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Descriptions of Two New Genera, *Scageliopsis* and *Glandothamnus* (Ceramiaceae, Rhodophyta), Including Five Previously Undescribed Species from Southern Australia[1]

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ABSTRACT: Two genera, *Scageliopsis* and *Glandothamnus*, including 5 new species (*Scageliopsis patens*, *Glandothamnus ramulentus*, *G. manifestus*, *G. flexilis*, and *G. acicularis*), are described from southern Australia. Both genera have some similarities with the northern hemisphere genus *Scagelia* Wollaston and with *Platythamnion* J. Agardh. *Scageliopsis* is characterized by whorls of equal whorl-branchlets, lateral gland cells, and carposporophytes produced on basal cells of fully developed whorl-branchlets which arise from axes capable of continued elongation. *Glandothamnus* is distinguished by unilateral initiation of whorl-branchlets at branch apices, adaxial branching of young whorl-branchlets, mature gland cells elongated obliquely to whorl-branchlet axes, and carposporophytes borne on fully formed whorl-branchlets arising from axes which only occasionally continue to elongate. *Scageliopsis* and *Glandothamnus* are placed with *Scagelia* in the tribe Antithamnieae (Ceramiaceae). Complete keys to all known genera of the tribes Antithamnieae and Heterothamnieae are included.

RECENT COLLECTIONS OF ALGAE obtained by diving have revealed several undescribed species of Ceramiaceae from the southern Australian coast. In this paper 2 genera, *Scageliopsis* gen. nov. and *Glandothamnus* gen. nov., including 5 species—*Scageliopsis patens*, *Glandothamnus ramulentus*, *G. manifestus*, *G. flexilis*, and *G. acicularis*—are described for the first time. Specimens of *Glandothamnus ramulentus* have previously been recorded as *Callithamnion* (or *Antithamnion*) *plumula*, but are now recognized as distinct from the northern hemisphere species *Antithamnion plumula* (Ellis) Thuret. The species is, however, closely similar to *Callithamnion bebbii* Reinsch from the Adriatic Sea, but unfortunately the type of this species has not been located.

Investigations have been made on fresh and preserved material, and although some collections have been limited, these species appear to be clearly distinct from previously described taxa. Both genera are closely related to *Scagelia* Wollaston, a genus represented by a single species, *S. occidentale* (Kylin) Wollaston, confined to the Pacific coast of North America. Although similar in various features of thallus structure and reproduction, *Scageliopsis* and *Glandothamnus* appear to be generically distinct from one another and from *Scagelia*.

Terminology used follows that of Wollaston (1968). "Gland cell" has been retained as implying a broader meaning than the term "secretory cell" used by some authors; it is considered preferable to leave the choice of a more appropriate term until the function of these cells is better understood.

Keys to all recognized genera of Antithamnieae and Heterothamnieae are included.

Scageliopsis gen. nov.

Thallus axium erectorum ramosorum in base per rhizoidea affixus; cellulae axiales maturae quaeque verticillum 2–4 ramulorum

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longitudine subaequorum, in apicibus ramorum inordinatim ortum, efferentes. Rami laterales in cellulis basalibus ramulorum verticillatorum portati. Cellulae glandulosae in cellulis ramulorum verticillatorum laterales sunt. Rami carpogoniales 4-cellulares in cellulis basalibus ramulorum verticillatorum in apicibus ramorum; ramuli verticillati fecundi in axibus ramorum qui post fecundationem vulgo longiores crescent portati; carposporophyta carposporangia globosa et aggregata continentia. Spermatangia in ramis brevibus ramulorum verticillatorum; tetrasporangia in cellulis ramulorum verticillatorum, cruciatim vel tetraedrice divisa.

The genus is named for the resemblance to *Scagelia* in certain distinctive features.

TYPE SPECIES: *Scageliopsis patens* sp. nov.

Scageliopsis is recognized by the following features:

i. A thallus of erect branches attached by basal rhizoids.
ii. Regular whorls of 2–4 whorl-branchlets equal or almost equal in length and initiated often in irregular sequence at branch apices.
iii. Short chains of small immature cells at branch apices and lateral branches borne on basal cells of whorl-branchlets.
iv. Gland cells developed laterally on cells of whorl-branchlets.
v. Carpogonial branches, 4 cells in length and few in number, borne on basal cells of whorl-branchlets at branch apices.
vi. Continued elongation of both axial apices and fertile whorl-branchlets after carposporophyte initiation. Carposporophytes with rounded groups of carposporangia.
vii. Spermatangia on short branches on whorl-branchlets.
viii. Tetrasporangia cruciately or tetrahedrally divided.

In most closely related genera, elongation of fertile axes ceases after fertilization and thallus growth is carried on by lateral branches. Continued elongation of fertile axes is, however, distinctive in the North American genus *Scagelia*, from which *Scageliopsis* differs mainly in detail of thallus morphology and especially in arrangement and branching pattern of whorl-branchlets. In *Scagelia*, whorl-branchlets are alternately or irregularly branched and differ in length in individual whorls. Fusions between cells of the carposporophyte and the axial cell upon which it is borne are also much more pronounced in *Scagelia* than in *Scageliopsis*. Thus although *Scageliopsis* resembles *Scagelia* in a number of features, a new genus is justified on the basis of the features outlined above.

Scageliopsis also possesses some features in common with *Glandothamnus*, and similarities with this genus are discussed later in this account.

Scageliopsis patens sp. nov.

Figures 1–11

Thallus ad 1(–2) cm altus, axibus ramosis verticilla 2–4 ramulorum ad 200 μm longos ex quaque cellula axiali pseudodichotome ramificantium, efferentibus, compositus. Cellulae glandulosae laterales in cellulis ramulorum verticillatorum. Carposporophyta portata in ramulis verticillatis fecundis, ex axibus longioribus interdum crescentibus, exorientibus. Spermatangia in ramis brevibus in ramulis verticillatis. Tetrasporangia ad 40 μm diam in cellulis interioribus centralibusque ramulorum verticillatorum, nata, ovoidea et cruciatim divisa.

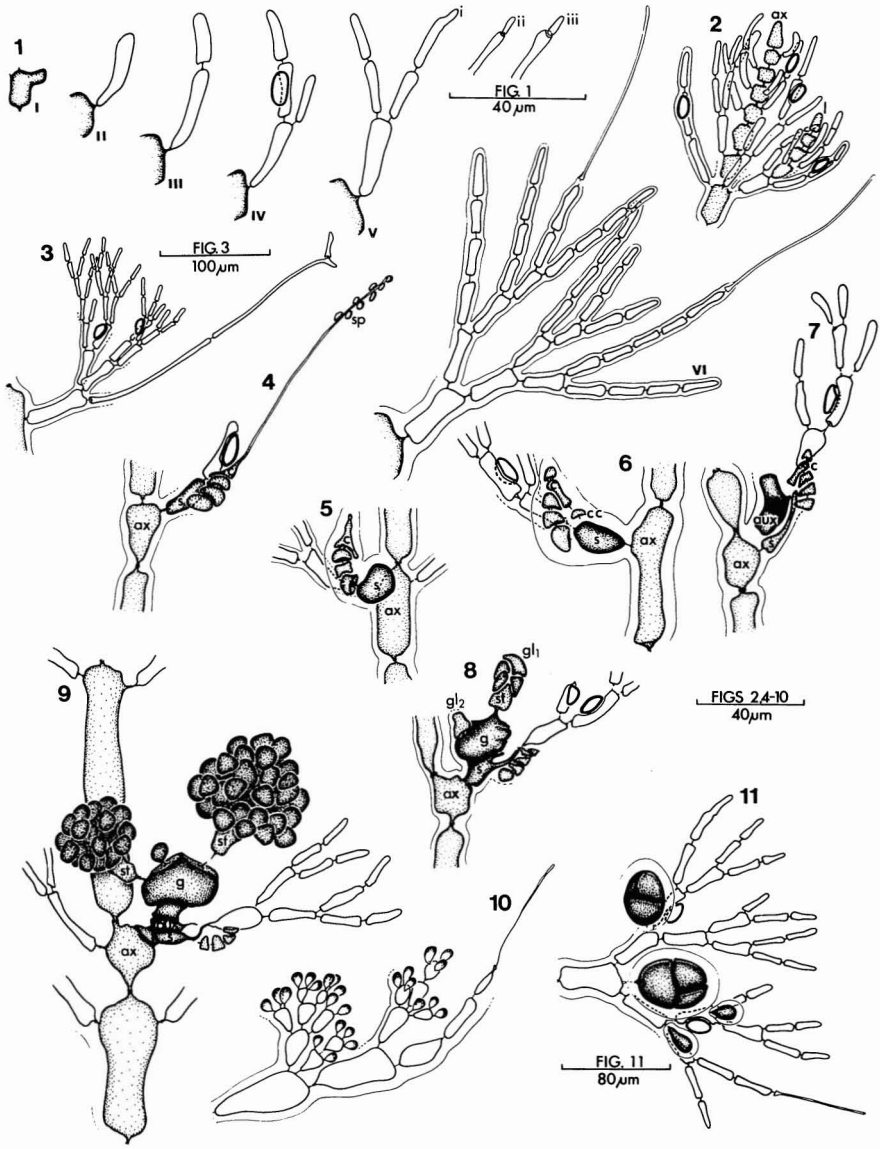
The species is named for the open, widely spreading whorl-branchlets oriented at almost 90° to branch axes.

