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## MORPHOLOGICAL AND TAXONOMIC STUDIES ON ANTARCTIC CERAMIACEAE (RHODOPHYCEAE). I. *ANTARCTICOTHAMNION* *POLYSPORUM* GEN. ET SP. NOV.

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*Antarcticothamnion polysporum* gen. et sp. nov. (Rhodophyceae: Ceramiaceae) is described from the South Shetland Is. and the Antarctic Peninsula. It differs from all previously described Ceramiaceae in vegetative structure: an indeterminate apex, which divides by alternating oblique septa, produces simple alternate-distichous determinate branches, while indeterminate branches are initiated on main axes in a verticillate arrangement. Reproductive structures are borne on modified indeterminate branch systems. Sporangia are polyhedrally divided. Spermatangia are formed in loose heads. Procarps are borne near the apex, but not always on the subapical cell, of a fertile branch. Two auxiliary cells may participate in the formation of a carposporophyte. A fusion cell is lacking and most cells of the gonimoblast develop into carposporangia, which are binucleate.

The suite of morphological characters exhibited by *Antarcticothamnion* sets this genus sufficiently apart from all previously described Ceramiaceae to warrant placement in its own tribe, *Antarcticothamnieae* trib. nov. It shares important features, however, with *Callithamnieae*, *Compsothamnieae*, and *Ptiloteae*.

Apical division is reviewed in the various tribes of Ceramiaceae. It is concluded that a pattern of alternating oblique septa is correlated with transitory or chronic structural imbalance resulting from a particular combination of timing and spatial sequence in the initiation and development of branches. The distribution of oblique apical division within Ceramiaceae is strongly correlated with features generally considered to be important at the level of tribe.

Phylogenetic relationships within *Ptiloteae*, a tribe characterized *inter alia* by oblique apical division, are suggested from an analysis of branching patterns. The validity of *Falklandiella* as a genus distinct from *Dasyptilon* is emphasized. *Gymnothamnion* and *Tokidaea* are removed from *Ptiloteae*, but without being assigned to another tribe. *Tanakaella* is removed from *Sphondylothamnieae* to *Compsothamnieae*, while *Mazoyerella* is removed from *Compsothamnieae* to *Spermothamnieae*.

*Spongoconium orthocladum* A. et E. S. Gepp is discussed as a possible species of *Antarcticothamnion*, while an undescribed alga from the South Orkney Is. is definitely indicated as a second species of the genus.

The Antarctic members of the red algal family Ceramiaceae are even more poorly known than the flora of which they are a part. One of the eight species, *Spongoconium orthocladum* A. et E. S. Gepp, is known only from the type collection (from the Ross Sea). A second, *Antithamnion antarcticum* Kylin, has been collected twice (Kylin & Skottsberg, 1919; Lamb & Zimmerman, 1977), but never in reproductive condition. Two others, *Georgiella confluens* (Reinsch) Kylin and *Plumariopsis eatonii* (Dickie) De Toni, were originally described from South Georgia and Kerguelen, respectively, but subsequently have been reported from the Antarctic Peninsula. One further species, *Ballia callitricha* (C. Ag.) Kütz., originally described from the Falkland Is., is widely distributed in the Antarctic and the South Temperate Zone. The remaining three species—*Antithamnion simile* (Hook. f. et Harv.) J. Ag. (type from Kerguelen), *Ceramium involutum* Kütz. (original material from Cape Horn and the Falkland Is., yet

to be lectotypified), and *Griffithsia antarctica* Hook. f. et Harv. (lectotype from Cape Horn; cf. Baldock, 1976, p. 534)—have been reported only once from the Antarctic, in each case as fragments.

Participation by one of us (Moe) in a programme of biological studies supported by National Science Foundation grants GV 31162 and OPP 74-12139 provided opportunities to collect marine algae on the Antarctic Peninsula during a 15-month period in 1973-75. Most specimens came from the vicinity of Palmer Station on Anvers I. Additional collections were made at several islands of the South Shetland group. Material at hand has proved adequate for detailed morphological studies of five species of Ceramiaceae. In the first paper of the present series, a new genus and species, *Antarcticothamnion polysporum*, will be described.

## DESCRIPTION

### VEGETATIVE STRUCTURE

The thallus (Fig. 1), which reaches a length of 6 cm, is dull red and flaccid. It is composed of a more or less percurrent, monosiphonous, erect axis with the largest cells 150  $\mu$ m diam.  $\times$  500  $\mu$ m long. The apical cell of the main axis divides by oblique septa, alternating left and right, and thus produces an alternate-distichous series of simple filaments (Fig. 2). Subsequently, these filaments may bear fertile branches and corticating rhizoids on their lowermost cells. Occasionally, the basal cell produces a short, simple, sterile filament. The apical cell of a filament is broadly rounded to pointed, 10-20  $\mu$ m diam.  $\times$  12-40  $\mu$ m long, dividing by transverse concave or convex septa (Figs 2, 3). The largest cells of a filament are in the middle, reaching 130  $\mu$ m diam.  $\times$  170  $\mu$ m long. Basal cells of a filament reach 60  $\mu$ m diam.  $\times$  75  $\mu$ m long. Filaments curve adaxially when young and short, but tend to be reflexed when old and long. Branches morphologically similar to the main axis are initiated on that axis at varying distances (7-30 cells) below the uppermost filament. The first such indeterminate branch is produced opposite a filament (Figs 2, 9-11), while one or two additional ones may arise at right angles, resulting maximally in a tetrastichous whorl. It should be emphasized that these whorls comprise only a single determinate branch (filament) combined with 1-3 indeterminate branches. The axes of these first-order indeterminate branches bear alternate-distichous simple filaments identical to those borne by the main axis. The oldest first-order indeterminate branches produce second-order indeterminate branches, arranged in whorls as they are along the main axis. Not all indeterminate branch primordia proceed to develop, nor do they develop in a regular acropetal sequence. While the most highly developed indeterminate branches tend to be borne on the lower portion of the main axis, it is common to find initials or short primordia lower on the axis than well-developed branches. Indeterminate branches may curtail their growth even when the thallus is wholly vegetative and thus in the absence of the inhibitory effect of reproductive structures. An axis that has ceased growing terminates in an acuminate tip with the cells separated by transverse walls (Fig. 3). Dehiscence and suppressed initiation of filaments frequently result in pectinate or irregular branching patterns. The lower portion of an axis is often devoid of filaments.



FIGS 1-3. *Antarcticothamnion polysporum*. Fig. 1. Habit (Moe 130 = holotype).  $\times 8$ . Fig. 2. Actively dividing apex. Note alternating oblique septa. Arrow indicates initial cell of indeterminate branch. Moe 109.  $\times 60$ . Fig. 3. Apex of inactive axis. Note transverse septa. Moe 109.  $\times 100$ .

