developed from cells of pseudolaterals. Lateral sympodial axes arise from the basal cell of pseudolaterals. Rhodoplasts discoid in small cells, becoming chained in larger cells.

**Reproduction.** Gametophytes dioecious. Procarps (Fig. 222C) formed on lower cells of the pseudolaterals which develop 5 pericentral cells in alternating sequence, the last formed facing the axis and developing a carpogonial branch and 2 sterile groups which divide to form the pericarp initials. Post-fertilization, the auxiliary cell, central cell of the fertile segment, lower gonimoblast cells and adjacent pericentral cells contribute to the fusion cell, with the upper much branched gonimoblast bearing ultimate rows of ovoid carposporangia 20–35 µm in diameter. Cystocarps (Fig. 221B) small, urceolate, 400–600 µm in diameter, usually developing a slightly flared neck 0.5–0.8 as long as the base, sessile or shortly pedicellate; pericarp 2–3 cells thick, with slight cortical on the outer pericentral cells. Spermatangial branches (Fig. 221C, D) occurring on pseudolaterals, with a monosiphonous (rarely polysiphonous) stalk and terminated by a row of 4–6 sterile cells, 150–400 µm in diameter, occasionally involving branches of pseudolaterals (Fig. 221D); axial cells with 4 pericentral cells producing initials which bear an outer layer of spermatangia.

Tetrasporangial stichidia (Fig. 222D) occur on cells of the pseudolaterals, sessile, basally polysiphonous, cylindrical to lanceoid and apically tapering with simple or branched apical filaments, 400–800 µm long and 120–175 µm in diameter with 15–25 fertile segments; each segment with 5 pericentral cells (Fig. 222E) formed alternately, each cell cutting off 2 pre-sporangial cover cells which divide transversely to form 4 cells covering each sporangium, and a tetrasporangium usually from each pericentral stalk cell, 35–65 (–70) µm in diameter.

**Type** from Port Jackson, N.S.W. (*Harvey, Alg. Aust. Exsicc. 211L, as Dasya subsecunda* Suhr?); holotype in Herb. Agardh, LO, 43630.

**Distribution:** Hopetoun, W. Aust., to Coffs Harbour, N.S.W. (Millar 1990, p. 436) and E Tasmania.


Baillouviana wrangelioideae (Harvey)Kuntze 1891: 885.

Dasya guichensis Reinbold 1897: 57.


**FIGS 222F-J, 223**

*Thallus* (Fig. 223A) medium to dark red, with numerous erect ecorticate axes (Fig. 223B) 6–12 cm high and (200–)300–700 μm in diameter, arising from prostrate axes. Attachment by rhizoids from prostrate axes: epiphytic usually on *Amphibolis* (and coralline algae?). *Structure*. Apices of axes sympodial and alternately distichous, developing 8–9(-11) pericentral cells (Fig. 222F) beginning 10–12 segments from the apex, cut off in alternating sequence. Pseudolaterals 2 segments apart (Fig. 223B), 0.7–1.5 (-2) mm long, each with 3–5 subdichotomies (Fig. 222G), cells 40–75 μm in diameter and L/D 0.8–2, tapering slightly to the last 2–3 cells of the acute apices, branches divergent, basal segments becoming polysiphonous. Rhizoids developed on modified pseudolaterals on prostrate axes. Rhodoplasts discoid, elongate or chained in larger cells.

*Reproduction*. Gametophytes dioecious. Procarps (Fig. 222H) formed on lower cells of pseudolaterals which develop 5 pericentral cells, the fifth bearing a carpogonial branch and 2
sterile groups, with pericentral cells forming 7–10 pericarp initials. Post-fertilization (with a connecting cell), the auxiliary cell, central cell, sterile pericentral cells and lower gonimoblast cells contribute to the fusion cell, with the much branched gonimoblast bearing rows of ovoid carposporangia 16–35 μm in diameter. Cystocarps (Fig. 223C) urceolate, 0.7–1.2 mm in basal diameter, with a tapering to flared neck of similar length, borne on a short polysiphonous stalk. Spermatangial branches (Figs 222 I, 223D) occur on lower cells of the pseudolaterals, with a basal cell and terminal simple or branched row of 6–8 sterile cells, cylindrical, (100–) 150–300 (=400) μm long and 60–80 μm in diameter; axial cells with 4 pericentral cells, dividing to form several initials each producing 4–5 spermatangia in the outer layer.

Tetrasporangial stichidia (Figs 222 J, 223E) occur on lower cells of the pseudolaterals, sessile and usually on polysiphonous stalks, lanceoid, 400–700 μm long and 160–200 (240) μm in diameter, with 10–20 fertile segments; each segment with 5–6 pericentral cells, all usually producing tetrasporangia 35–55 μm in diameter, each with 2 divided cover cells covering the sporangia.

Type from Fremantle, W. Aust. (Harvey); lectotype Harvey, Alg. Aust. Exciss. 207A, in Herb. Harvey, TCD.

Distribution: Fremantle and Rottnest I., W. Aust., to Walkerville, Vic., and N Tasmania.


H. wrangelioides is mainly epiphytic on Amphibolis (usually A. antarctica).


FIGS 224, 225

Thallus (Fig. 224A, B) medium to dark red, erect, with one to several main axes 5–25 cm high, heavily corticated below and 3–4 mm in diameter, bearing alternately distichous lateral branches at intervals of 1–2 mm, in turn bearing alternately distichous, tufted, pseudolaterals; lower axes (probably perennial) clothed with monosiphonous, mostly unbranched, adventitious filaments (Fig. 224C). Holdfast flat to conical, rhizoidal, 2–7 cm across; epilithic or rarely epiphytic. Structure. Apices of axes and branches sympodial and distichous, developing 7–8 pericentral cells in alternating sequence, commencing 16–18 segments from the apex. Pseudolaterals 2–3 (5) segments apart, (1–) 1.5–2.5 mm long, each with 3–5 lower subdichotomies (1–) 2–3 cells apart and upper unbranched ends 10–15 cells long; the basal 3–4 segments usually become polysiphonous, with 4–8 pericentral cells; lower cells of
Heterosiphonia pseudolaterals 70–110 μm in diameter and L/D 1–1.5, tapering gradually, upper cells 20–35 μm in diameter and L/D 1.5–2.5. Cortication commences early by small cells cut off the lower end of pericentral cells, developing rhizoidal filaments which rapidly develop a thick cortex, the cells becoming of similar size to the pericentral cells which become indistinct. Adventitious filaments 1–2 mm and 12–25 cells long, curved upwards, tapering apically and basally, some cells slightly swollen, 70–110 μm in diameter and L/D 1–1.4. Lateral branches develop from lower cells of the pseudolaterals.