TYPE LOCALITY: Port Stanvac, St. Vincent Gulf, S. Aust., 3–12 m deep on bryozoans on jetty pylons (*Clarke and Engler*, 14.iv.1979).

HOLOTYPE: ADU, A50327.

DISTRIBUTION: Known from the type locality and from Semaphore and Port Noarlunga, St. Vincent Gulf, S. Aust.

The thallus, seldom over 1 cm high, consists of branched axes arising from a prostrate base. Axial cells are up to 300 μm long and to 10 times as long as broad; cells of the central mature thallus are usually 80–100 μm long



FIGURES 1–11. *Scageliopsis patens* sp. nov. 1, *I–VI*. Stages in development of a whorl-branchlet from (*I*) at initiation to (*VI*) at maturity showing pseudodichotomous branching. (*V*) includes series *i–iii* showing stages in cell development. 2. Axial apex with young lateral branch (*l*) initiated on the basal cell of a developing whorl-branchlet. Gland cells prominent. *ax*, axial cell. 3. Attachment rhizoid, with developing digital process, borne on basal cell of a whorl-branchlet. 4. Four-celled carpogonial branch with spermatia (*sp*) adhering to the elongate trichogyne, borne on basal cell of immature whorl-branchlet. *s*, supporting cell.

5. Carpogonial branch prior to fusion showing base of carpogonium (*c*) elongating toward the supporting cell (*s*) which is enlarging upwardly before the auxiliary cell is cut off. 6. Protrusion with connecting cell (*cc*) from the carpogonium (*c*) extended toward the supporting cell (*s*) prior to cutting off of the auxiliary cell. Remnant of trichogyne remains as a small capping cell above the carpogonium. 7. Auxiliary cell (*aux*), immediately after fusion with the carpogonium (*c*), elongating upwardly prior to cutting off of the gonimoblast cell. 8. First-formed gonimolobes (*gl*) developing from upper part of gonimoblast cell (*g*). First carposporangia cut off from sterile cell of first-formed gonimolobe. *st*, sterile cell.

9. Carposporophyte with rounded groups of carposporangia; fertile whorl-branchlet borne on axial cell (*ax*) which remains smaller than adjacent axial cells; broad connections between axial cell and supporting cell (*s*) and between old auxiliary cell (*aux*) and gonimoblast cell (*g*); axis continuing to elongate as carposporophyte matures. 10. Spermatangia borne on terminal cells of short special branches on whorl-branchlets. 11. Tetrasporangia borne on inner cells of whorl-branchlets.

and 18–25 μm broad. Each mature axial cell bears a whorl of 2–)3–4 pseudodichotomously branched whorl-branchlets, each to 200 μm long, with orientation at almost 90° to branch axes and which, although appearing dichotomously branched when mature, are formed by successive branching during whorl-branchlet development (Figure 1, *I–VI*). Terminal cells of whorl-branchlets may bear long colorless hairs (Figure 1, *VI*). Axial growth occurs by transverse division of apical cells which gives rise to a short chain, often curved, of immature axial cells at each branch apex. Whorl-branchlets are initiated in irregular sequence from young cells at branch apices (Figure 2).

Lateral branches arise from the outer end of basal cells of whorl-branchlets (Figure 2); thus the basal cell of each parent whorl-branchlet forms the apparent basal cell of each mature lateral branch and bears only two branchlets which were formed as the first pseudodichotomy of the parent whorl-branchlet; adjacent cells of a mature lateral branch axis bear the usual complement of 3–4 whorl-branchlets per cell. Gland cells are prominent and are cut off laterally from whorl-branchlet cells with the first-formed gland cells initiated on young whorl-branchlets at branch tips; usually several gland cells occur on each mature whorl-branchlet (Figures 2, 3). Attachment rhizoids, each composed of several elongate cells, are developed from basal cells of whorl-branchlets and form digitate attachment organs on contact with the host (Figure 3).

Carpogonial branches are borne from the abaxial part of the outer end of basal cells (= supporting cells) of immature whorl-branchlets near branch apices (Figure 4); each fertile whorl-branchlet continues to grow during carposporophyte development and the branch axis bearing the fertile whorl-branchlet may also continue to elongate (Figure 9). Lateral branches sometimes develop from axial cells close below that which bears the fertile whorl-branchlet. Each carpogonial branch is 4-celled, including the terminal carpogonium with upwardly directed trichogyne (Figure 4). Numerous spermatia have been noted adhering to single trichogynes. After receiving the sperm nucleus the carpogonium becomes elongated in the direction of the auxiliary cell (Figure 5), a fusion tube is developed, and the nucleus is transferred to the developing auxiliary cell by means of a small connecting cell (Figure 6). A small remnant of the trichogyne base remains above the carpogonium. The auxiliary cell appears to form rapidly from the upper part of the supporting cell and is probably cut off almost simultaneously with the fusion process. As the fusion tube of the carpogonium develops, the upper part of the supporting cell becomes swollen and stains densely, while the next observed stage, apparently soon after fusion, shows a distinct auxiliary cell already elongating upwardly to form a gonimoblast cell initial (Figure 7). As the initial of the gonimoblast cell enlarges, the lower portion of the auxiliary cell, which includes the point of fusion, becomes modified to form a broad connection between the gonimoblast cell and the supporting cell (Figure 8). The connection between supporting cell and axial cell of the main axis also becomes enlarged, presumably to allow adequate nutrients to reach the developing carposporangia (Figures 8, 9). Carposporangial groups are formed successively from the gonimoblast cell with the first-formed gonimolobes cut off from the upper part of the gonimoblast cell (Figure 8). Each mature group is rounded in form and consists of a single sterile cell bearing numerous carposporangia (Figure 9). During development of the procarp and carposporophyte, the axial cell which bears the fertile whorl-branchlet contracts and becomes reduced in size in comparison with other cells of the axes (Figure 9).

Spermatangial clusters are borne on the upper side of cells of whorl-branchlets scattered over the thallus. Each cluster consists of a short special branch, either branched or unbranched, bearing up to 4 spermatangia from the outer end of each terminal cell (Figure 10).

Tetrasporangia are borne from the outer part of inner and central cells of whorl-branchlets. Each mature tetrasporangium is sessile, ovoid, up to 40 μm long, cruciately

divided (Figure 11), and liberated by an apical slit in the enveloping gelatinous sheath.

Glandothamnus gen. nov.

Thallus, axium erectorum ramosorum per fila rhizoidea affixus; cellulae axiales maturae quaeque verticillum (2–) 3–4 ramulorum plerumque ordinatim in apicibus ramorum vulgo ortum. Rami laterales ex extremitate superna cellularum axialium exorti, vel ex cellulis basalibus ramulorum verticillatorum exorti. Cellulae glandulosae maturae vulgo prominentes, versus axes ramulorum verticillatorum oblique elongatae. Rami carpogoniales, 4-cellulares in cellulis basalibus ramulorum verticillatorum; ramuli verticillati fecundi ex axibus ramorum qui post fecundationem raro longiores crescent, exorti. Spermatangia in ramis brevibus ramulorum verticillatorum. Tetrasporangia in cellulis ramulorum verticillatorum plerumque cruciatim divisa.

The genus is named for the prominent and distinctive gland cells.

TYPE SPECIES: *Glandothamnus ramulentus* sp. nov.

Glandothamnus is characterized by the following features:

i. An erect, branched thallus attached by rhizoidal filaments from the base of the thallus. In some species attachment rhizoids are also formed by terminal elongation of axes and presumably new plants can be formed vegetatively by this means.
ii. Whorl-branchlets in whorls of (2–) 3–4 from each mature cell of branch axes and near equal in length when mature.
iii. Apical development often with unilateral initiation of whorl-branchlets, and lateral branches borne directly on the upper part of axial cells or on basal cells of whorl-branchlets.
iv. Gland cells initiated laterally on cells of whorl-branchlets, usually prominent, and, when mature, elongated obliquely to the long axes of the cells upon which they are borne.
v. Carpogonial branches few in number, usually 1–3, borne on basal cells of whorl-branchlets at apices of lateral branches. Whorl-branchlets continue to develop as the carposporophyte forms and axial growth of the fertile lateral branch is continued by further lateral branches produced on cells below the developing carposporophyte. Occasionally the branch axis bearing the fertile whorl-branchlet continues to elongate and further carpogonial branches may develop.
vi. Spermatangia on short branches on whorl-branchlets.
vii. Tetrasporangia cruciately or tetrahedrally divided.