Fertile branches or branch systems are borne either (1) on the main axis, (2) on the lower portion of the axis of an indeterminate branch, or (3) on the lower portion (often the basal cell) of a filament. Although their basic pattern of development is like that of the indeterminate branches, with a tendency to form alternate-distichous filaments, irregularities occur, possibly as a result of crowding, and vegetative growth essentially ceases with the initiation of reproductive structures. Fertile thalli are much more profusely branched than sterile ones and appear banded because of the whorls of fertile branches. Spermatangial plants appear less congested than other reproductive phases.

The lower portion of the main axis and of well-developed indeterminate branches is loosely covered with decurrent branched rhizoids which originate from the basal cells of determinate and indeterminate branches (Fig. 13). The rhizoids form a web that attaches the thallus to the substrate. They terminate simply, without forming the digitate haptera characteristic of many Ceramiaceae. At times they terminate by forming secondary pit-connections with other rhizoids or with cells in the lower portion of a branch.

All vegetative cells are multinucleate and contain numerous elongate plastids.

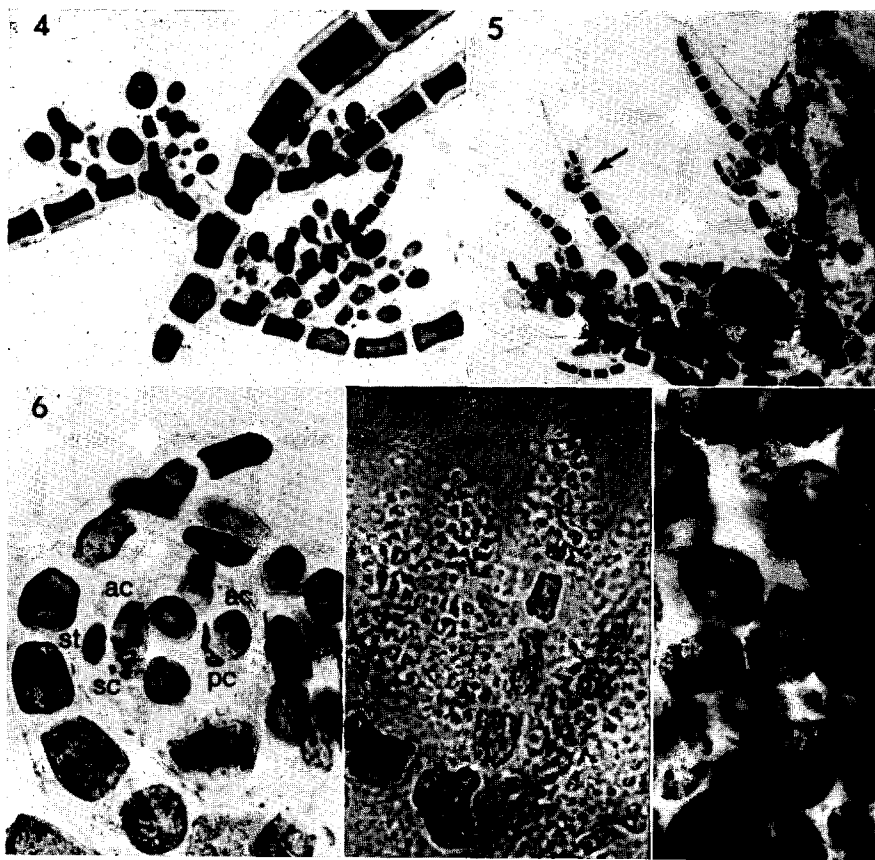
#### REPRODUCTIVE STRUCTURES

Polysporangia result from metamorphosis of apical cells of ordinary filaments of very short fertile branches (Figs 4, 16). The sporangial mother cell contains at first a single nucleus which then undergoes a series of asynchronous divisions to produce 12–24 nuclei. Nuclear division is followed by simultaneous cytoplasmic cleavage, resulting in a spherical polysporangium containing 12–24 walled spores. The sporangium enlarges after cleavage, reaching a maximum diameter of 120  $\mu\text{m}$ .

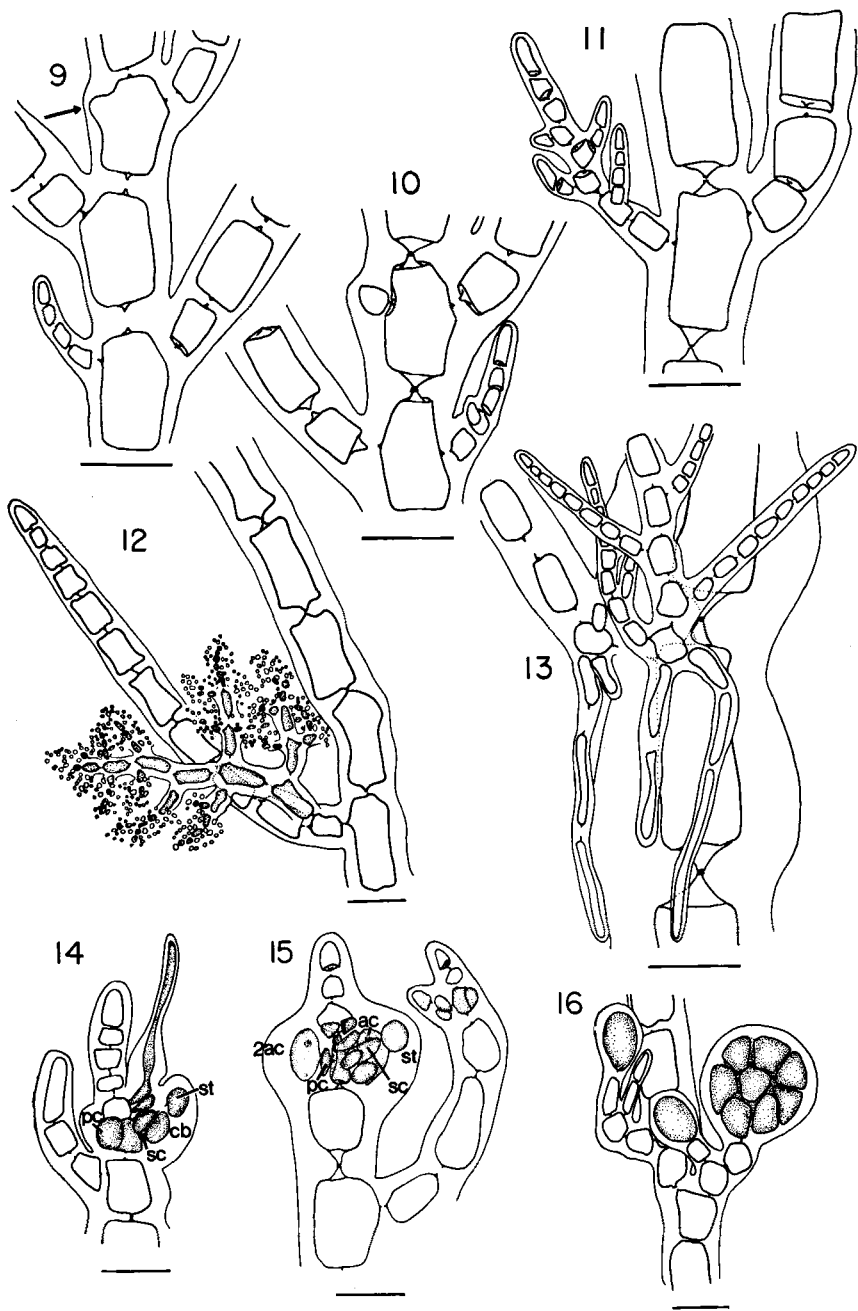
Spermatangia are produced in loose heads on specialized branchlets of short fertile branches (Figs 7, 12). After the fertile branch has produced a few vegetative filaments, the lowermost of which may be rebranched, all of the apical cells begin to cut off in rapid succession a series of cells which, without elongating, produce branchlets 1–3 cells long in partial or complete whorls of 1–4. Even before spermatangia are cut off, a spermatangial branch is recognizable by its condensed habit and the angularity and paleness of the cells. A mature spermatangial branch system is roughly conical, with all terminal cells (including the apical cell of each component branch) and some subterminal cells functioning as spermatangial mother cells. As spermatangia form, the axial cells of the branch system elongate and become less angular. Spermatangia are cut off singly. As one matures, another is initiated. They are subspherical, 4–5  $\mu\text{m}$  diam., and contain a distal nucleus and a proximal vacuole.