Reproduction. Gametophytes dioecious. Procarps (Fig. 225A) develop usually on the third subdichotomy of pseudolaterals, with the fifth pericentral cell bearing a carposporial branch and 2 groups of sterile cells, with up to 10 and 8 cells in each group. Post-fertilization, a fusion cell occurs with an upper much branched gonimoblast bearing terminal lachrymiform to clavate carposporangia 18–25 μm in diameter. Cystocarps (Figs 224D, 225B) prominent, ovoid to subspherical, 1–2 mm in diameter, with little or no neck, borne on short polysiphonous laterals; pericarp with the erect filament cells cutting off 1–3 outer pericentral cells which form a 2–4 layered cortex of small cells. Spermatangial branches (Figs 224E, 225C) developed as branches of pseudolaterals, with a monosiphonous stalk 4–6 cells long and terminal filament

of up to 10 cells, 100–300 μm long and 35–50 μm in diameter, with 10–15 fertile segments each with 4 pericentral cells (Fig. 225D) producing a layer of initials each forming 3–4 outer spermatangia.

Tetrasporangial stichidia (Figs 224F, 225E) occur as pseudolateral branches, usually with a polysiphonous stalk and a short terminal filament 1–6 cells long, lanceoid, 150–1500 μm long and 80–120 (230) μm in diameter, with 20–35 fertile segments each with 6 pericentral (Fig. 225F) cells and ovoid tetrasporangia 40–55 μm in diameter, and 2 (subdivided) cover cells.

**Type** from Port Phillip, Vic. (Mueller, 1.xi.1852); lectotype Herb. Sonder, MEL, 1006526.

**Distribution:** Lancelin, W. Aust., to Walkerville, Vic., and N Tasmania.

N Indian Ocean.


_H. muelleri_ is one of the commonest species of _Heterosiphonia_ on southern Australian coasts, from shallow water on rough-water coasts to deeper water on calmer coasts where current flow occurs. It has been recorded from India, Indonesia and Sri Lanka (see Silva et al. 1996, p. 443), but Parsons (1975, p. 627) questioned these records.


_Baillouvialba crassipes_ (Harvey) Kuntze 1891: 885.

**FIG. 226**

_Thallus_ (Fig. 226A) medium red-brown to grey-red, erect, with one to numerous axes 300–800 μm in diameter below with few lateral branches but densely clothed above with slender, plumose, pseudolaterals, lower pseudolaterals coarse and terminally acute; base of axes becoming heavily corticated and with outer anticlinal filaments 200–500 μm long. Holdfast becoming massive, rhizoidal, 2–30 mm across; epitheca. Structure. Apices of axes sympodial and distichous, developing 10–11 pericentral cells (Fig. 226B) commencing several cells below apical cells. Pseudolaterals (Fig. 226D) 2 segments apart, of 2 differing forms; upper pseudolaterals 3–5 mm long, each with 4–5 lower dichotomies 2–4 cells apart and with upper unbranched monosiphonous ends 12–18 cells long, cells tapering (Fig. 226D, E) from 60–80 μm to 15–20 μm in diameter and L/D 2–3 to 6–8; the basal dichotomous segments become monosiphonous and 100–200 μm in diameter, L/D 0.5–1; lower pseudolaterals (Fig. 226D, E) 2–3 mm long, with basal segments 300–500 μm in diameter and L/D 0.4–0.7, monosiphonous upper branches 100–200 μm in diameter, cells L/D 0.8–1, tapering over the last 3–5 cells to an acute apex. Cortication of lower axes by cells cut off the pericentral cells,
Heterosiphonia with rhizoidal filaments developing a pseudoparenchymatous cortex 5–8 cells thick, with outer anticlinal filaments (Fig. 226B) 250–400 μm and 8–15 cells long, cells 35–45 μm in diameter and L/D 0.7–1. Rhodoplasts discoid.

Reproduction. Gametophytes unknown.

Tetrasporangial stichidia occur as terminal branches of pseudolaterals, with a polysiphonous stalk and short blunt apex, lanceoid to cylindrical, 180–600 μm long and 120–

Fig. 226. Heterosiphonia crassipes (A, B, D, E, AD, A34148; C, AD, A32940). A. Habit. B. Transverse sections of young and old axes. C. Pseudolaterals with gradually tapering branches. D. Axis with coarse pseudolaterals. E. A coarse pseudolateral with basal polysiphonous segments and terminal mucronate cells.
180 μm in diameter, segments with several tetrasporangia 30–40 μm in diameter and 2 cover cells, each dividing horizontally.

**Type** from Rottnest I., W. Aust., on jetty reef (Harvey); lectotype in Herb. Harvey, TCD (Alg. Aust. Exsic. 213A), Trav. Set 189 not located.


*H. crassipes* was recorded from Coffs Harbour and Sydney Harbour, N.S.W., and from Lord Howe I., by Millar (1990, p. 437) and may be more widespread around northern Australia than records indicate. It apparently occurs from shallow to deep water. Further study is needed to clarify the change from stout, abruptly terminally tapering, lower pseudolaterals to upper slender and gradually tapering ones (both types occuring on single plants), and also to discover gametophytes. The only tetrasporangial specimen seen is the lectotype.

*H. multiceps* (Harvey) Falkenberg (1901, p. 654), also from Rottnest I., is closely related to *H. crassipes*, having largely ecorctic axes with 10–11 pericentral cells and a corticate base; it differs in having a few cortical cells cut off over the nodes of the axial segments. Further studies on Rottnest I. material are needed to clarify the species.