The most distinctive single feature of *Glandothamnus* is the form of the obliquely oriented gland cells which are usually numerous and widely distributed over the thallus. Gland cell form and position are recognized as remarkably consistent generic indicators, especially in genera of the tribes Antithamnieae Hommersand and Heterothamnieae Wollaston of Ceramiaceae as, for example, in *Antithamnion*, *Macrothamnion*, *Acrothamnion*, and *Hollenbergia*.

Although similar in some features to both *Scagelia* and *Scageliopsis*, *Glandothamnus* differs from both these genera in the branching pattern of whorl-branchlets, unilateral initiation of whorl-branchlets at branch apices, oblique orientation of mature gland-cells, and in only occasional continuation of elongation of fertile branch axes after carposporophyte initiation. In most cases axial growth is continued by lateral branches borne on axial cells below the developing carposporophyte. Whorl-branchlets in species of *Glandothamnus* are at first branched adaxially, although further branching may produce a pseudodichotomous (*G. manifestus*) or opposite (*G. ramulentus*, *G. flexuosus*) branching pattern. In *Scagelia* whorls consist of unequal whorl-branchlets which are oppositely, alternately, or irregularly branched, and in *Scageliopsis* whorls and whorl-branchlets are regular in form and branching in all parts of the thallus.

KEY TO THE SOUTHERN AUSTRALIAN SPECIES OF *Glandothamnus*

1. Whorl-branchlets short, 300 (–400) μm long, not flexuous. Spined structures often present on whorl-branchlets of upper thallus. ..... *G. acicularis.*
1. Whorl-branchlets longer, 600–1500 μm long, semi- to very flexuous. Spined structures absent. ..... 2.
   2. Mature whorl-branchlets pseudodichotomously branched, to 650 μm long, semi-flexuous; branch axes not elongated into terminal attachment rhizoids. .*G. manifestus.*
   2. Mature whorl-branchlets adaxially to oppositely branched, 800–1500 μm long, flexuous; branch axes occasionally elongated into terminal attachment rhizoids. ..... 3.
3. Whorl-branchlets to 900 μm long, branch axes not conspicuously flexuous; unilateral development of whorl-branchlets from 3–9 cells at each branch apex. ... *G. ramulentus.*
3. Whorl-branchlets to 1500 μm long, branch axes, as well as whorl-branchlets, long and flexuous; unilateral development of whorl-branchlets from up to 25 cells at distinctly curved branch apices. ..... *G. flexilis.*

Glandothamnus ramulentus sp. nov.

Figures 12–18, 41

Callithamnion plumula sensu Hooker and Harvey 1847:412. Harvey 1860:333; 1863 synop. 690.

Antithamnion plumula sensu May 1946: 123.

Thallus ad 5 cm altus, erectus axibus ramosis verticilla 2–4 ramulorum ex quaque cellula axiali efferentibus, compositus, et apice in rhizoideum ad affixendum interdum productus. Ramuli verticillati ad 850 μm longos in thallo superiori vel medio adaxialiter ramosi, ramis oppositis saepe inferis. Rami laterales vel in cellulis axialibus ipsis portati, vel in cellulis basalibus ramulorum verticillatorum portati. Cellulae glandulosae oblique elongatae ad 30 μm longas, prominentes. Rami carpogoniales prope apices ramorum portati. Carposporophyta carposporangia globose aggregata continent. Spermatangia ignota. Tetrasporangia pedunculata 1–3 cellularia longa in cellulis interioribus et centralibus ramulorum verticillatorum, raro sessilia, globosa ad 30 μm diam cruciatim divisa.

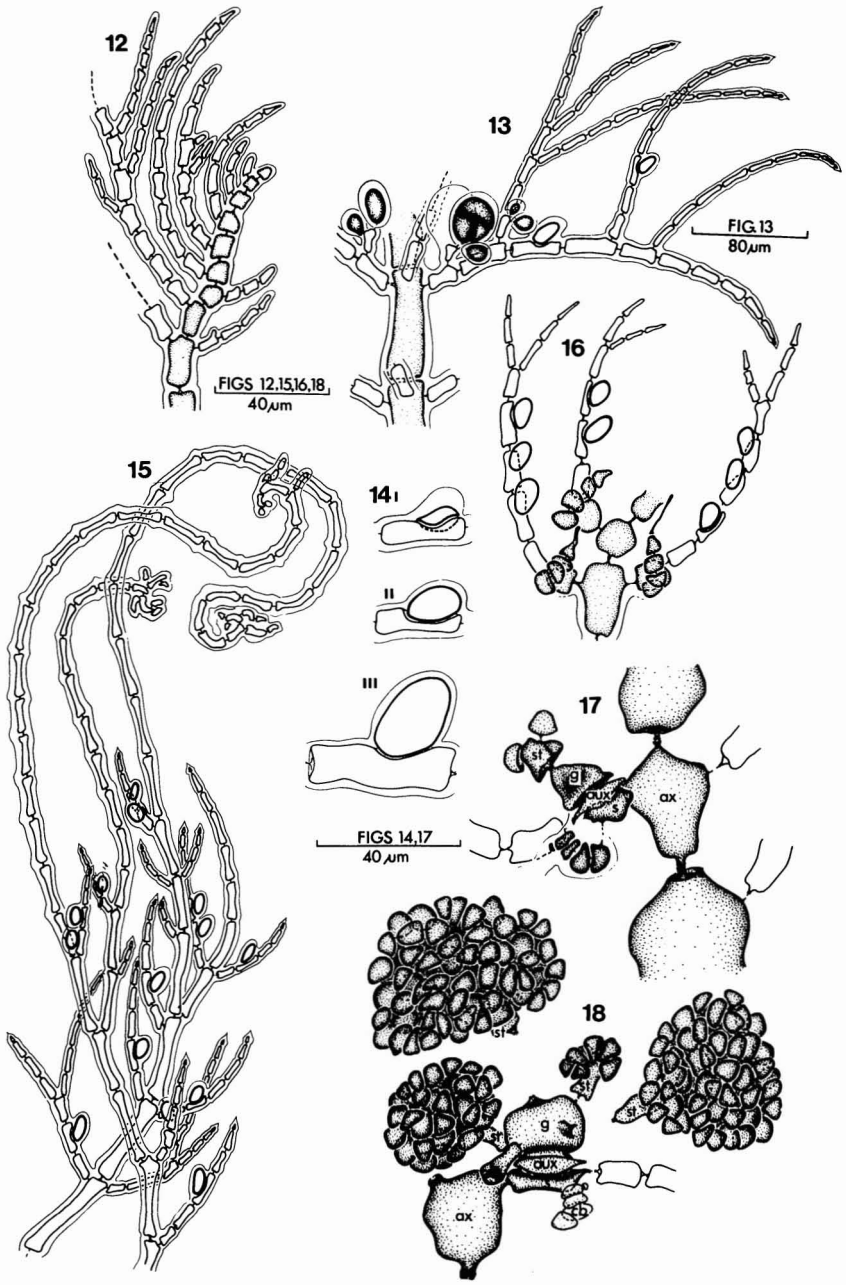
The species is named for the conspicuous and flexuous form of thallus axes and whorl-branchlets.

TYPE LOCALITY: Georgetown, Tasmania.

HOLOTYPE: MEL 516229, Herb. Sonder (*Harvey*, Alg. Aust. Exsicc. 544I) (tetrasporangial).

DISTRIBUTION: Recorded from southern and southeastern coasts of Australia from Investigator Str., S. Aust., to Ulladulla, N.S.W., including the north coast of Tasmania.

The thallus, up to 5 cm or more high, is erect and consists of much-branched axes which appear somewhat annular to the naked eye. Axes are composed of closely articulating cells up to 900 μm long and 300 μm broad in the older parts of the thallus, but 200–400 μm long and 50–150 μm broad in the central mature thallus, and covered by a distinct gelatinous sheath; cells of axes are (2–)3(–5) times as long as broad. Each axial cell bears a whorl of (2–)4 whorl-branchlets, each up to 850 μm long when mature, which are initiated at axial apices, often with unilateral development of the first-formed whorl-branchlets (Figure 12). Whorl-branchlet initials give rise to a rachis which soon develops lateral branches adaxially from the rachis cells, so that whorl-branchlets in the upper to central part of the thallus are secundly branched and up to 900 μm long with branches up to 650 μm long (Figure 13). Branches of the whorl-branchlets may become further branched, often unilaterally, and mature whorl-branchlets may bear pairs of opposite, branched or unbranched, laterals from lower and central cells of the rachis. Whorl-branchlet rachides are often curved downward at the outer end, and, like their branches, appear elongate and flexuous, gradually narrowing to an acute tip. Axial



FIGURES 12–18. *Glandothamnus ramulentus* sp. nov. 12. Branch apex with unilateral development of whorl-branchlet initials. 13. Whorl-branchlet from upper part of thallus with adaxial branching, gland cell, and tetrasporangia which are either sessile or borne on short stalks 1(–3) cells long. 14, *I–III*. Stages in development of gland cell cut off laterally from whorl-branchlet cell: (*I*) with sheath swelling prior to enlarging of gland cell, (*II*) oblique elongation of gland cell, (*III*) mature form of gland cell. 15. Branch axes elongating to form terminal rhizoids with digitate attachment processes. Numerous gland cells on branches.