The female fertile branch produces a few vegetative filaments, the lowermost of which may be rebranched, before the initiation of procarys. Procarys are produced at a distance of 2–4 cells below the apical cell either of the axis of the fertile branch or of a first-order filament. Several may occur on one branch system (Fig. 5), but only one develops into a carposporophyte. The cell that initiates a procary cuts off two pericentral cells at right angles to one another (Fig. 14). The one in the plane of branching—the supporting cell—cuts off first a sterile cell apically and then the carpogonial branch initial from its lower surface. The pericentral cell perpendicular to the plane of branching—the

mother cell of a second auxiliary cell—is cut off after the supporting cell but before the carpogonial branch is initiated. Both pericentral cells are uninucleate. The sterile cell is multinucleate. The four-celled carpogonial branch, which is produced by sequential division, curves upward around the supporting cell on the side towards the second pericentral cell (that is, towards the site of the future second auxiliary cell). The two basal cells of the carpogonial branch contain more than one nucleus—usually two, occasionally three. The third cell and the carpogonium are uninucleate. The trichogyne is long and straight with a basal swelling. Following presumptive fertilization, two auxiliary cells are cut off—one from the upper surface of the supporting cell and one terminally from the second pericentral cell (Figs 6, 15). Either or both of the auxiliary cells, after fusing with a cell cut off from the fertilized carpogonium, divides



FIGS 4-8. *Antarcticothamnion polysporum*. Fig. 4. Branch bearing undivided polysporangia. Moe 123.  $\times 95$ . Fig. 5. Female branch system showing subterminal procarys (arrows). Moe 41.  $\times 100$ . Fig. 6. Post-fertilization stage showing two auxiliary cells; ac = auxiliary cell, pc = pericentral cell, sc = supporting cell, st = sterile cell. See also Fig. 15. Moe 109.  $\times 460$ . Fig. 7. Spermatangial branch system. Moe 109.  $\times 390$ . Fig. 8. Carposporangia. Note two nuclei in each sporangium. Moe 136.  $\times 300$ .



FIGS 9-16.

to form a foot cell and a primary gonimoblast cell. No fusion cell forms in the developing carposporophyte. After fertilization, the apical cell of the fertile axis undergoes a few successive divisions, the prolongation forming part of the involucre. The sterile cell borne on the supporting cell sometimes divides to form a two-celled sterile branch. Cells below the procarp produce abundant involucre branches which loosely envelop the carposporophyte (and, together with omnipresent epiphytes, obscure the details of carposporophyte development). Gonimolobes are of different sizes, indicating development in sequence or at different rates. Most cells of the carposporophyte become spheroidal carposporangia, the largest of which measure 40–50  $\mu\text{m}$  diam. Mature as well as immature carposporangia contain two nuclei (Fig. 8).

### ECOLOGY

*Antarcticothamnion polysporum* was usually found growing on a bryozoan which in turn grew on *Phyllophora ahnfeltioides* Kylin and *Myriogramme manginii* Gain, but one collection was made from a tunicate. Plants grew at depths of 13–26 m in clear offshore water. All plants were densely epiphytized by diatoms and by the green alga *Entocladia*. In some instances, the latter formed an entire corticating sheath around branches. Since plants were found only in October and January, it is possible that *Antarcticothamnion* is a spring–summer annual, but more observations are needed to settle this point. The substrates on which it was found are available throughout the year.

### DISTRIBUTION

South Shetland Is.: Elephant I.: Moe 130, 139; Livingston I.: False Bay: Moe 188a; Deception I.: Moe 104, 964b, 982.

Antarctic Peninsula: Anvers I.: Palmer Station: Moe 14, 41, 674.

### DISCUSSION

The suite of characters exhibited by *Antarcticothamnion polysporum* not only sets this alga far apart from all previously described genera of Ceramiaceae, but precludes its assignment to any existing tribe. Most characters seem at least moderately advanced. The vegetative structure is unique: an apical pattern of alternate-distichous determinate filaments changing below, through delayed branch initiation, into a situation in which there are pairs or whorls composed of a determinate filament and 1–3 indeterminate branches. If the assumption is made that the most primitive structure in Ceramiaceae is a monosiphonous axis

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FIGS 9–16. *Antarcticothamnion polysporum*. Camera lucida drawings. (Figs 9–11 and 13, bar = 100  $\mu\text{m}$ ; Fig. 12, bar = 50  $\mu\text{m}$ ; Figs 14–16, bar = 25  $\mu\text{m}$ .) Fig. 9. Initiation of indeterminate branch (arrow). Moe 109. Fig. 10. Stages in development of indeterminate branch. Moe 109. Fig. 11. Later stage in development of indeterminate branch, showing alternating oblique divisions of apical cell and alternate branching. Moe 109. Fig. 12. Spermatangial branch system. Moe 123. Fig. 13. Development of rhizoids from basal cells of determinate and indeterminate branches. Moe 109. Fig. 14. Procarp; cb = carpogonial branch, pc = pericentral cell, sc = supporting cell, st = sterile cell. Moe 982. Fig. 15. Early post-fertilization stage; ac = auxiliary cell, 2ac = second auxiliary cell, pc = pericentral cell, sc = supporting cell, st = sterile cell. Moe 109. Fig. 16. Polysporangial branch. Moe 139.



bearing whorls of determinate laterals (Hommersand, 1963, p. 291) or pairs of indeterminate laterals (Wollaston, 1971, p. 297), *Antarcticothamnion* must be considered highly derived. Evidence that the verticillate branching in this genus has evolved secondarily is provided by (1) the apices of indeterminate axes, which, when active, divide by oblique septa to produce alternate-distichous laterals, and (2) the composition of the whorls, which is unlike the pairs of indeterminate branches bearing determinate branchlets in the Warrenieae (Wollaston, 1971) or the whorls of determinate branches (whorl-branchlets) in the Antithamnieae, Heterothamnieae, Crouanieae, Wrangelieae, Sphondylothamnieae and Griffithsieae (Wollaston, 1968; Gordon, 1972; Baldock, 1976). The only tribes having members with an alternate-distichous pattern of indeterminate axes are the Callithamnieae and Compsothamnieae, so that it is not surprising that the apex of the actively growing indeterminate axis of *Antarcticothamnion* is most like that of certain species of *Callithamnion* and *Pleonosporium*. In all three genera, the only manifestation of a primitive whorled structure is the cutting off of pericentral cells in the formation of a procarp and, in some cases, in the formation of spermatangial mother cells.