**FIG. 227**

**Thallus** (Fig. 227A) dark red-brown, erect, 10–30 cm high, with a single axis bearing long lateral branches 2–3 (–4) mm in diameter, heavily corticated and denuded over lower half or more (probably perennial with annual re-growth). Branches bearing relatively slender laterals 2–5 cm long, with distichous pseudolaterals. Holdfast discoid, 2–10 cm across; epithectic. **Structure.** Apices of axes sympodial and distichous, developing (12-) 13 pericentral cells (Fig. 227B) commencing shortly below the apical cell. Pseudolaterals 4–5 segments apart, 2–3 mm long, each with subdichotomous, more or less distichous, coarse branches (2-) 3–4 segments apart, becoming polysiphonous (5–8 pericentral cells) but with monosiphonous terminal branches, cells tapering abruptly to an acute end cell (Fig. 227C, D, right), some pseudolaterals developing markedly slender terminal tufts (Fig. 227C, E, left); monosiphonous branches 90–120 μm in diameter, cells L/D 0.7–1.2, but the slender filaments basally 35–45 μm in diameter, cells L/D 1.5–2, tapering gradually to upper cells 10–12 μm in diameter and L/D 4–7. Cortication commencing on polysiphonous lower segments of pseudolaterals from small cells cut off pericentral cells, developing rapidly and on axes and lateral branches forming a pseudoparenchymatous cortex 0.7–1.5 mm and many cells thick, with smaller cells between the prominent axial cell and the ring of pericentral cells; outer cortex without anticlinal filaments. Rhodoplasts discoid to elongate or in chains in axial cells.

**Reproduction.** Gametophytes dioecious. Procarps unknown. Cystocarps (Fig. 227C) large and prominent, ovoid, 1.5–2.5 mm in diameter, with a slight neck, sessile on polysiphonous branches; pericarp dense, with an outer layer of irregular cells; carposporophytes much branched, with a basal fusion cell and rows of ovoid carposporangia, 20–45 μm in diameter. Spermatangial branches (Fig. 227D) developed as terminal branches of the slender monosiphonous tufts, 90–120 μm long and 30–40 μm in diameter.

Tetrasporangial stichidia (Fig. 227E, F) situated on lower polysiphonous branches of coarse pseudolaterals, lanceoid to cylindrical, 400–1400 μm long and 200–280 μm in diameter, with 6 sporangia per whorl, each with 2 pre-sporangial cover cells (Fig. 227F) divided horizontally, largely covering the sporangia; tetrasporangia 60–90 μm in diameter.
**Heterosiphonia**

Type from S. Australia (*Curdie*); holotype in Herb. Agardh, LD, 43802.

**Distribution**: Eyre, W. Aust., to Nora Creina, S. Australia.


_H. curdieana_ is a distinctive species, in size and in the heavily corticated, bare, axes and lower branches (probably perennial) bearing tufts of small branches and coarse pseudolaterals. It is probably a deep-water species.

There are 2 Curdiea species in Herb. Harvey, TCD, bearing Harvey’s name, and one in LD, from which J. Agardh described the species.


**Polysiphonia gunniana** Harvey 1844: 437.


**Eupogonium gunnianum** (Harvey)Kützing 1849: 798.

**FIGS 228, 229**

**Thallus** (Fig. 228A) medium to dark red-brown, erect, with one to several main axes 10–20 (-30) cm high and strongly developed lateral branches, denuded below, axes 1–1.5 (2) mm in diameter where heavily corticated, lateral branches alternately distichous, mostly 2–10 (-50) mm apart, usually with further similar branching. Lesser branches terminating in flabellate tufts (Figs 228F, 229A, B) of rhodoplastic, ecorticate, basally polysiphonous but mostly monosiphonous, filaments to 4 mm long. Holdfast discoid, 2–15 mm across; epilithic.

**Structure.** Apices of axes sympodial and distichous, developing 8–10 (-12) pericentral cells (Figs 228B, 229C), commencing 10–16 segments below the apical cell, produced in alternating sequence. Pseudolaterals (2-) 3–5 (-7) segments apart, each with several slender subdichotomous, tapering, upper monosiphonous filaments (Fig. 229B), lower cells 30–70 μm in diameter and L/D 1.3–3, tapering gently to upper cells 6–12 μm in diameter and L/D 8–15; the basal 5–7 segments becoming polysiphonous with 4–9 pericentral cells; segments 100–175 μm in diameter and L/D 0.8–2 (longer in deep water plants). Cortication commences well below the apices, by small cells cut off from the base of pericentral cells, developing into descending rhizoids which form a cortex 4–8 cells thick, outer cortical cells 12–25 μm in diameter, with contorted rhizoids (Fig. 228C). Lateral branches develop from lower cells of pseudolaterals. Rhodoplasts discoid, in chains in larger cells.

**Reproduction.** Gametophytes dioecious. Procarps (Fig. 229D, E) develop on lower segments of the pseudolaterals subtending a subdichotomy, which develop 5 pericentral cells, the fifth formed bearing a carpogonial branch and 2 sterile groups which divide to form a number of pericarp initials. Post-fertilization, the auxiliary cell, residual supporting cell, axial cell and lower gonimoblast cells form a fusion cell (Fig. 229G) below the much branched gonimoblast with terminal or short rows of ovoid carposporangia 45–65 μm in diameter, with later carposporangia developing from below. Cystocarps (Figs 228D, 229F) large, ovoid to subspherical, 1–1.5 mm in diameter, with little or no neck, on polysiphonous branches, often with remains of monosiphonous filaments protruding through the pericarp which is corticated with 3–4 layers of cells. Sporangial branches (Figs 228E, 229H) occur as branches of the
Fig. 228. *Heterosiphonia gunniana* (A, AD, A60832; B-F, AD, A31893). A. Habit. B. Transverse section of young axis. C. Transverse section of old axis. D. Cystocarp. E. Spermatangial branches. F. Branch with pseudolaterals and stichidia.
**Heterosiphonia**

DASYACEAE

Pseudolaterals, cylindrical with a short monosiphonous stalk and a terminal filament 6–12 cells long, 150–300 μm long and 30–50 μm in diameter, the axial cells with 5 pericentral cells (Fig. 229 I) which divide to form initials each producing 4–5 spermatangia. Tetrasporangial stichidia (Figs 228F, 229J) occur on basal polysiphonous segments of the pseudolaterals, cylindrical to lanceoid, 500–1500 μm long and 250–400 μm in diameter, terminated by a monosiphonous filament 4–8 cells long, with 14–25 fertile segments; each segment with 6 or 7 pericentral cells (Fig. 229K), all producing subspherical to slightly ovoid tetrasporangia 100–150 μm in diameter, decussately divided, each covered by the 4 cover cells.