16. Carpogonial branches borne on basal cells of whorl-branchlets. 17. Carposporophyte with early stage of development of the first terminal gonimolobe borne on the gonimoblast cell (*g*) and consisting of a large sterile cell (*st*) with 2 carposporangial initials. Axial cell (*ax*), bearing the fertile whorl-branchlet, is smaller than adjacent axial cells. *aux*, auxiliary cell; *st*, sterile cell. 18. Rounded groups of carposporangia borne successively from gonimoblast cell (*g*) of carposporophyte. *cb*, carpogonial branch.

growth occurs by transverse divisions of apical cells. Lateral branches of the thallus develop either directly from axial cells or from the basal cells of whorl-branchlets. Gland cells, up to 30 μm long, are prominent on all parts of the thallus and often particularly abundant near branch tips (Figure 15). Gland cells are cut off laterally from whorl-branchlet cells and elongate obliquely to the long axes of the cells upon which they are borne (Figure 14, *I–III*). Attachment rhizoids are developed from the base of the thallus. Elongate rhizoidal filaments may also be produced by terminal elongation of branch axes, and these may produce digitate attachment processes which presumably can give rise to new individual plants (Figure 15).

Carpogonial branches are 4-celled and borne on basal cells (= supporting cells) of whorl-branchlets near branch apices (Figure 16). Although fertile branch axes occasionally continue to elongate after initiation of carposporophyte development, it is usual that axial growth is continued by lateral branches borne on axial cells below the carposporophyte. Carposporophyte development follows fusion between the auxiliary cell, cut off from the supporting cell, and the carpogonium of the carpogonial branch; a gonimoblast cell is formed from the upper part of the auxiliary cell and gives rise to a succession of rounded groups of carposporangia of which the first is terminal in position (Figures 17, 18). As the carposporophyte develops, the axial cell which bears the fertile whorl-branchlet becomes obviously smaller and stains more densely than adjacent axial cells.

Spermatangia unknown.

Tetrasporangia are usually borne on short stalks which are 1(–3) cells long and occasionally branched, and develop on the inner to central cells of whorl-branchlet rachides in the position of whorl-branchlet branches. Occasionally sessile tetrasporangia are also produced from the lower cells of inner branches of whorl-branchlets (Figure 13). Tetrasporangia are produced successively, and are released through apical slits in the gelatinous sheaths which surround them during development; up to 8 empty sheaths, as well as further developing tetrasporangia, have been observed on a single parent cell. Each mature tetrasporangium is spherical, up to 30 μm diameter when mature, and cruciately or tetrahedrally divided (Figure 13).

The species is distinguished by the length and form of whorl-branchlets usually with curved rachides which are adaxially branched in the upper thallus but usually oppositely branched in the lower thallus, and the occasional presence of filamentous rhizoids developed terminally from branch apices.

Glandothamnus ramulentus is the plant which Harvey distributed (Alg. Aust. Exsicc. 544I) as *Callithamnion plumula* from Georgetown, Tasmania, and which was first recorded from this locality by Hooker and Harvey (1847:412, *Gunn*). Agardh (1851:29) also refers to *Callithamnion plumula*, as recorded by Harvey, from Cape Horn and Tasmania. However Harvey (1860:333) recognized that the Tasmanian plant differed in branching of "ramuli" from the usual form of *Callithamnion plumula*, including the Cape Horn plant which he had previously (1847:489) considered to be the same as the European and North American species.

Later collections indicate that *Glandothamnus ramulentus* is widespread along southern and southeastern coasts of Australia and that the European species, *Antithamnion* (*Callithamnion*) *plumula*, is probably confined to the northern hemisphere.

Glandothamnus ramulentus agrees closely with the description and figures given by Reinsch (1875) for *Callithamnion bebbii* from the Adriatic Sea. However, Australian plants are 3–4(–6) cm in height and more robust than those recorded by Reinsch as 8–12 mm high. Unfortunately the type specimen of *Callithamnion bebbii* has not been located, hence for the present the identity of the Australian plant remains doubtful. It is also apparent that Feldmann (1942:285, figures 35–37) did not see the type of *Callithamnion bebbii* when he described *Antithamnion plumula* var. *bebbii* based upon the descriptions and figures published by Reinsch.

Glandothamnus ramulentus differs in habit and branching from *Antithamnion plumula* var. *bebbii*, and is also less variable in form,

although plants may become attenuated when growing in deep water (30–100 m) or are subjected to water currents such as occur in Investigator Strait between Kangaroo Island and the mainland of South Australia.

Although Harvey reported the species as rare, numerous plants have now been collected through diving, and May (1946) regarded the species as prevalent and spreading rapidly along parts of the New South Wales coast.

Glandothamnus manifestus sp. nov.

Figures 19–30, 42

Thallus ad 8 cm altus, erectus, axibus ramosis verticilla 2–4 ramulorum ad 650 μm longos ex quaque cellula axiali pseudodichotome ramificantium efferentibus compositus. Rami laterales vel in cellulis axialibus ipsis portati, vel in cellulis basalibus vel secundis ramulorum verticillatorum portati. Cellulae glandulosae oblique elongatae, 20(–25) μm longae, crebrae. Rami carpogoniales prope apices ramorum lateralium plerumque portati. Carposporophyta carposporangia globose aggregata continent. Spermatangia in ramis brevibus in ramulis verticillatis. Tetrasporangia ignota.

The species is named for the unusually clear stages of carposporophyte development revealed in the holotype specimen.

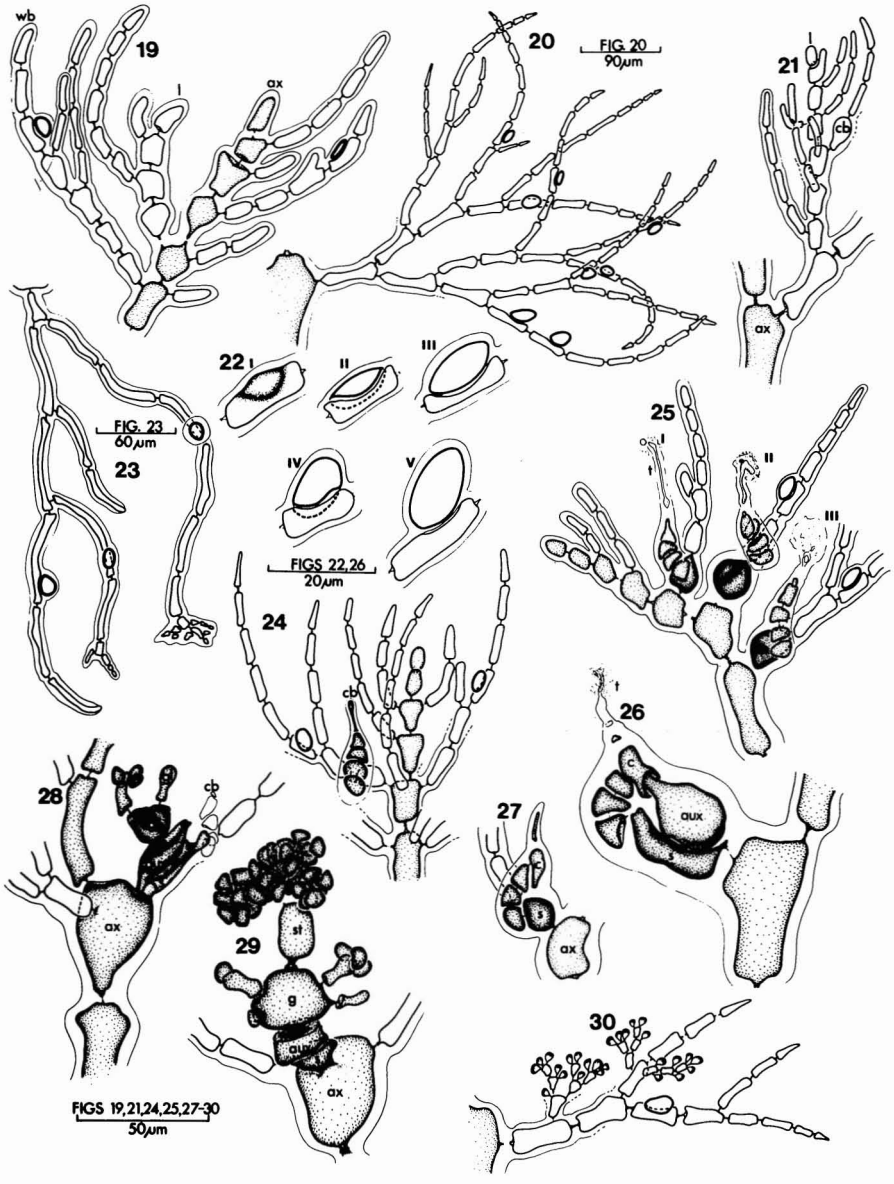
TYPE LOCALITY: Woody Island, D'Entrecasteaux Channel, Tasmania, 0–2 m deep (*Shepherd*, 17.ii.1972).