Certain fundamental aspects of apices—specifically, the shape and relative size of the apical cell and its immediate derivatives, and the form and orientation of the septa of successive divisions—have not been accorded sufficient importance in the taxonomy of Ceramiaceae, in our opinion. Even in detailed and precise descriptions, the apex is often treated superficially. The form of the septa is rarely stated and gradations in obliqueness are seldom distinguished. Among those authors who have made comprehensive surveys of the family, Feldmann-Mazoyer (1941, p. 121) stated that the apical cell of Ceramiaceae generally divides by a septum perpendicular to the axis of the frond. She listed three exceptional instances of oblique septa: *Crouaniopsis annulata* (Berth.) J. et G. Feldm. (= *Gulsonia mediterranea* Kylin), *Wrangelia penicillata* (C. Ag.) C. Ag., and *Spyridia*. Kylin (1956), while describing and illustrating the apical cell and its division in certain genera (especially Ptiloteae), did not generalize. Hommersand (1963, p. 292) stated that in simple monosiphonous Ceramiaceae axial growth is initiated by an apical cell that divides transversely into two daughter cells of nearly the same size. He also (p. 179) described the division of the apical cell in *Spyridia filamentosa* (Wulf.) Harv., in which oblique concave septa result in a spiral series of trapezoidal segments, and thus confirmed the classical work of Cramer (1863). In the Ceramiaceae, Hommersand distinguished between axial growth by transverse septa and the initiation of apical branches (holoblastic branching) by oblique septa. The most extensive consideration of the apical cell and its mode of division is to be found in Itono (1977), who, in discussing all species of Ceramiaceae from southern Japan, assessed the taxonomic significance of morphological details. Itono recognized four types of divisions: (1) transverse; (2) oblique, with the high sides of the segments arranged on the same side of the axis; (3) oblique, with the high sides of the segments arranged alternately; and (4) oblique, with the high sides of the segments arranged in a spiral. He concluded that the four types occurred irregularly, without close relationship to phylogeny. From a reading of his carefully prepared descriptions and an examination of his Table II, however, we draw the opposite conclusion, as will be shown in the following discussion.

The patterns of division of the apical cell in Ceramiaceae do not represent an independent evolutionary trend, but rather are correlated with patterns of branching and subsequent thallus development. Since the latter are accorded great importance at the tribal level in this family, it follows that patterns of apical division are also highly significant. It is probably this close correlation that has led to underrating the taxonomic importance of the details of apical division.

An obliquely dividing apical cell seems to be correlated with a primary growth pattern involving transitory or chronic structural imbalance resulting from a particular combination of timing and spatial sequence in the initiation and development of branches. A simple illustration of this point is provided by alternate-distichous members of the Callithamnieceae and Compsothamnieceae, such as *Callithamnion* and *Pleonosporium*. In certain species of these genera (e.g. *C. rupicola* Anders. and *P. squarrulosum* (Harv.) Abb.; cf. Abbott & Hollenberg, 1976, figs 557 & 561) the alternating oblique septa are retained for varying distances below the apex, the zigzag axis thus comprising a series of segments that compensate, left and right, for a chronically unbalanced thallus.

Even in genera with symmetrically opposite or whorled branching, imbalance exists to a degree dependent upon the delay in initiating the second branchlet of a pair or the complementary branchlets of a whorl. In most species with symmetrically opposite branching (e.g. *Antithamnion calloclados* Itono; cf. Itono, 1977, fig. 3D) the two members of a pair of branchlets are initiated in rapid succession and in a regular alternating sequence. Imbalance is thus effectively eliminated or confined to a single apical derivative. In a few instances (e.g. *A. plumula* (Ell.) Thur.; cf. Nägeli in Nägeli & Cramer, 1855, pl. VII), however, the apex curves sinusoidally as it cuts off groups of first-formed laterals in an alternating second pattern, always bending away from the side from which the last group of initials is being formed. The apical cell divides by a septum that is perpendicular to the tangent of the curve and successive septa are therefore slightly oblique with respect to one another. In species with whorled branching, apical imbalance appears to be obviated or at least minimized by the circumstance that the first-formed branchlets are initiated from successive segments in a spiral involving small angular intervals, followed closely by the initiation of complementary branchlets of each whorl. While the precise form of apical septa in most Crouanieae has not been described, it seems reasonable to expect some degree of obliqueness in certain species. The occurrence of oblique septa in *Gulsonia mediterranea* was mentioned above. From an examination of liquid-preserved material of *G. annulata* Harv. (Kangaroo I., Australia, Womersley A10613) we conclude that the septa are slightly oblique with the high sides of the cells arranged spirally. This observation agrees with the statement by Wollaston (1968, p. 277) that the first-formed initials are cut off in a  $1/8$  spiral. The imbalance suggested by the oblique septa seems to be related to the timing of initiation of the complementary branchlets of each whorl, which in turn seems to be related to the position of the axis on the thallus. The apex of an indeterminate branch (Wollaston & Womersley, 1959, fig. 2c) must undergo numerous divisions before it breaks through the gelatinous matrix and dense investiture of whorl-branchlets of the parent axis. While it is within the matrix, initiation of complementary branchlets appears to

be inhibited. Our examination of a main axis reveals an apex which is shorter and which initiates complementary branchlets much more rapidly than that of a lateral branch.

Among Ceramieae with whorl-branchlets, only *Wrangelia* has a pattern of alternating oblique septa. In this genus, which stands apart in its own tribe chiefly because of its highly specialized mode of carposporophyte development, oblique septa are undoubtedly related to the trend towards bilaterality (e.g. *W. nobilis* Hook. f. et Harv.), presaged in less advanced species (e.g. *W. penicillata*) by the alternating position, left and right, of the first-formed whorl-branchlet on successive axial segments.