**Type** from Georgetown, Tas. (Gunn); lectotype Gunn 1265 in Herb. Harvey, TCD.

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


**H. gunniana** is a common species, from shallow to deep water, often prolific in pools and on reef edges under rough-water conditions. It is closely related to **H. lawrenciana** (see below) but has cortication commencing well below the apices so that most upper parts are clearly polysiphonous, and differs in transverse section appearance.


**Dasya gunniana** f. lawrenciana (Harvey) Agardh 1863: 1201.

**FIG. 230**

**Thallus** (Fig. 230A) medium to dark red-brown, erect with one to a few main axes, 10–40 cm high, axes becoming 2–3 mm in diameter for 5–30 cm (probably perennial) and denuded apart from regrowth, lesser branches alternately distichous, mostly 2–5 mm apart, terminating in flabellate tufts of rhodoplast filamentous, with the polysiphonous segments soon becoming corticated and obscured. Holdfast discoid to conical, 2–10 mm across; epilithic. Structure. Apices of axes sympodial and distichous, developing 8–9 (10) pericentral cells (Fig. 230B). Pseudolaterals (2)–3–5 segments apart, each with 2–4 lower subdichotomies 2–4 cells apart, the lower several segments becoming polysiphonous and with upper monosiphonous filaments (Fig. 230D), lower cells 35–65 μm in diameter and L/D 0.5–1.3, tapering gradually to upper cells 15–30 μm in diameter and L/D 2–3.5. Cortication commences by cells cut off the pericentral cells and soon becomes complete, with the central axial cell and the pericentral cells obscured (Fig. 230D). Rhodoplasts discoid.

**Reproduction.** Gametophytes dioecious or monocious. Procarps on lower segments of pseudolaterals, becoming polysiphonous, with a pericarp developed pre-fertilization (Fig.
Thuretia

DASYACEAE

230D), adjacent pseudolaterals usually slenderer than normal pseudolaterals. Cystocarps (Fig. 230E) large, ovoid, 1–1.5 mm in diameter, with little or no neck, on polysiphonous corticated branches; gonimoblast much branched, with a basal fusion cell and ovoid carposporangia 40–50 μm in diameter; pericarp with a cortex 2–3 cells thick. Spermatangial branches (Fig. 230F) as terminal branches of pseudolaterals, lanceoloid to cylindrical with short monosiphonous pedicels and terminal filaments, 90–400 μm long and 35–45 μm in diameter.

Tetrasporangial stichidia (Fig. 230G) as ultimate branches of pseudolaterals, with a polysiphonous (becoming corticated) base and blunt apex, cylindrical, 500–1000 μm long and 200–300 μm in diameter, with 6 pericentral cells and tetrasporangia per whorl with 2 cover cells divided horizontally and somewhat irregular; sporangia 60–90 μm in diameter.

Type from Georgetown, Tas.; lectotype Gunn 1268, in BM.

Distribution: Cottesloe, W. Aust., to Port Phillip Heads, Vic., and N Tasmania.


H. lawrenciana is closely related to H. gunniana, especially in reproductive organs, as was discussed by Parsons (1975, pp. 618, 625). H. lawrenciana is characterised by cortication of the polysiphonous segments starting early, so that only few polysiphonous segments are visible near the apices; this early cortication also occurs on the stalks of the stichidia. The basal parts of the axes become heavily corticated, and transverse sections show a large central cell but the pericentral cells are inconspicuous amongst the similar-sized rhizoidal corticating cells. This basal thickened part is probably perennial, many specimens showing slender regrowth from its upper parts. In contrast to the above, H. gunniana has polysiphonous segments visible well below the upper parts, cortication commencing much later, and in old corticated axes the pericentral cells remain conspicuous around the axial cell and are of similar size.

Detailed studies are still needed of these differences, especially to follow seasonal development.

Genus THURETIA Decaisne 1844: 236

Thallus erect, terete or with flat and complanate branches. Axes sympodially developed, becoming polysiphonous are soon corticate, with rhodoplastic pseudolaterals forming a network surrounding the axes; holdfast discoid, rhizoidal. Structure. Axes with 4 pericentral cells produced in alternating sequence. Pseudolaterals arising from each segment of the axes, subdichotomous and linking by cell adhesion to form the network, with outer filaments unbranched.

Reproduction. Gametophytes dioecious. Procarps formed on basal cells of the pseudolaterals, with a 4-celled carpogonial branch and 2 groups of sterile cells, the supporting cell being the fourth pericentral cut off on the fertile segment; the sterile pericentral cells divide before fertilization to form the pericarp initials. Post-fertilization, fusion between the carpogonium and auxiliary cell occurs via a connecting cell, and the auxiliary cell, residual supporting cell, adjacent pericentral cells and lower gonimoblast cells contribute to the fusion cell. Carposporangia are terminal, with further ones developing laterally from below. Cystocarps have an urceolate pericarp, usually with a prominent neck. Spermatangial branchlets are subglobeose and terminal on lateral monosiphonous branches within the pseudolateral network; 4–5 axial cells divide to form small initials and ultimately a surface layer of spermatangia.
Tetrasporangial stichidia develop from lower parts of the pseudolaterals, with each axial cell cutting off in alternating sequence usually 6 pericentral cells which divide to form 2–3 presporangial cover cells and the tetrasporangium.

**Type species:** *T. quercifolia* Decaisne 1844: 236.

A genus of 3 species, the type and *T. australasica* from southern Australia and *T. bornetii* Vickers (1903, p. 63) from the West Indies (see Parsons 1975, p. 650).