HOLOTYPE: ADU, A41641 (carposporangial).

DISTRIBUTION: Known only from the type locality.

The thallus, to 8 cm high, consists of branched axes composed of cells up to 900 μm long and 200 μm broad in lower parts, but 200–400 μm long and 70 to 150 μm broad in the central thallus; cells may be up to 6 times as long as broad. Axial cells at the extreme base of the thallus are often proportionately shorter and broader. Each axial cell bears a whorl of 2–4 whorl-branchlets which are initiated at axial apices often with unilateral development of the first-formed whorl-branchlets (Figure 19). Whorl-branchlet initials develop acute-tipped rachides, the cells of which give rise to tapered, acute branches so that mature whorl-branchlets are pseudodichotomously branched and up to 650 μm long (Figure 20). Axial growth occurs by transverse division of apical cells to form a short chain of immature axial cells at each branch apex (Figure 19). Lateral branches are borne either directly on axial cells near branch apices (Figure 19), or on the basal or second cells of whorl-branchlets (Figure 21). Lateral branches borne directly on axial cells are distinguished from young whorl-branchlets in having abaxial initiation of whorl-branchlets while young whorl-branchlets develop adaxial branches first (Figure 19). Lateral branches of the second type are particularly prominent on female plants and usually bear carpogonial branches and carposporophytes. Fertile lateral branches are often borne from the outer end of the second cell, rather than the basal cell, of whorl-branchlets. Gland cells up to 20(–25) μm long are prominent on all parts of the thallus and mature whorl-branchlets may each bear up to 40 gland cells. Each gland cell is cut off laterally from an immature whorl-branchlet cell (Figures 19, 22, *I–III*) and when fully developed is usually elongated obliquely, or almost at right angles, to the long axes of the cell upon which it is borne (Figure 22, *IV–V*). Gland cells are notably abundant on fertile lateral branches of female plants and near the base of the thallus; they occasionally occur on cells of attachment rhizoids (Figure 23). Branched filamentous attachment rhizoids are developed from the basal cells of whorl-branchlets near the base of the plant and attach by means of small, terminal, digital processes (Figure 23) which are formed on contact with the host.

Carpogonial branches are 4-celled and are initiated on basal cells (= supporting cells) of developing whorl-branchlets near branch apices (Figures 21, 24). In female plants a succession of fertile lateral branches often occurs at close intervals along axes. Each fertile branch apex bears 1–3 carpogonial



FIGURES 19–30. *Glandothamnus manifestus* sp. nov. 19. Branch apex showing whorl-branchlets initiated in unilateral sequence, abaxially branched lateral branch (*l*) initiated directly on cell of axis, adaxial position of first-formed branches of whorl-branchlet (*wb*), and lateral initiation of gland cells. *ax*, axial cell. 20. Mature pseudodichotomously branched whorl-branchlet with oblique mature gland cells. 21. Young lateral branch (*l*) borne on basal cell of whorl-branchlet with a swollen cell representing the first stage toward initiation of a carpogonial branch (*cb*). 22, *I–V*. Sequence in development of a gland cell from initiation to fully developed "oblique" form.

23. Rhizoids with digital attachment processes and bearing gland cells. 24. Four-celled carpogonial branch (*cb*) borne on the basal cell of whorl-branchlet near the apex of a lateral branch. 25. Apex of lateral branch showing 3 carpogonial branches: (*I*) with mature trichogyne (*t*), (*II*) with degenerating trichogyne, (*III*) with degenerated trichogyne. 26. Tubular extensions from carpogonium (*c*) and from auxiliary cell (*aux*) in process of fusion. *s*, supporting cell.

27. Carpogonial branch showing degenerating trichogyne and carpogonium (*c*) elongating toward the supporting cell (*s*) before the auxiliary cell is apparent. 28. Carposporophyte showing supporting cell (*s*), auxiliary cell (*aux*), and gonimoblast cell (*g*) with young gonimolobes (*gl*); pit-connections present between cells of carposporophyte and broadened connection between supporting cell and axial cell (*ax*). 29. Rounded groups of carposporangia developing from gonimolobes produced on the gonimoblast cell (*g*). *st*, sterile cell. 30. Spermatangia borne on special branches on whorl-branchlets.

branches (Figure 25), although only one carposporophyte matures. As the procarp develops, the axial cell upon which the fertile whorl-branchlet is borne becomes contracted in form and stains densely. Occasionally further elongation of the branch axis may occur and another sequence of carpogonial branches may be developed. However, thallus growth is usually continued by lateral branches borne from axial cells below the carposporophyte. A short terminal trichogyne develops from the carpogonium of each carpogonial branch (Figure 25). The tip of the trichogyne becomes expanded to receive the sperm nucleus (Figure 21, *I*) and, following fertilization, is soon lost (Figure 25, *II*, *III*). Clearly defined stages of the fusion process have been observed. The carpogonium develops a tubular process extended toward the auxiliary cell which is cut off from the upper side of the supporting cell; the auxiliary cell also develops a tube-like process which extends outward to link with the fusion tube from the carpogonium (Figure 26). A small cell-like structure, the "capping cell," referred to by Wollaston (1968) for genera of Antithamnieae, remains at the base of the degenerate trichogyne. The supporting cell enlarges prior to cutting off the auxiliary cell, but the actual process of auxiliary cell formation is almost, if not exactly, simultaneous with the development of the fusion tube preceding fusion. Elongation of the carpogonium prior to fusion occurs before the auxiliary cell and its fusion tube is apparent (Figure 27). Following auxiliary cell formation the lower remnant of the supporting cell remains as a narrow cell connecting the developing carposporophyte to the branch axis (Figure 28).

After fusion, the carpogonial branch including the carpogonium gradually degenerates, and the auxiliary cell develops a rounded gonimoblast cell from its upper part. Pit connections are visible between the remaining portions of the supporting cell and auxiliary cell, and between the auxiliary cell and the gonimoblast cell. Rounded groups of carposporangia are developed successively from the gonimoblast cell. Each group is initiated as an elongate protrusion from which carposporangial initials are cut off from the outer end. At this stage the connection between the supporting cell of the carposporophyte and the axial cell upon which it is borne becomes broadened (Figure 28). Rounded groups of carposporangia are formed by successive divisions of the carposporangial initials (Figure 29).

Spermatangia are borne in clusters on the upper side of inner and central cells of whorl-branchlets (Figure 30). Each cluster consists of a special short branch with 1–4 spermatangia developed outwardly from each terminal cell. The first-formed cluster are initiated on cells of immature whorl-branchlets near branch apices.

Tetrasporangia unknown.

Glandothamnus manifestus most closely resembles *G. ramulentus* but is distinguished by the pseudodichotomously branched whorl-branchlets arising from simple, unilaterally developed initials at branch apices, and by carposporophytes borne on lateral branches which occasionally elongate as the carposporophyte matures. To the present time this species is known only from southern Tasmania and has not been recorded from the Australian mainland.

Glandothamnus flexilis sp. nov.

Figures 31–36, 43

Thallus ad 8 cm altus, erectus, compositus axibus ramosis verticilla 2–4 ramulorum ex quaeque cellula axiali efferentibus et apice in rhizoideum ad affixendum interdum productus. Ramuli verticillati ad 1500 μm longos in apicibus ramorum unilateraliter ordinatim orientes, in thallo superiori vel melio adaxialiter ramosi, ramis oppositis inferis. Rami laterales in cellulis axialibus ipsis portati, vel in cellulis basalibus ramulorum verticillatorum portati. Cellulae glandulosae, oblique elongatae ad 25 μm longas, prominentes. Rami carpogoniales, carposporophyta et spermatangia ignota. Tetrasporangia stipitata, 1(–2)-cellularia longa in cellulis interioribus ramulorum verticillatorum, raro sessilia, globosa ad 30 μm diam cruciatim vel tetraedrice divisa.

The species is named for the tapering, flexuous form of whorl-branchlets.

TYPE LOCALITY: Approximately 20 km WSW of Outer Harbour, S. Aust., 22–25 m deep on shells (*McFarlane*, 11.ix.1975).

HOLOTYPE: ADU, A46637 (tetrasporic).

DISTRIBUTION: Known only from the type locality.