Among Ceramieae, Itono (1977) described the septa as wholly or partly oblique in *Reinholdiella*, *Herpochondria*, *Campylaeophora*, *Ceramium* and *Centroceras* (and thus in disagreement with previous authors, including Hommersand, 1963). Oblique septa in these genera are associated with two patterns of initiation of pericentral cells. In most instances the apex is curved as a result of unilateral initiation of first-formed pericentral cells from the high side (convex side) of successive segments. In a few species (e.g. *Ceramium serpens* S. et G.) the high sides of successive segments lie in a spiral, as do the first-formed pericentral cells. As mentioned above, oblique septa are also involved in holoblastic branching, which is restricted within the Ceramieae to certain genera of Ceramieae (e.g. *Centroceras*, *Ceramium*, *Herpochondria* and *Microcladia*). In this instance the septum separating the branch initial must be oblique in order that the remainder of the apical cell be in a position to proceed with axial elongation.

The occurrence of oblique septa in *Griffithsia*, while not mentioned by Baldock (1976), is carefully described by Itono (1977). In this genus, it is correlated with a subdichotomous pattern of branching. The apical cell divides by an oblique septum in those species in which branches arise from the subapical cell (e.g. *G. japonica* Okam.; cf. Itono, 1977, fig. 28G), but by a transverse septum in those species in which branches arise well behind the apex (e.g. *G. rhizophora* Grun.; cf. Itono, 1977, fig. 28L).

Among Dohrnielleae, a small group of radially branched species in which reproduction remained largely unknown until recently, oblique septa were described by Taylor (in Taylor & Arndt, 1929) when establishing *Actinothamnion antillarum* (transferred to *Dohrniella* by Feldmann-Mazoyer in 1941). Taylor carefully distinguished apical division in indeterminate axes from that in determinate laterals. The apex of a main axis divides by slightly oblique septa, with a lateral being initiated from the high side of each segment. Determinate apices, by contrast, elongate by transverse divisions, but cut off by oblique septa the nodal cells characteristic of *Dohrniella*. According to Taylor, the first lateral of an indeterminate axis is generally initiated by the subapical cell. The laterals develop rapidly, exceeding the apex, and curve adaxially, tightly enclosing the apex subcorymbosely. Our examination of liquid-preserved material of *D. antillarum* (Jamaica, V. J. Chapman) generally confirms Taylor's observations. In our material, however, it is the third or fourth rather than the second axial cell that usually initiates the first lateral. Moreover, the incurving of determinate laterals is seen to be caused by one or two unilaterally oblique divisions immediately following their initiation.

Oblique septa do not occur in Spermothamnieae, a tribe in which branching tends to be sparse and irregular or subdichotomous, but is opposite in *Ptilothamnion pluma* (Dillw.) Thur.

The tribe Delesseriopsidae, in our opinion, comprises only *Delesseriopsis elegans* Okam., an unusual plant with asymmetrically opposite branches that cohere to form a membrane. Itono (1977, p. 78) described elongation of the thallus by means of a transversely dividing apical cell, but available illustrations (Okamura, 1931, pl. CCLXXIV: fig. 2; Tanaka, 1965, fig. 12A) strongly suggest a pattern of oblique divisions. Unfortunately, material has not been available to us to clarify the situation.

The Ptiloteae are generally considered to constitute one of the most advanced tribes of Ceramiaceae. Vegetatively they are characterized by a branching pattern that is basically opposite, but usually effectively alternate, and by specialized cortication. On the basis of the mode of apical division in indeterminate axes, Yoshida (1974) recognized two groups of Ptiloteae: *Diapse*, *Euptilota*, *Georgiella*, *Neoptilota* and *Ptilota*, with oblique divisions; *Gymnothamnion*, *Tokidaea*, *Plumaria*, *Plumariella* and *Plumariopsis*, with transverse divisions. Our survey of Ptiloteae shows that this distinction is untenable. First, contrary to published reports, oblique divisions occur in all genera, with the possible, but unlikely exception of *Plumariella*. Unfortunately, material of that genus has not been available for us to determine the correctness of published descriptions specifying transverse divisions (Okamura, 1930; Kylin, 1956). Second, there is more than one pattern of oblique septa.

As postulated earlier in this paper, oblique septa are related to structural imbalance, and while they are predictably conspicuous in alternate-distichous branching patterns, they may be equally conspicuous in opposite-distichous patterns involving delayed initiation or delayed and even permanently suppressed development of the second members of alternating pairs of branch primordia. Depending upon the degree of delay and suppression, the branching pattern may be transitorily alternate, permanently and effectively alternate, or truly alternate. From this point of view, the various Ptiloteae can be arranged as follows.

(1) *Plumaria*, in which branching is basically opposite-distichous but with the addition on indeterminate axes of short cortex-initiating primordia perpendicular to the plane of the thallus. Each member of a pair of laterals develops usually into a determinate branch, occasionally into an indeterminate branch, the two members usually disparately developed. The first-formed laterals are initiated unilaterally by two or three successive apical derivatives, the series of initials alternating left and right (cf. Cramer, 1863, pl. III: fig. 1, incorrectly as *Ptilota plumosa*). Since the first-formed laterals are cut off from the high side of slightly trapezoidal cells, the tip of the apex (2-4 cells) curves away from the most recent series of initials, later changing its direction in preparation for cutting off a new series on the opposite side. The apical cell of indeterminate axes divides by a convex septum perpendicular to the tangent of the curve of the apex so that successive septa are slightly oblique with respect to one another.

(2) *Dasyptilon*, *Falklandiella*, *Georgiella*, *Plumariopsis* and *Plumariella*, in which two branch primordia are initiated by each axial cell, with the first-formed primordium developing more extensively than the second. The two members

of a pair alternate on successive axial cells. In most genera of this group, indeterminate branches arise by an alteration in the growth pattern of certain of those branches that develop from first-formed primordia. In *Plumariopsis eatonii* (Dickie) De Toni, however, indeterminate branches develop from special second-formed primordia (Askenasy, 1888, p. 37, confirmed by our observations). In all genera of this group (with the possible exception of *Plumariella*, for which details are not available), apical division of indeterminate axes follows a pattern of alternating, markedly oblique, nearly planar septa. The tip of the apex is strongly flexuous (*Dasyptilon pellucidum* (Harv.) G. Feldm.; cf. G. Feldmann, 1950, fig. 10), slightly flexuous (*Falklandiella harveyi* (Hook. f.) Kylin; cf. Cramer, 1863, pl. I: fig. 1a, as *Euptilota harveyi*), or approximately straight (*Georgiella confluens* (Reinsch) Kylin; cf. Kylin & Skottsberg, 1919, fig. 33a, as *Euptilota confluens*; *Plumariopsis eatonii*, original observations).