**KEY TO SPECIES OF THURETIA**

1. Thallus network flat, 5–25 mm broad; stichidia ovoid, in transverse rows across the thallus forming sori at the branch tips; mature cystocarps covered by corticate filaments of the network .................................................................................................................. 1. *T. quercifolia*

1. Thallus network terete or only slightly compressed, up to 4 mm broad; stichidia branched, fan-shaped, distichous on the main axis; mature cystocarps covered by ecorcticate filaments of the network ........................................................................................ 2. *T. australasica*


**FIGS 231, 232, 233A, B**

*Thallus* (Fig. 231A, B) medium to dark red, erect to decumbent, 10–25 cm high, complanately and laterally branched with flat branches mostly 1–2.5 cm broad and 0.5–1 mm thick, with polysiphonous axes bearing a network of monosiphonous filaments with surface unbranched filaments becoming spine-like on the margins (Fig. 231D), denuded below with slender axes. Holdfast conical, rhizoidal, 1–3 mm across, spreading by stolons. *Structure*. Apices sympodial (Fig. 232A), forming alternately distichous pseudolaterals which develop into determinate sympodial laterals forming the flat branches. Pericentral cells 4, formed in alternating sequence. Pseudolaterals occur alternately on each cell of the determinate laterals (Fig. 232A), and the monosiphonous network develops by branchlets becoming linked by small lateral cells (Fig. 232B), with free curved filaments (Figs 231D, 232F) on the surface of the network, more spine like on the thallus margin. Inner cells 25–55 μm in diameter and L/D 0.6–2, cells of free surface filaments 15–40 μm in diameter and L/D 1–3, when spine like, cells 50–150 μm in diameter and L/D 0.5–1. Mature axes become corticated by filaments arising from the pericentral cells which are no longer recognisable in older axes (Fig. 231C). Lateral axes arise from pseudolaterals near the apices. Rhodoplasts discoid in smaller cells, becoming chained or ribon like in larger cells.

*Reproduction*. Gametophytes dioecious. Procarps occur (Fig. 232C) on basal branches on determinate sympodia, with 5 pericentral cells, the fourth of which forms a sterile group and a carpogonal branch; the supporting cell forms a second sterile group. Post-fertilization a fusion cell develops from the auxiliary cell and central cell of the fertile segment and involves also the other pericentral cells and lower goniomblast cells (Fig. 232D); the sterile groups divide extensively. The goniomblast (Fig. 231F) is much branched with terminal clavate carpogorangia 25–35 μm in diameter. Cystocarps (Figs 231B, E, 232E) lie within the filamentous network, ovoid, on a short corticate stalk, 1–2 mm in diameter, corticated, with a prominent neck 0.7–1.2 mm long protruding through the network; the pericarp arises pre-fertilisation by division of the sterile pericentral cells, with the erect filaments becoming 3–6 layered with small outer cortical cells. Spermatangial branches (Figs 232F, 233A) are terminal on short filaments within the network, subglobose and 70–150 μm in diameter, with 3–4 axial...
Fig. 231. Thuretia quercifolia (A, AD, A27130; B, AD, A33720; C-F, AD, A20110). A. Habit. B. Thallus with cystocarps. C. Transverse section of lower denuded axis. D. Longitudinal section of young thallus with free surface filaments and apical filaments anastomosing. E. Cystocarp with slender neck within thallus network. F. Carposporophyte with terminal clavate carposporangia.
cells (Fig. 232G) each cutting off 4 pericentral cells which divide irregularly to form initials which each form 3-4 spermatangia.

Stichidia (Fig. 232B) occur in 2 rows on polysiphonous axes of determinate symposial laterals, formed on 4-6 cells (Fig. 232H) of a monosiphonous network filament, ovoid and 150–200 μm in diameter, each with 6 pericentral cells and ovoid tetrasporangia (40–55 μm in diameter) plus 2–3 pre-sporangial cover cells.

*Type* from “Australia”; lectotype in PC.

enveloping the basal cells of the pseudolaterals. Lateral axes arise from basal cells of fertile segment, sterile pericentral cells and lower gonimoblasts 4-5 cells thick. Spermatangial branches (Figs 233D, 234F) ovoid, 20-25 μm long, with each cell forming 4-5 pericentral cells which cut off initials each of which produces 3-4 spermatangia. Tetrasporangial stichidia (Fig. 233E, 234F) develop from lower branched parts of the pseudolaterals, becoming 300-500 μm in diameter and 10-15 segments long, with each central cell cutting off 6-10 pericentral cells most of which form tetrasporangia (Fig. 234I) 25-50 μm in diameter and 3 pre-sporangial cover cells.

Structure. Apices of axes and laterals sympodial, forming alternately distichous pseudolaterals which become semicircular with laterals developing to similar length and thus producing the terete network of monosiphonous filaments, with outer, free, short filaments (Fig. 234A, F) 0.2-0.6-1 mm in diameter and L/D 0.2-0.6-1. Pericentral cells are elongate, with the sterile groups becoming corticated from close to the apex, the thick mature cortex (Fig. 234A) 20-25 μm thick. Rhodoplasts discoid, becoming elongate or chained in larger cells. Tetrastromatous branches (Figs 233D, 234F) ovoid, 60-100 μm in diameter, borne terminally on short monosiphonous stalks within the network, 3-6 cells long (Fig. 234G) with each cell forming 4-5 pericentral cells which cut off initials each of which produces 3-4 spermatangia.

Reproduction. Gametophytes dioecious. Procarps (Fig. 234B) occur on lower cells of the pseudolaterals, with 5 pericentral cells the fourth of which (occasionally also the fifth) is the supporting cell and cuts off the carpogonial branch and 2 groups of sterile cells. Post-fertilization the fusion cell (Fig. 234C) develops from the auxiliary cell, central cell of the fertile segment, sterile pericentral cells and lower gonimoblasts, and the sterile groups divide. The much branched gonimoblast bears terminal clavate to ovoid carposporangia (Fig. 234E) 20-25 μm in diameter. Cystocarps (Fig. 234D) lie within the monosiphonous network, urceolate and 0.6-1.2 mm in diameter with a relatively long protruding neck, opening straight to flared; the pericarp arises pre-fertilization from the sterile pericentral cells and becomes 4-5 cells thick. Spermatangial branches (Figs 233D, 234F) ovoid, 60-100 μm in diameter, borne terminally on short monosiphonous stalks within the network, 3-6 cells long (Fig. 234G) with each cell forming 4-5 pericentral cells which cut off initials each of which produces 3-4 spermatangia.