The thallus is flexuous, to 8 cm high, and consists of erect branched axes composed of narrow, elongate cells within a thick gelatinous sheath. Cells of lower main axes are closely articulating, up to 800 μm long and 450 μm broad, while cells of axes in the upper thallus are longer (to 300 μm) in proportion to breadth (to 50 μm) and less closely articulated. Each mature axial cell bears from its upper part a whorl of 2–4 whorl-branchlets which are initiated in unilateral sequence from the second immature axial cell at the tip of characteristically curved branch apices (Figure 31). Whorl-branchlets at first consist of an elongating rachis (Figure 32, *I*) which soon develops adaxial lateral branches (Figure 32, *II*, *III*). Mature whorl-branchlets are up to 1500 μm long and are adaxially branched in upper to central parts of the thallus, but usually bear opposite pairs of long filamentous branches, up to 800 μm long, below (Figure 32, *IV*). Axial growth takes place by transverse divisions of apical cells. Lateral branches arise directly from the upper end of axial cells (Figure 31), or from the basal cells of whorl-branchlets (Figure 33), and although they are rarely formed from the basal cell of whorl-branchlets on tetrasporic plants it is probable that they develop more commonly in this position on female plants, as occurs in *G. manifestus*. Gland cells, up to 25 μm long, are prominent on all parts of the thallus and are initiated early on young whorl-branchlets (Figure 31). Gland cell initials are cut off laterally from part or in young cells from the whole length of whorl-branchlet cells and elongate obliquely to the long axis of the cells upon which they are borne (Figure 34, *I–III*). Attachment rhizoids are developed from near the base of the thallus. Also, as in *G. ramulentus*, elongate rhizoidal filaments may be produced by terminal elongation of branch apices (Figure 35) and may twine around available support or, by developing digitate attachment structures, may presumably give rise to new individual plants.

Carpogonial branches, carposporophytes, and spermatangia unknown.

Tetrasporangia are borne on short stalks, 1(–2) cells long, on inner cells of whorl-branchlets, or occasionally are sessile. A terminal tetrasporangium is developed first on each stalk-cell followed by the development of lateral tetrasporangia. Mature tetrasporangia are spherical, up to 30 μm diameter, and cruciately or tetrahedrally divided (Figure 36, *I*, *II*).

The species is characterized by the form of the long flexuous whorl-branchlets, rhizoids which occasionally terminate branch axes, and the distinctive curved branch apices with unilateral development of whorl-branchlets. Although sexual plants have not been available, vegetative and tetrasporangial features indicate that the plant belongs to this genus.

Glandothamnus acicularis sp. nov.

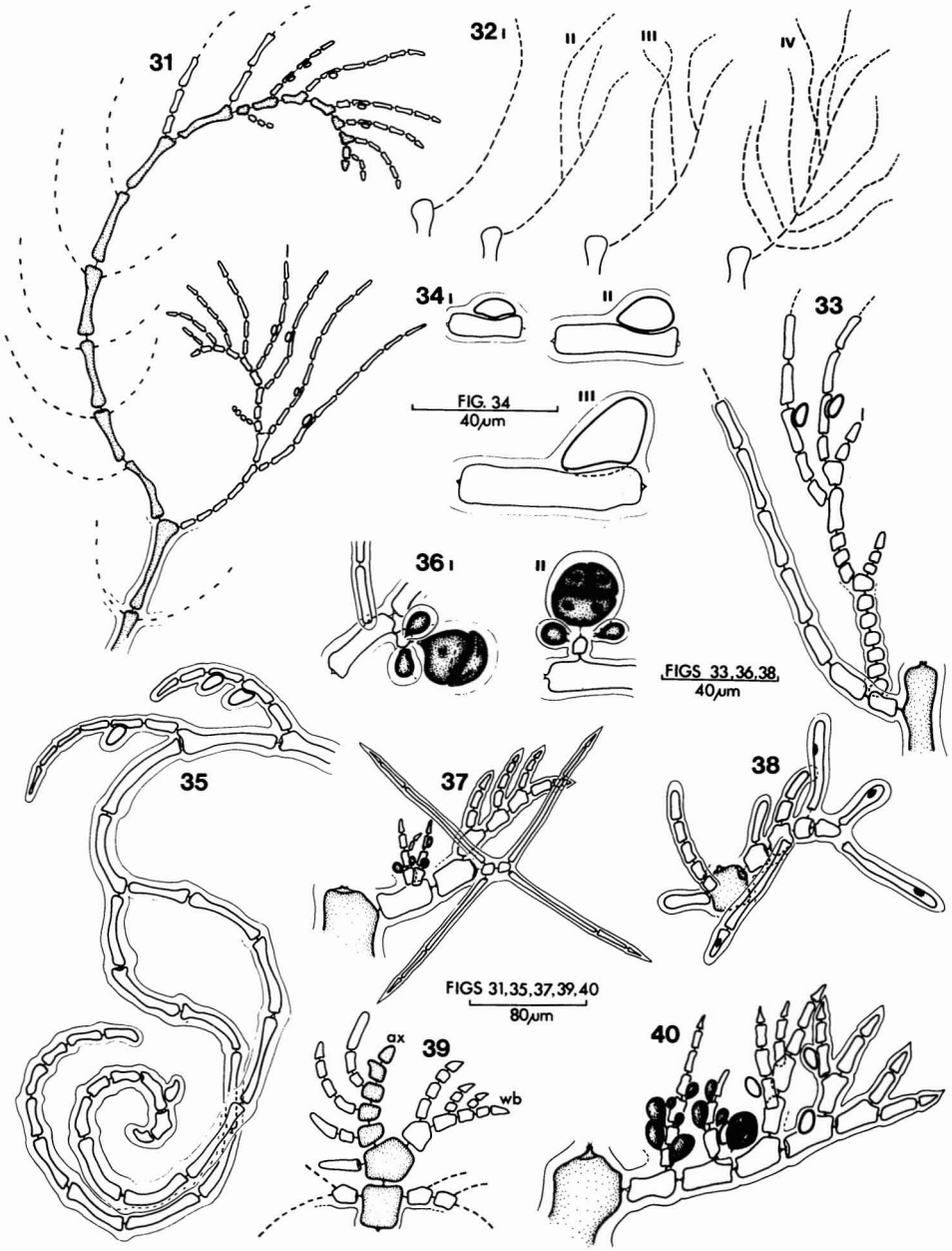
Figures 37–40

Thallus ad 2 cm vel ultra altus, erectus, compositus axibus ramosis, verticilla 2–4 ramulorum ex quaque cellula axiali efferentibus. Ramuli verticillati, ad 300(–400) μm longos, ramulis acutis ad 250 μm longos adaxialiter ramosi et in thallo superiori spinulas 4 spinis acutis ad 150 μm longas ferentes. Ramuli laterales in cellulis axialibus ipsis portati vel in cellulis basalibus ramulorum verticillatorum portati. Cellulae glandulosae oblique elongatae ad 20 μm longas. Rami carpogoniales, carposporophyta et spermatangia ignota. Tetrasporangia sessilia in cellulis interioribus ramulorum verticillatorum, globosa ad 36 μm diam cruciatim vel tetraedrice divisa.

The species is named for the needle-like spines occurring near branch tips.

TYPE LOCALITY: Taroona, Tasmania, 2–3 m deep, near jetty on vertical rock faces (*Shepherd*, 19.iii.1975).

HOLOTYPE: ADU, A46154 (tetrasporic).



FIGURES 31–36. *Glandothamnus flexilis* sp. nov. 31. Branch apices showing unilateral development of whorl-branchlet initials, lateral initiation of gland cells, and a primary lateral branch (*I*) developed from the upper end of an axial cell. 32, *I–IV*. Stages in development of a whorl-branchlet (diagrammatic). 33. Lateral branch (*I*) initiated from the basal cell of a whorl-branchlet. 34, *I–III*. Stages in development of a gland cell: (*I*) shortly after initiation, (*II*) further enlarged, (*III*) near maturity. 35. Branched attachment rhizoid developed by terminal elongation of a branch axis. 36, *I*, *II*. Tetrasporangia. Development of terminal tetrasporangia followed by lateral tetrasporangial initials borne on a small stalk cell.

FIGURES 37–40. *Glandothamnus acicularis* sp. nov. 37. Immature whorl-branchlet with spinous process terminal on rachis, and elongation continued from a branch borne on the rachis cell below the spinous structure. 38. Development of a spinous process by formation of elongate cells from the "corners" of the two terminal rachis cells of the developing whorl-branchlet. 39. Axial apex (*ax*) showing unilateral whorl-branchlet initiation from uppermost cells, and nearly mature whorl-branch (*wb*) immediately below. 40. Whorl-branchlet with gland cells and stages of tetrasporangial development.

DISTRIBUTION: Known only from the type locality.