(3) *Ptilota* and *Neoptilota*, in which branch primordia are initiated only by every second or third axial cell and the two branches of each pair are disparately developed. Both members are potentially indeterminate in *Ptilota*, whereas in *Neoptilota* the first member remains determinate while the second forms either a greatly reduced fertile branch or an indeterminate vegetative branch. Each member alternates left and right with its counterpart on successively branched segments. The pattern of apical division in this group is rather sophisticated. In *P. plumosa* (Huds.) C. Ag., for example, the tip of the indeterminate axis is alternately branched, since there is delayed initiation of the second member of each pair of laterals. The apical cell weaves from left to right, changing direction after every second division. It first cuts off, by a transverse septum, a short rectangular cell that does not bear laterals. It then turns away from the side where the next lateral is to be initiated and cuts off, by a slightly oblique septum, a derivative with one side higher than the other. A lateral is soon initiated from the high side, but by that time the apical cell has cut off (by a transverse septum) another flat cell and has turned back towards the initial as it cuts off (by an oblique septum) the asymmetrical derivative that will initiate the next lateral (cf. Cramer, 1863, pl. V, as *Pterota plumosa*).

(4) *Diapse*, in which two branch primordia are initiated by each axial cell, but only one, alternating left and right on successive segments, develops into a branch, the other contributing solely to cortication. The pattern of apical division is like that in *Georgiella* and *Plumariopsis* (cf. Kylin, 1956, fig. 307D).

(5) *Euptilota*, in which branching is truly alternate (cf. Kylin, 1956, fig. 307B). The pattern of apical division is similar to that in groups (2) and (4).

The foregoing series, while indicating vegetative phylogenetic trends, is not to be construed as a single evolutionary line. The interplay between obliqueness of apical division and structural imbalance seems especially interesting and important.

Discrepancies between Yoshida's list of Ptiloteae and our list call for a brief discussion.

*Dasyptilon* exhibits a suite of characters that makes its tribal affiliation controversial. When establishing the genus, G. Feldmann (1950) noted that the position of the tetrasporangia—sessile, on the adaxial side of branchlets of determinate branches—was unlike that in most Ptiloteae, where they terminate short branchlets. Their position is like that in certain species of *Antithamnion*,

although Feldmann did not make the comparison. On the basis of vegetative structure, however, she aligned the new genus with Ptiloteae. Erskine (1955) discovered procarps, and finding that they are borne on the basal cell of short branches (i.e. the minor member of each pair of branches)—another antithamnoid character, he reviewed the evidence pertinent to the intrafamilial placement of the genus. Erskine concluded that “it may best be considered as the genus of the Ptiloteae least departing from the primitive condition of the Crouanieae.” On the basis of procarp position, Yoshida (1974) removed *Dasyptilon* to the Antithamnieceae. We attach primary significance to its vegetative structure. The pattern of apical division by alternating oblique septa resulting in pairs of branches, one long and one short, each type alternating left and right on successive segments, is characteristic of Ptiloteae. Because we do not believe that the procarp-bearing short branches are equivalent to whorl-branchlets, we prefer to consider *Dasyptilon* a primitive member of the Ptiloteae while recognizing the validity of an alternative course—placing it in its own tribe.

*Falklandiella* was not mentioned by Yoshida, but presumably he followed Papenfuss (1958) in considering it congeneric with *Dasyptilon*. The two genera must be kept separate, however, since they exhibit several significant differences. As mentioned above, the procarp in *D. pellucidum* is produced directly by the basal cell of a determinate branch, while in *F. harveyi* it is produced by a pericentral cell cut off from an axial cell near the apex of a determinate branch. In *D. pellucidum* the supporting cell lies in the plane of thallus branching and the carpogonial branch bends upward around that cell, while in *F. harveyi* the supporting cell is perpendicular to the plane of thallus branching and the carpogonial branch bends horizontally around the axis bearing the supporting cell (our observations on material from the Falkland Is. collected by Mrs E. P. Vallentin and housed at BM), as in *Georgiella confluens* and *Euptilota articulata* (J. Agardh) Schmitz (Kylin, 1956). Moreover, the tetrasporangia in *D. pellucidum* are cruciately divided and in a position characteristic of Antithamnieceae—adaxial and sessile on branchlets of a determinate branch—while in *F. harveyi* they are tetrahedrally divided and in a position characteristic of Ptiloteae—terminal on the axis and numerous branchlets of a determinate branch.

*Gymnothamnion* is enigmatic. Branching is basically opposite-distichous, with all degrees of intermediacy between short and long branches occurring in some thalli, and thus suggests Ptiloteae. These branches, however, while not equivalent to whorl-branchlets (as emphasized by J. & G. Feldmann, 1966), are not arranged in pairs that are markedly unequal in time of initiation, time of development, and degree of development, nor does apical division involve alternating oblique septa, as in Ptiloteae. Cortication characteristic of that tribe is lacking. Although the usual position of the procarp—on the antepenultimate cell of the axis of a lateral—is an advanced character that is in general agreement with Ptiloteae, the exceptional position—the carpogonial branch being borne directly on the basal cell of an ultimate lateral—is primitive and, as in *Dasyptilon*, points towards Antithamnieceae. *Tokidaea*, a genus established by Yoshida (1974) and placed by him in the Ptiloteae next to *Gymnothamnion*, differs from that genus in several important characters, despite similarities in procarp position and development. While branching, as in *Gymnothamnion*, is basically opposite-distichous, without a sharp distinction

between short and long branches, the pattern in *Tokidaea* is much more profuse and specialized, including the sporadic production of poorly developed branches perpendicular to the plane of the thallus. *Tokidaea* has no prostrate system, the erect main axis being attached to the substrate by rhizoidal filaments that corticate the lower portion of all principal branches. In *Gymnothamnion*, by contrast, the erect axes are uncorticated and arise from a prostrate system which is attached to the substrate by short multicellular rhizoids. The tendency in *Tokidaea* for the two members of a pair of branches to develop unequally recalls the situation in Ptiloteae, but only slightly. At present, we are not prepared to assign either *Gymnothamnion* or *Tokidaea* to an existing tribe of Ceramiaceae.

Before continuing our survey of the incidence of oblique septa in Ceramiaceae, we must clarify our concept of the remaining tribe, Dasyphileae. As established by Schmitz & Hauptfleisch (1897, p. 484), this tribe was characterized by rhizoidal cortication originating from whorled determinate branches and included *Dasyphila*, *Psilothallia* and *Muellerena*. Kylin (1956) defined the group as having four to six branch initials cut off in a rhodomelacean sequence, the last in each segment lying opposite the first. (All Ptiloteae *sensu* Kylin have two branch initials except *Plumaria*, in which four are cut off in a delesseriacean sequence.) Kylin transferred *Rhodocallis* from the Ptiloteae (where Schmitz & Hauptfleisch had placed it) to the Dasyphileae, while removing *Muellerena* (as *Muellerella*) to an unspecified position near *Crouania*. Hommersand (1963, p. 169) found that in *Muellerena* the branch initials (incorrectly reported by him as four rather than five per segment) are cut off in a rhodomelacean sequence. On the basis of this character and the position of the procarp (on dwarf indeterminate branches) as described by Schmitz (in Schmitz & Hauptfleisch, 1897, p. 496), Hommersand returned *Muellerena* to the Dasyphileae. Wollaston (1972) confirmed the rhodomelacean sequence of branch initiation in *Muellerena*, but suggested that it could have arisen from the sequence typical of Ceramiaceae by a delayed cutting off of the last (adaxial) initial, which at times is lacking at the base of lateral branches. Moreover, Wollaston (1977) showed that in *Dasyphila preissii* Sonder (the type of its genus), the sequence of branch initiation is not truly rhodomelacean, since the fourth initial lies directly opposite the first while the fifth and sixth lie on either side of the fourth. She suggested the possibility that this sequence is a modification of the one typical of Ceramiaceae in that the first three initials are formed as a group on one side of the axis, the last three on the opposite side. Wollaston (1977) concluded that *Muellerena* and *Dasyphila* probably are phylogenetically advanced forms in the crouanioid line which merit recognition as a tribe. Hommersand (1963, p. 333) had previously concluded that Dasyphileae, despite their resemblance to Ptiloteae, probably arose from Antithamnieae.