Type from Wilsons Prom., Victoria (Mueller, June 1853); holotype in MEL, 1006620.

Distribution: Hopetoun, W. Aust., to Wilsons Prom., Victoria.

*Thuretia australasica* occurs just below low tide level and deeper on rough-water coasts, both on larger algae or *Amphibolis* or directly on rock.

**Genus COLACODASYA** Schmitz in Schmitz & Falkenberg 1897: 473

*Thallas* pulvinate to globular, 1-5 mm across, pale in colour, parasitic on species of *Dasya* or *Heterosiphonia* with rhizoids penetrating between the host cells, with a basal pseudoparenchymatous tissue and erect, surface, polysiphonous branches sympodially branched and with radially or distichously arranged pseudolaterals; laterals 1 or 2 segments apart; pericentral cells 4-6, in some species divided horizontally, often lightly corticated.

**Reproduction.** Gametophytes monoecious or dioecious. Procarps borne on basal cells of pseudolaterals which develop 5 pericentral cells, with a 4-celled carpogonial branch and sterile cells. Carposporophytes ovoid, sessile on polysiphonous bases, with a much branched gonimoblast bearing terminal chains of carposporangia, and a pericarp lightly corticated. Spermatangial branches developed from branches of pseudolaterals.

Tetrasporangial stichidia borne on branches of pseudolaterals, with 4-6 pericentral cells and tetrasporangia per whorl, each with 2 or 3 usually undivided cover cells.

**Type species:** *C. inconspicua* (Reinsch) Schmitz 1897: 473.

A genus of 3 species, the type from the subantarctic and *C. californica* Hollenberg (1970, p. 65) from California, both parasitic on species of *Heterosiphonia*, and *C. australica* parasitic on *Dasya clavigera* on southern Australian coasts.

**Calacodasya australica** Womersley, *sp. nov.*

**FIGS 235**

*Thallas* light red-brown, pulvinate to globose, 2-4 mm across, with a central pseudoparenchymatous tissue and short, peripheral, free polysiphonous branches (Fig. 235C). Attachment by rhizoids (Fig. 235A) penetrating between host cells; epiphytic on axes of *Dasya clavigera*. *Structure*. Central tissue of irregularly branched filaments linked laterally by secondary pit-connections, cells elongate to ovoid, inner cells 40-90 μm in diameter, outer cells 25-40 μm in diameter; attachment rhizoids penetrating between host cells, 15-25 μm in diameter with cells L/D 2-4, cells later becoming irregular and 30-60 μm across. Peripheral free filaments (Fig. 235C) becoming polysiphonous (Fig. 235G) with 5 pericentral cells, 70-170 μm in diameter with segments L/D 0.8-1.5, ecorticate but with ovoid cells 12-25 μm in diameter cut off from both ends (Fig. 235B) of the pericentral cells. Apices probably sympodial, with pseudolaterals borne radially from each segment and branched from each (occasionally second) cell, upper filaments unbranched and 5-10 cells long. Pseudolaterals with lower cells 20-45 (-60) μm in diameter and L/D 1-2.5 (-4), tapering to apical cells (often lost) 12-22 μm in diameter, subapical cells L/D (1-2) 2-4, apical cell short. Rhodoplasts discoid, pale in colour.

**Reproduction.** Gametophytes monoecious. Procarps borne on basal cells of pseudolaterals which cut off 5 pericentral cells, with a 4-celled carpogonial branch and associated sterile cells. Cystocarps (Fig. 235D, E) ovoid, broad based, 200-450 μm in diameter with a slightly broad neck and borne laterally on a polysiphonous branch; gonimoblast much branched, with basal cells scarcely fusing, carposporangia in short terminal chains, ovoid, 7-15 μm in diameter. Pericarp with 12-14 erect filaments, 3 cells thick with ovoid, irregularly shaped and placed outer cortical cells 12-25 μm in diameter. Spermatangial branches (Fig. 235F) on the same...
Fig. 235. *Colacodasya australica* (AD, A31895). A. Rhizoids of *Colacodasya* (above) penetrating the host. B. Erect branch showing pericentral cells and small nodal corticating cells. C. Outer part of pulvinate base with young erect branches. D. Cystocarps on erect branches. E. A cystocarp with ovoid carposporangia. F. Spermatangial branches on erect surface branches. G. An erect branch with stichidia.
thallus as cystocarps, developed as single or paired terminal branches of pseudolaterals, 75–150 \( \mu \text{m} \) long and 25–35 \( \mu \text{m} \) in diameter, with or without a terminal row of sterile cells.

Tetrasporangial stichidia (Fig. 235G) lanceoid to cylindrical, 100–400 \( \mu \text{m} \) long and 50–70 \( \mu \text{m} \) in diameter, borne as branches of pseudolaterals on a monosiphonous base, with 5 pericentral cells and tetrasporangia per whorl, tetrasporangia 15–25 \( \mu \text{m} \) in diameter, each with 2 (undivided) ovoid cover cells which remain more or less erect and cover the lower half of the sporangia.

**Thallus** pulvinatus ad globosus, 2–4 mm latum, cum contexto centrali pseudoparenchymato et ramis brevibus peripheralibus discretis polysiphonis; epiphyticus in *Dasya clavigera*. Filamenta peripheralia cum 5 cellulis pericentralibus, segmenta 70–170 \( \mu \text{m} \) diametro et L/D 0.8–1.5, ecorticata sed cum cellulis parvis ovoideis in finibus cellularum pericentralium. Pseudolaterales radiales plerumque e quoque segmento, cellularae inferiores 20–45 (–69) \( \mu \text{m} \) diametro et L/D 1–2.5 (–4), decrescentes ad cellulas apicales 12–22 \( \mu \text{m} \) diametro, cellulas subapicales L/D (1–) 2–4.

**Reproductio.** Gametophyta monoecia. Procarpia in cellulis basalis cum 5 cellulis pericentralibus, cystocarpia ovoidea, 200–450 \( \mu \text{m} \) diametro cum collo levi, portato lateraliter in ramo polysiphono. Carposporangia in catenis brevibus terminalibus. Percarpium 3 cellulares crassum, cellularae inferioriores irregulariares. Rami spermatangiales in pseudolateribus, 75–150 \( \mu \text{m} \) longi et 25–35 \( \mu \text{m} \) diametro.