The thallus, to 2 cm high, consists of erect branched axes composed of closely articulating cells within a thick gelatinous sheath. Cells of the lower axes are up to 800 μm long and 450 μm broad, while, in upper parts of the plant, cells are smaller, up to 500 μm long and 200 μm broad with length to breadth in the proportion of 3(–4):1. Each mature axial cell bears from its upper part a whorl of 4 whorl-branchlets, each to 300(–400) μm long, and branched from the adaxial side with often densely branched, acute-tipped branchlets up to 250 μm long; these branchlets are often borne in 2s, side by side, from the upper side of lower and central cells of the rachis. The rachides of whorl-branchlets are oriented at 45° to 90° to branch axes and are usually curved with downturned tips. Whorl-branchlets of the lower thallus are usually more densely branched than those above. Peculiar spinous structures, usually consisting of 2 small cells each bearing (1–)2–3 celled, tapered, acute spines, each to 150 μm long, are occasionally formed by modified development of the 2 terminal cells of whorl-branchlet rachides in upper parts of the thallus (Figure 37). The 4 radiating spines are developed from the corners of the cells which support them and the spinous structure thus formed replaces further elongation of the rachis in young whorl-branchlets (Figures 37, 38). Whorl-branchlet elongation is continued from a branch initiated on the rachis cell behind the spinous structure (Figure 37). Spinous processes are not often found on central and lower parts of the thallus and are thus probably caducous. Axial growth takes place by transverse division of apical cells forming 3–8 small cells at each branch tip; whorl-branchlets are initiated in unilateral sequence from these cells (Figure 39) but mature rapidly so that the next lower axial cells are distinctly larger and bear nearly mature whorl-branchlets (Figure 39) which overarch the small cells of the axial apex. Occasionally lateral branches replace immature whorl-branchlets in this region. Lateral branches may be initiated either directly from axial cells in place of whorl-branchlets or from the basal cells of whorl-branchlets and, as in *G. manifestus*, it is likely that lateral branches borne on basal cells of whorl-branchlets occur more abundantly on female plants. Gland cells are initiated laterally on cells of whorl-branchlets and elongate obliquely to the long axes of the cells upon which they are borne (Figure 40). When mature they are up to 20 μm long and scattered prominently over the thallus. Attachment rhizoids are developed from the base of the thallus. Filamentous rhizoids developed terminally from branch axes, as occur in *G. ramulentus* and *G. flexilis*, are not known to occur.

Carpogonial branches, carposporophytes, and spermatangia unknown.

Tetrasporangia occur abundantly and are formed successively on inner cells of whorl-branchlets. Mature tetrasporangia are sessile, spherical, to 36 μm diameter and cruciately, or occasionally tetrahedrally, divided (Figure 40).

This species is distinguished by the presence of spinous processes, the form of the abruptly tapered and acute-tipped whorl-branchlet branches, and the sessile position of tetrasporangia. It is tentatively placed in *Glandothamnus* on account of the unilateral whorl-branchlet initiation at branch apices, obliquely elongated gland cells, and adaxial branching of whorl-branchlets. In general habit, however, the thallus is less flexuous than in other species of *Glandothamnus*, and lower whorl-branchlets seldom develop opposite branches. Also, tetrasporangia lack stalk cells such as commonly occur in *G. ramulentus* and *G. flexilis*, although both these species may also produce occasional sessile tetrasporangia.

In several features *G. acicularis* resembles some species of *Platythamnion*, particularly in the form of whorl-branchlets which are characterized by curved rachides and adaxial branches, often in 2s, with abruptly tapered acute tips. However, *Platythamnion* is distinct in having whorl-branchlets arraged in whorls made up of 2 long and 2 shorter whorl-branchlets, while in *G. acicularis* the whorl-branchlets of each whorl are always approximately equal in length. *Glandothamnus acicu-*

laris also resembles species of *Platythamnion* in tetrasporangial features, in increased branching of whorl-branchlets toward the base of the thallus, and in rapid development of whorl-branchlets, or lateral branches, to overarch branch apices; however, in *Platythamnion* overarching usually occurs only from lateral branches. Unfortunately, sexual plants of *G. acicularis* have not been available for study, and confirmation of its identity awaits further collections and observations.

TAXONOMIC CONSIDERATIONS

From the foregoing descriptions it is clear that *Scageliopsis* and *Glandothamnus* possess a number of features in common with one another and with the genus *Scagelia*. One of the most significant is the ability of the fertile branch axis to continue growth following carposporophyte initiation. Similar axial elongation occurs in species of *Ballia* Harvey, but as shown by Wollaston (1974), this genus is also unique in features of procarp and carposporophyte development.

In describing *Scagelia*, Wollaston (1971) placed the genus in the tribe Heterothamnieae on account of its close resemblance to *Antithamnionella* in some features, including inconsistency in number of whorl-branchlets per whorl, irregularity in sequence of whorl-branchlet initiation at branch apices, and the small number of carpogonial branches produced at each branch apex. It should be noted, however, that some genera of Antithamnieae also show inconsistency in whorl-branchlet features (e.g., *Macrothamnion*, *Platythamnion*, *Hollenbergia*) and that adaxial branching of whorl-branchlets, especially of the form developed in *Glandothamnus acicularis*, is characteristic of some species of *Platythamnion* (Antithamnieae). Further. Wollaston (1971), in describing species of *Platythamnion* from the Pacific coast of North America, pointed out that although the fertile axes in species of this genus may or may not continue to elongate, they never remain as small and undeveloped as in *Antithamnion*. Hence in features of whorl-branchlet form and elongation of fertile axes, *Scageliopsis*, *Glandothamnus*, and *Scagelia* are probably not far removed from *Platythamnion*. In fact Wollaston (1971) suggested that *Scagelia* probably lay phylogenetically close to both *Antithamnionella* and the more stable thallus forms of *Platythamnion*. It now appears that *Scageliopsis* and *Glandothamnus*, while showing distinct relationship with *Scagelia*, are probably more closely allied to *Platythamnion* than is *Scagelia*, especially in stability of vegetative features. Fusions between cells of the developing earposporophyte in *Scageliopsis* and *Glandothamnus* are also more like those of *Platythamnion* than are the very pronounced fusions characteristic of *Scagelia* (Wollaston 1971).

The occurrence of both cruciate and tetrahedral division in tetrasporangia of *Scageliopsis* and *Glandothamnus* is also possibly indicative of an intermediate phylogenetic position. However, tetrasporangial features are not reliable taxonomic indicators in these groups. Although cruciate division of tetrasporangia occurs commonly in Antithamnieae and tetrasporangia are usually tetrahedrally-divided in Heterothamnieae, observations have shown that tetrasporangial division is often variable and both types can occur even on a single plant.

In separating Heterothamnieae from Antithamnieae, Wollaston (1968) emphasized the consistency of features associated with procarp and carposporophyte development within each tribe, and the consequent necessity for genera to be distinguished primarily using vegetative features.

Scageliopsis, *Glandothamnus*, and *Scagelia* can be satisfactorily separated generically by differences in thallus morphology and development. However, in procarp and carposporophyte features the genera are notably similar and again appear to lie between Heterothamnieae and Antithamnieae. The small number of procarps developed at each fertile branch apex and the less pronounced fusions between cells of the carposporophyte (except in *Scagelia*) are Heterothamnieae-like features, while the continued elongation of the fertile whorl-branchlet during carposporophyte development is Antithamnieae-like. Ability for axial growth to occur after

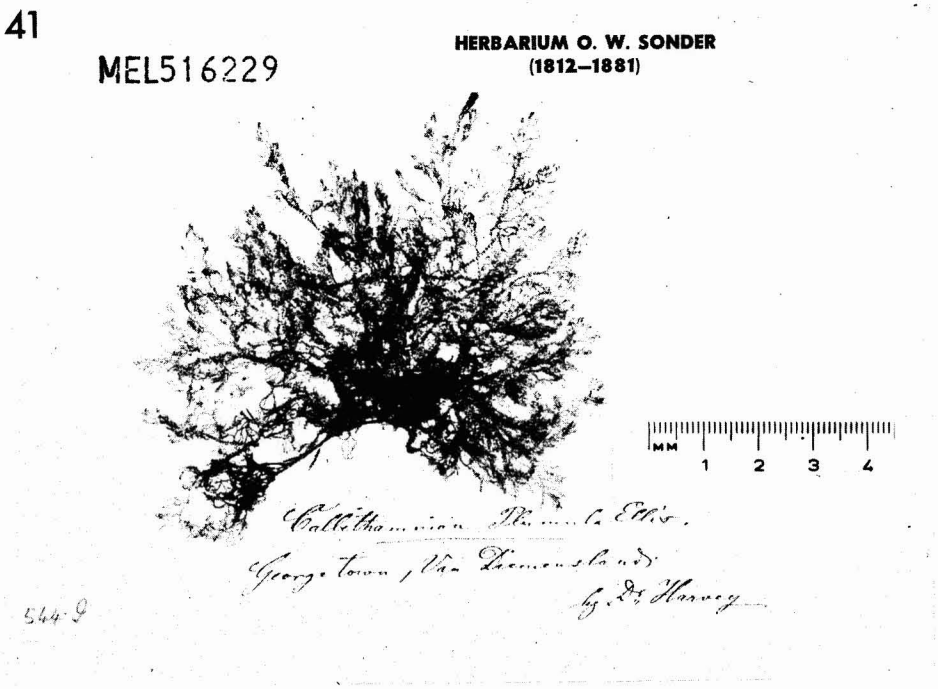


FIGURE 41. Type specimen of *Glandothamnus ramulentus* (Georgetown, Tas. *Harvey*, Alg. Aust. Exsicc. 544I, MEL 516229).