In both *Muellerena* and *Dasyphila*, the apical cell of an indeterminate axis divides by a slightly oblique septum correlated with sinusoidal growth. Long branches develop only from lateral initials and have an alternate-distichous arrangement. The most detailed information on apical division in Dasyphileae is to be found in the description and figures of *Dasyphila plumarioides* Yendo given by Itono (1977, p. 141, fig. 22). In this species, oblique septa occur in both indeterminate and determinate apices. The indeterminate apex is similar

to that of *Plumaria* in that the first-formed branch initials are cut off unilaterally by two or three successive derivatives, the series of initials alternating left and right. The septa at the tip of the apex are slightly oblique with respect to one another. Of the determinate apices, those that develop from the four transverse pericentral cells have transverse septa and produce only rudimentary branches (Itono, 1977, fig. 22E–G). Those that develop from the two lateral pericentral cells have alternating oblique septa and produce alternate-distichous filaments, one per segment (fig. 22C). Occasionally, one of the latter type of branch develops desultorily, with many axial cells failing to produce filaments. In such an instance, apical division shifts back and forth between oblique septa (when filaments are being initiated) and transverse septa (when filaments are omitted) (fig. 22D). A similar phenomenon is readily observable in *Antarcticothamnion*, in which apical division of indeterminate apices changes from oblique to transverse when growth ceases (Fig. 3).

*Rhodocallis* probably does not belong with the Dasyphileae. The indeterminate axis is nearly straight, the apical cell dividing by a markedly oblique septum. The four branch initials are cut off in a rhodomelacean sequence, but Hommersand (1963, p. 333) did not consider this difference of sufficient importance to exclude the genus from the Ptiloteae, with which he believed it conformed in all other characters. According to Kylin (1956, p. 395), both determinate and indeterminate branches develop only from the first initial, which alternates left and right on successive segments, the remaining initials producing short unbranched filaments or contributing to the cortication. In a mature thallus, the determinate branches, of uniform length, are thus alternate-distichous, with occasional ones replaced by indeterminate branches. While this branching pattern is typical of Ptiloteae, we believe that a careful study of *Rhodocallis* may reveal reproductive characters which, when combined with the rhodomelacean sequence of branch initiation, will warrant the establishment of a new tribe.

*Psilothallia* also probably does not belong with the Dasyphileae. According to Kylin (1956, p. 394), the apical cell of an indeterminate axis divides by a slightly oblique septum. The six branch initials are cut off in a rhodomelacean sequence. The first initial of every second to fourth segment develops into a branch. In a mature thallus, the branching pattern is similar to that in *Rhodocallis*. A meaningful statement about the affinities of *Psilothallia* must await a detailed morphological study.

Similarities between *Muellerena* and *Dasyphila*, in addition to the rhodomelacean sequence of initiation of more than four branches per segment, include a curious event in carposporophyte development—the formation of a secondary pit-connection between the auxiliary cell and the fertile axial cell. In *Muellerena*, however, the supporting cell is one of a whorl of four cells cut off by the terminal cell of a special short branch that replaces a vegetative branch of a whorl-branchlet, while in *Dasyphila* the supporting cell is the basal cell of a whorl-branchlet. This reproductive specialization in *Muellerena* is puzzling in view of the fact that the vegetative structure of this genus is more crouanioid (and hence relatively less advanced) than that of *Dasyphila*. At present we prefer to limit the Dasyphileae to *Dasyphila* and to suggest the possibility of establishing a new tribe to accommodate *Muellerena*.



We conclude that although oblique septa constitute an adaptable functional character rather than an invariable intrinsic character, their occurrence in indeterminate apices of Ceramiaceae shows a high degree of correlation with features generally considered to be important at the level of tribe. Oblique divisions are apparently absent in Warrenieae, Sphondylothamnieae, Spermothamnieae, and certain Ceramiaceae and Griffithsieae. They occur in connection with holoblastic (apical) branching in certain Ceramiaceae and with subapical subdichotomous branching in certain Griffithsieae. They also occur in certain Ceramiaceae with unilaterally or spirally arranged first-formed pericentral cells and in all Wrangelieae (quasi alternate-distichous), Spyrideae (spiral), Callithamnieae, Dohrniellaeae and Compsothamnieae (alternate-distichous or spiral), Ptiloteae and Dasyphileae (alternate-distichous or effectively so). They probably also occur regularly in Delesseriopsidae, but are rare in Antithamnieae, Heterothamnieae and Crouanieae.

Before leaving the topic of apical division, we should like to comment on *Tanakaella*, a genus established by Itono (1977, p. 46) and considered by him a primitive member of the Sphondylothamnieae. Itono was aware of significant differences between his new genus and all previously described Sphondylothamnieae, including the absence of a large fusion cell and the metamorphosis of almost all gonimoblast cells into carposporangia, but accorded primary importance to the production of involucre branchlets by the sterile cells associated with the procarp. We would downgrade the latter character and emphasize vegetative structure, which Itono ignored. The alternate-distichous branching in *Tanakaella*, involving alternating oblique septa, in our opinion precludes the assignment of this genus to the Sphondylothamnieae, a tribe characterized by verticillate branching, and points instead to the Compsothamnieae. The chief obstacle to placing *Tanakaella* in the Compsothamnieae is its involucre, but that feature probably has evolved independently in several tribes (Spermothamnieae, Sphondylothamnieae and Compsothamnieae). Gordon-Mills & Womersley (1974) previously made a similar suggestion in connection with their establishment of *Mazoyerella*, which they assigned to the Compsothamnieae despite the formation of involucre filaments from the sterile cells associated with the procarp in that genus. Those authors hesitated to place *Mazoyerella* in the Spermothamnieae, with which it generally agrees in reproductive details except for the involucre, because a prostrate system is lacking. We believe, however, that the rather sparse subdichotomous branching points to Spermothamnieae rather than Compsothamnieae.