Stichidia tetrasporangialia 100–400 \( \mu \text{m} \) longa et 50–70 \( \mu \text{m} \) diametro, portata in pseudolateribus, cum 5 cellulis pericentralibus et tetrasporangiae per segmentum, cum 2 cellulis ovoideis tegentibus.

**Type** from Port Elliot, S. Aust., on *Dasya clavigera* (on *Amphibolis antarctica*), upper sublittoral (Parsons, 1.xi.1967; AD, A31895 -- "Marine Algae of southern Australia" No. 401).

**Distribution:** Hopetoun, W. Aust., to Port MacDonnell, S. Australia.


*C. australica* is often common on *Dasya clavigera* and is to be expected anywhere the host occurs.

The other 2 species of *Colacodasya*, while similar in habit, show clear differences from *C. australica*. The type species, *C. inconspicua* (Reinsch) Schmitz occurs on *Heterosiphonia merenia*, is distichously branched and has 6 tetrasporangia per segment, with undivided cover cells; Levring (1945, p. 25) considered it closest to *Heterosiphonia*. The other species, *C. californica* Hollenberg (1970, p. 65), occurs on *Heterosiphonia erecta*, branching is uncertain, and there are 4 tetrasporangia per whorl with divided and transversely elongate cover cells.
REFERENCES


ADAMS, N.M. (1994). Seaweeds of New Zealand. (Cant. Univ. Press; Christchurch.)


REFERENCES


ATHANASIADIS, A. (1987). A survey of the seaweeds of the Aegean Sea with taxonomic studies on the species of the tribe Antithamnieae (Rhodophyta). (University of Gothenburg, Department of Marine Botany.)


REFERENCES


REFERENCES


FELDMANN-MAZOYER, G. (1941). Recherches sur les Céramiaciées de la Méditerranée occidentale. (Algiers.)


REFERENCES

REFERENCES


REFERENCES

KÜTZING, F.T. (1849). Species Algarum. (Leipzig.)
LYNGBYE, H.CH. (1819). Tentamen Hydrophytologiae Danicae. (Copenhagen.)
REFERENCES


REFERENCES


OLTMANNNS, F. (1904). Morphologie und Biologie der algen. 1. (Jena.)


ROTH, A.G. (1797). *Catlelecta botanica quibus plantae novae et minus cognitae describuntr atque illustrantur. Fasc. 1.* (Lipsiae.)

ROTH, A.G. (1806). *Catlelecta Botanica.* Vol. 3. (Lipsiae.)
REFERENCES


REFERENCES


WEBER van BOSSE, A. (1921). Liste des algues du Siboga. II. Rhodophyceae, Premier partie. Siboga-Expeditie Monogr. 59b, pp. 185–310, Plates VI–VIII. (Leiden.)


REFERENCES


GLOSSARY

abaxial: on the side of the branch facing away from the axis.
accessory: additional to the normal branches or structures.
acropetal: produced in succession towards the apex.
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.
adpressed: lying flat against a structure.
adventitious: an organ or structure arising in an abnormal position.
alantoid: sausage-shaped.
alternate: with branches arising at different levels along an axis.
ampulliform: flask-shaped.
anastomosing: union of cells or filaments laterally to form a network (if extensive).
annular: ring-shaped or arranged in a circle.
annulations: marked with rings.
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.
apomeiotic: formation of reproductive cells without meiosis.
appressed: lying flat along the length of an organ.
assurgent: inclined upwards (usually curved) from its origin.
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.

bilateral: arranged on opposite sides.
bispore: a spore from a sporangium bearing only two spores.
blade: the lamina or part of a flat frond.
caducous: dropping off early.
campanulate: bell-shaped.
cap layer: one or two layers (polysaccharide) over each side of the pit-plug between two cells.
carpogonial branch: the uniseriate branch, usually four cells long (Ceramiales), 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 fusion cell and gonimoblast filaments bearing carposporangia.
cartilaginous: firm and tough but somewhat flexible.
clavate: club-shaped, broadest near the apex.
cmpplanate: flattened or branched in one plane.
compressed: flattened but not strongly so, with an ovate cross section.
conca-co-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.
connecting cell: a cell, through which the zygote nucleus is transferred from the carpogonium to the auxiliary cell.
cortex: the outer layer of cells or tissue of a thallus, outside the medulla.
corticate: covered with an outer layer, usually of smaller cells.
cover cell: a cell overlying the tetrasporangium, cut off from the sporangium initial.
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.
cupulate: cup-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.
decurrent: running down the side of an organ.
decussate: divided into pairs alternately at right angles; a sporangium with cross walls in different planes.
dentate: with marginal teeth.
determinate: having a fixed limit to growth.
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.
dioecious: having the male and female gametes produced on different plants.
diplloid: the generation or cells with nuclei bearing 2N chromosomes.
discoid: forming a flattened disc with a rounded outline.
discrite: separate, not joined or coalescent.
distal: furthest from the point of attachment of an organ.
distichous: in two opposite rows along an axis or branch and thus lying in one plane.
divaricate: branching at wide angles.
doliform: barrel-shaped.
dorsiventral: a structure with distinct upper and lower surfaces.
ecorticate: without a cortex.
emergent: growing out from a structure.
endophyte: an organism living within the tissues of a host plant.
epilithic: living attached to rock or stones.
epiphytic: living attached to a plant, but not parasitic.
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).

farinaceous: with a greyish starchy appearance.
fascicle: a compact cluster or bundle.
fastigiate: with branchlets clustered, erect and subparallel, but tapering above.
filament: a long row of cells attached end to end, usually uniseriate, or a very elongate and narrow coenocytic cell or part thereof.
flange: slightly projecting longitudinal rims on a branch.
flared: spread out or broadened above the base.
flexuous: axes or branches with zig-zag development, usually with alternate branches on each side.
foliose: broadly flattened and leaf-like.
foot cell: a basal cell below an upper structure.
frond: the thallus or a main branch thereof.
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.