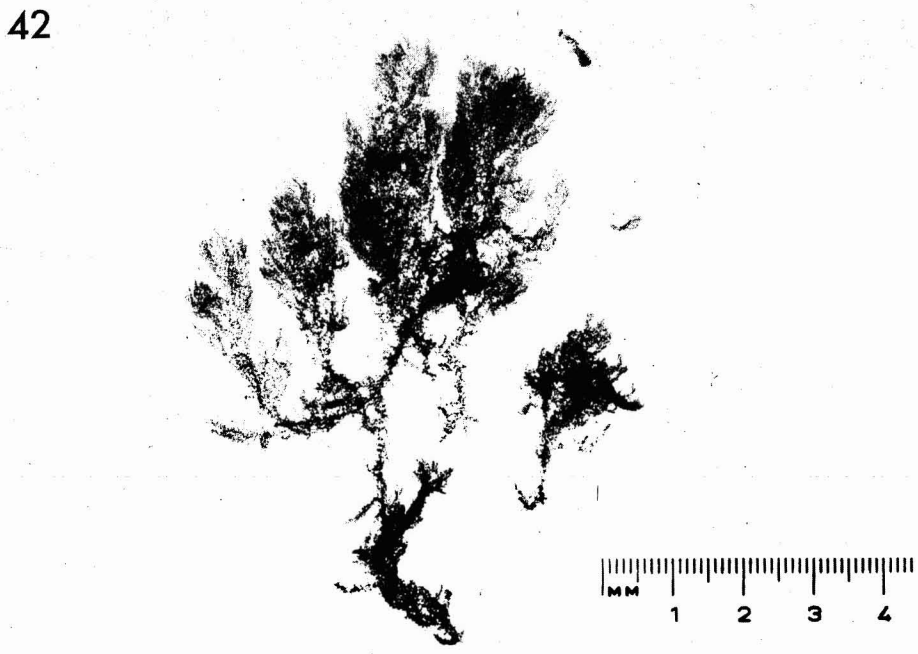


FIGURE 42. Type specimen of *Glandothamnus manifestus* (Woody I., D'Entrecasteaux Channel, Tas. *S. A. Shepherd*, 17.ii.1972, ADU A41641).

FIGURE 43. Type specimen of *Glandothamnus flexilis* (approx. 20 km, WSW of Outer Harbour, S. Aust. *J. McFarlane*, 11.ix.1975, ADU A46637).

carposporophyte initiation is not characteristic of either tribe although, as indicated previously, this potential has been observed in *Platythamnion*.

According to Wollaston (1968), Heterothamnieae is primarily characterized by the presence of 1(–2–3) sterile cells, probably representing a reduction of the fertile whorl-branchlet, on the supporting cell of the carpogonial branch, while in Antithamnieae the normal whorl-branchlet is developed. Hence as *Scageliopsis*, *Glandothamnus*, and *Scagelia* appear, in a combination of most characters, to lie between Heterothamnieae and Antithamnieae, it seems logical to place them firstly upon this basic tribal feature. It is thus proposed that *Scageliopsis* and *Glandothamnus* should be placed in Antithamnieae, and that *Scagelia*, because of development of the fertile whorl-branchlet and similarity to these genera in other features, should be transferred from Heterothamnieae and included with *Scageliopsis* and *Glandothamnus* in the tribe Antithamnieae of the Ceramiaceae. On the basis of vegetative features particularly, *Scagelia* is probably not far removed from Heterothamnieae while *Scageliopsis* and *Glandothamnus* are more closely allied to some genera of Antithamnieae.

KEYS TO GENERA OF ANTITHAMNIEAE AND HETEROTHAMNIEAE

Antithamnieae Hommersand

Antithamnieae is distinguished from Heterothamnieae by having carpogonial branches (2–20) developed at branch apices on basal cells of successive whorl-branchlets which continue to elongate during carposporophyte development. Whorl-branchlets are often distichously

arranged and secundly or pinnately branched. Tetrasporangia are frequently cruciately divided.

1. Thallus less than 10 cm high, erect or partly prostrate, attached by rhizoids; axes without rhizoidal cortication (except *Platythamnion nodiferum*). ..... 2.
1. Thallus erect, 8–30 (–40) cm high (to 3 cm in *Macrothamnion pectenellum*), usually with distinct fibrous holdfast. Axes corticated with rhizoids, at least in lower thallus. ..... 8.
   2. Whorl-branchlets in 2s, opposite on each axial cell. Gland cells borne on special short branches on whorl-branchlets. ..... *Antithamnion.*
   2. Whorl-branchlets verticillate, 1–4 per axial cell. Gland cells borne directly on cells of whorl-branchlets. ..... 3.
3. Whorls of 2 long opposite whorl-branchlets at right angles to 2 short opposite whorl-branchlets. (See 9 for *Platythamnion nodiferum.*) ..... *Platythamnion.*
3. Whorls 2–4 on each axial cell, sometimes varying in number and form in each whorl. 4.
   4. Mature gland cells terminal on rachides of pinnately branched whorl-branchlets. ..... *Acrothamnion.*
   4. Mature gland cells not terminal on rachides of whorl-branchlets. ..... 5.
5. Gland cells almost spherical near outer tips of whorl-branchlet branches, initiated terminally. Fertile axes cease elongation with carposporophyte initiation. ..... *Hollenbergia.*
5. Gland cells seldom spherical, usually abundant, scattered on whorl-branchlets, initiated laterally on whorl-branchlet cells. Fertile axes capable of continued elongation after carposporophyte initiation. ..... 6.
   6. Mature gland cells often elongated obliquely to whorl-branchlet axes. *Glandothamnus.*
   6. Mature gland cells with long axis lateral on cells of whorl-branchlets. ..... 7.
7. Whorls of (2–) 3–4 whorl-branchlets usually with 1 (–2) distinctly longer than the others. ..... *Scagelia.*
7. Whorls of 2–4 whorl-branchlets, all equal in length. ..... *Scageliopsis.*
   8. Whorls of (2–) 3 evenly spaced equal whorl-branchlets; gland cells on special short branches on whorl-branchlets. ..... *Macrothamnion.*
   8. Whorls distichously (or tristichously) arranged, sometimes with short whorl-branchlets between the longer ones or with branchlets irregularly developed, not in whorls. Gland cells sessile or absent. ..... 9.
9. Gland cells sessile on rachides of whorl-branchlets. ..... *Platythamnion nodiferum.*
9. Gland cells absent. ..... *Ballia.*

Heterothamnieae Wollaston

Heterothamnieae is distinguished from Antithamnieae by having carpogonial branches (1–4) developed at branch apices on basal cells of successive whorl-branchlets which are reduced to 1–2 (–3) cells in length and appear as sterile cells on the supporting cell of the carpogonial branch. Whorl-branchlets are usually not distichous, simple or branched irregularly or by whorls. Tetrasporangia are frequently tetrahedrally divided.

1. Whorl-branchlets unbranched, or consisting of a distinct rachis from which branches arise. ..... 2.
1. Whorl-branchlets branched by successive whorls of cells, mostly with at least one whorl of 3 branches, sometimes unequal in length, from the outer end of a large basal cell. ..4.
   2. Whorls variable in number (1–4) and form of whorl-branchlets; branching of whorl-branchlets often increasing toward base of thallus. ..... *Antithamnionella.*
   2. Whorls of 4 whorl-branchlets (3–5 in *Trithamnion*) usually decreasing in length and branching toward base of thallus. ..... 3.

3. Plants in tufts, only known to occur on receptacles of *Cystophora* species. Whorl-branchlets equally spaced in each whorl. Gland cells sessile usually on 3rd–5th cell of whorl-branchlet rachis. ..... *Heterothamnion.*
3. Plants not in tufts. Whorl-branchlets 3 (–5), unilaterally placed in each whorl. Gland cells on branches of whorl-branchlets. ..... *Trithamnion.*
   4. Lateral branches forming apparent dichotomies with axes. Whorl-branchlets usually short in relation to size of axial cells. ..... *Amoenothamnion.*
   4. Lateral branches not equivalent nor appearing dichotomous with axes. Whorl- branchlets not conspicuously short. ..... 5.
5. Lateral branches often crowded on axes and limited in growth. Tetrasporangia usually on special short branches borne on inner cells of whorl-branchlets. ..... *Perithamnion.*
5. Lateral branches spaced along axes and not obviously restricted in growth. Tetrasporangia sessile on central to outer cells of whorl-branchlets. ..... *Tetrathamnion.*

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