gametophyte: the multicellular sexual (N) gamete-producing phase of the life history of a plant.
gland cell: a small, ovoid to subspherical cell with highly refractive contents, darkly staining, which may function in secretion or storage.
globose (globular): nearly spherical.
glomeruliferous: bearing rounded clusters of filaments.
gonimoblast filament: a filament, usually becoming multicellular and branched, produced by the zygote or fusion cell and which produces the carposporangia.
gonimolobe: a lobe, becoming branched, of the young carposporophyte.
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: curved or hooked at the tip.
haptera: branched or multicellular attachment organs.
hemicapulate: half cup-shaped.
hirsute: hairy, with prominent hairs.
holdfast: a basal attachment organ.
holotype: the single specimen or sheet on which an author bases the description of a new taxon.
hypogenous cell: the cell immediately below another structure.
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 specialized cells originate.
tercalary: situation or growth occurring between the apex and base.
ternode: the region between two nodes.
involute: rolled inwards.
isodiametric: with approximately equal diameters or dimensions.
isolate: a duplicate of the lectotype.
isomorph: organisms with the gametophyte and sporophyte of similar morphology and size.
isotype: a duplicate specimen to the holotype.

L/D: length divided by diameter.
lacerate: torn or irregularly cleft.
lachrimiform: tear-shaped.
lanceolate: a solid form, lance-shaped; long and narrow, tapering to both ends, especially to the upper.
lectotype: a specimen of the type collection selected as the basis of the taxon in the absence of a holotype.
leptolocular: 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.

macroscopic: structures seen clearly with the unaided eye.
medulla: the central region of a thallus, internal to the cortex.
meiospore: a spore formed directly as a result of meiosis.
membranous: delicate and often transparent.
meristem: a region of cells actively dividing.
moniliform: arranged like a string of rounded beads.
monoecious: producing male and female gametes usually in separate structures but on the same individual.
monopodial: growth by means of a continuous apical growing point.
monosiphonous: a filament with a single row of cells.
monostromatic: single layered, usually only one cell thick.
mucilaginous (mucoid): slimy, with surface and/or internal mucilage.
mucro: a sharp terminal point.
mucronate: possessing a short, straight point.
multinucleate: with many nuclei in each cell.

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.
nutritive cells (filaments): cells or filaments supplying nutrition to other cells (e.g. the developing carposporophyte), usually darkly staining.

obloid: a 3-dimensional figure oblong in section.
obovoid: egg-shaped, but broadest near the upper end (a three-dimensional term).
obtuse: blunt or rounded at the apex.
octosporangia: sporangia containing 8 spores.
ontogeny: development of an individual in its various stages.
orthostichous: with vertical rows of laterals from the apex down.
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).

palisade-like: rows or tiers of elongate cells, usually on the surface of tissues, with primary pit-connections on the short basal wall.
papillose: covered with papillae (soft protuberances).
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.
pedicle: 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.

peripheral: surrounding, either inside or outside, a round tissue.
peronaxial 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.

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.
polyhedral: a solid with many bases.
polysiphonous: a filament several cells broad, usually with 4 or more pericentral cells around an axial filament.
polysporangia: meiosporangia with more than 4 (usually 8–32) spores.
procarp: the supporting cell, carpogonial branch, and auxiliary cell closely associated in the one branch-system.
GLOSSARY

procumbent: lying along the substrate.
proliferous: bearing branchlets as irregularly placed offshoots.
prostrate: lying flat on the substrate.
proximal: nearest to the point of attachment of an organ.
pseudolateral: a hair or branch system displaced from apical 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.
pyriform: pear-shaped, attached at the narrower end.
rachis: the axis of a frond bearing lateral structures.
radial: on the radii of the structure or around an axis.
rhizoid: a single- or few-celled (without differentiation) attaching or absorptive structure or produced from inner cells.
rhodoplast: the photosynthetic plastid of the Rhodophyta, with single thylakoids which bear the phycobilin pigments.
rosette: a ring of small cells around the margin of a larger inner cell.
septate: with cross walls to the cells or filaments.
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.
siliculose: resembling a small siliqua or pod.
simple: unbranched or undivided.
sinuous: with a wavy margin.
sorus(-i): a cluster of reproductive organs, occurring as a surface patch or slightly raised group.
spermatangia: the cells which contain or cut off the spermatia.
spermatia: the non-motile male cells of the Rhodophyta, usually without a cell wall.
spicate: spike-like.
spine: a stiff, sharp-pointed projection on a cell or tissue.
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.
stichidium: a specialised branch bearing tetrasporangia.
stichidiose: resembling a stichidium in shape.
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.
subapical: shortly below the apex; one (or more) cells below the apex.
subdichotomous: almost dichotomous but not truly so.
subhypogenous: directly below the hypogenous cell (which is below a particular structure).
sublittoral: the photic zone below the eulittoral region, from about mean low tide level to the lower limit of algal growth.
subspherical: almost spherical.
subulate: awl-shaped, tapering from a broader base to a fine point.
supporting cell: the cell which bears one or more carpogonial branches.
synchronic: 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.
terinal: 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.
tomentum: a dense covering of hairs.
torulose: cylindrical with swollen lumps at intervals.
transverse: from the flat sides of a compressed structure.
trapeziform: an asymmetrical 4-sided figure.
trichoblast: a colourless, usually branched, hair-like appendage produced near branch apices (Rhodolomelaceae).
trichogyne: the slender prolongation from the carpogonium to which spermatia become attached.
trichotomous: branching to give 3 equal branches.
triphasic: with three phases in the life history.
tubercle: a wart like or knobby excrescence.
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.

umbonate: with a rounded projection (umbo) in the centre.
unialaxial: 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.
uniseriate: arranged in a single row or series, not more than one cell broad.
urceolate: shaped like an urn; hollow and contracted at the mouth.
urnicle: a swollen, often elongate-clavate, terminal part of a filament.
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.
villose (branchlets): long, slender and soft branches.

wart: verrucose; covered with wart-like protuberances.
whorl-branchlet: one of 2–5 short determinate branchlets arranged in a whorl (vertical) on the axis (Cladophoraceae).

zygote: the diploid cell resulting from fusion of gametes.
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