Returning to a consideration of the position of *Antarcticothamnion* within the Ceramiaceae, we find that the lack of a prostrate system and the absence of gland cells offer no phylogenetic insight, while the multinucleate cells point to Callithamnieae, Griffithsieae, Compsothamnieae and Spermothamnieae. Reproductive features provide conflicting indications. Polysporangia are known only in certain Callithamnieae, Compsothamnieae and Spermothamnieae. The arrangement of spermatangia—loose heads produced on short, modified branches—most closely resembles that in Compsothamnieae and Spermothamnieae. The position of the procarp near the apex, but not on a specific cell, of a modified indeterminate branch indicates a level of advancement beyond Callithamnieae, in which the procarp is borne near the apex of an ordinary

indeterminate branch, but approximated by Ptiloteae and far exceeded by Griffithsiae, Sphondylothamnieae, Compsothamnieae and Spermothamnieae. In the latter four tribes, the procarp is always borne on the subapical cell of a short fertile axis and the second-formed pericentral cell always serves as the supporting cell. In *Antarcticothamnion*, as in all Ptiloteae, the procarp is not restricted to the subapical cell of the fertile axis and, as in certain members of that tribe, the first-formed pericentral cell serves as the supporting cell. The metamorphosis of most gonimoblast cells into carposporangia and the lack of a fusion cell agree with both Compsothamnieae and Ptiloteae. Binucleate carposporangia appear to be unique to *Antarcticothamnion*, although multinucleate carposporangia are found in *Pleonosporium squarulosum* (Kugrens, 1976, as *P. dasyoides*, confirmed by our observations).

We conclude that *Antarcticothamnion* stands sufficiently apart from all other Ceramiaceae to warrant placement in its own tribe, Antarcticothamnieae trib. nov. It shares important features, however, with Callithamnieae, Compsothamnieae and Ptiloteae. Our ideas of possible phylogenetic relationships among the various tribes of Ceramiaceae are depicted in Fig. 17.

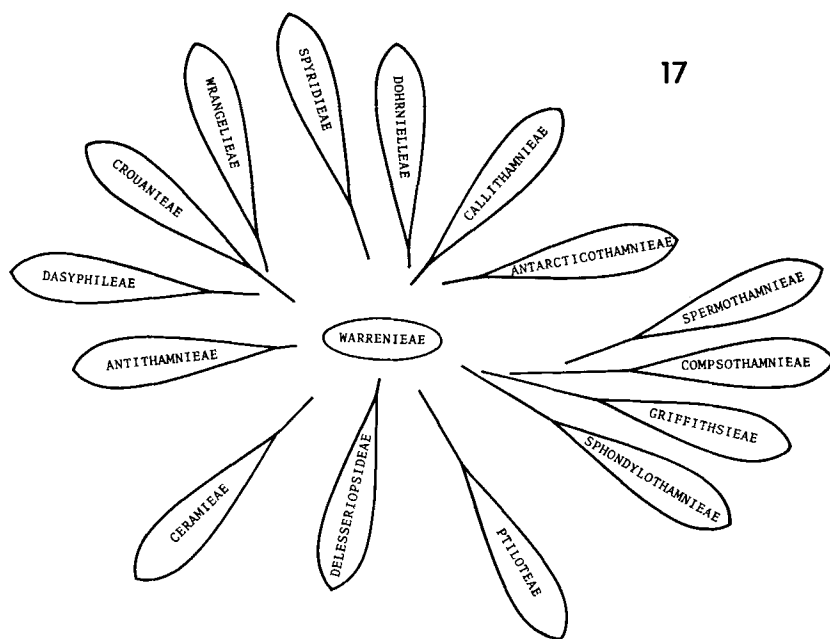


FIG. 17. Two-dimensional scheme showing possible phylogenetic relationships among the various tribes of Ceramiaceae. (Heterothamnieae is merged with Antithamnieae.) The scheme represents a tree as seen from above, the present-day organisms forming the canopy and each tribe attached by a branch from ancestral stock below the canopy. The direction of each branch as it reaches the surface indicates postulated relationships with other branches. Distance from the centre indicates assumed degree of advancement in selected vegetative and/or reproductive characters.

After having written the foregoing part of this paper, we were able to examine at the British Museum (Natural History) the type collection of *Spongoconium*

*orthocladum* A. et E. S. Gepp (1907) from Cape Adare, Ross Sea, Antarctica. This alga is clearly not congeneric with *S. conspicuum* Sonder (1855) from Australia, the type of its genus, but seems closely related to *Antarcticothamnion polysporum*. As noted by the Gepps, the plant is so thickly infested with diatoms as to obscure the branching. Another difficulty is imposed by the abundance of fertile branches with numerous branchlets composed of very small cells, which congests the sides of the main axes. While a definitive statement must await a study of fresh material from the type locality, it seems certain that the basic branching pattern is alternate, as in *A. polysporum*, but with an important difference: alternately branched laterals are initiated at the apex along with unbranched laterals, in no perceptible sequence. The origin of major indeterminate branches has not been ascertained. Female branch systems are borne, as in *A. polysporum*, either directly on a main axis or on the lower portion of a lateral. If on a main axis, the axial cell may be devoid of other branches or may bear either a primary lateral or another fertile branch or both. The female branch systems are much more elaborate than in *A. polysporum* and are ramified both pectinately and alternately. Details of the procarp are similar to those in *A. polysporum*. A male thallus was present in the type material, although not mentioned by the Gepps. The spermatangial branch systems, like the female, are more elaborate than in *A. polysporum* and ramify both pectinately and alternately.

Through the kindness of Mr James Price of the British Museum (Natural History), we have been privileged to examine excellent liquid-preserved and herbarium material of an undescribed alga from the South Orkney Is. This species is clearly congeneric with *Antarcticothamnion polysporum*, but shows an important vegetative difference in the origin of indeterminate branches. In *A. polysporum* they are always produced secondarily along an axis. In the South Orkney species they may be primary (i.e. one of the alternate-distichous laterals, as in *Spongoclonium orthocladum*) or secondary. If secondary, they may be borne (1) opposite a determinate lateral (as in *A. polysporum*, but not more than one per axial cell), (2) opposite a primary indeterminate lateral, (3) on an axial cell lacking a primary lateral, or (4) on the basal cell of a determinate lateral, usually with a rhizoid emitting from the bottom side of the same cell. (The last position suggests that the short simple filaments occasionally observed on the basal cell of determinate laterals in *A. polysporum* are equivalent to primordia of indeterminate branches, although they apparently never develop further in that species.) A minor vegetative difference is that in the South Orkney species the alternate-distichous branching of indeterminate axes tends to be restricted to the apex. For example, in a lateral of about 22 cells, branching was restricted to the apical 6 cells. Although the South Orkney species will remain undescribed at this time, with the permission of Mr Price we have adjusted the generic and tribal diagnoses to accommodate the variable branching pattern that it introduces into *Antarcticothamnion*.

#### ANTARCTICOTHAMNION GEN. NOV.

##### DIAGNOSIS

Ceramiceae cum ramificatione principalia disticha-alterna; rami determinati simplices, rami indeterminati primarii (ad apicem initiati) vel secundarii (ex axibus principalibus initiati)

verticilli 1–4 ramosi facientes vel e cellula basili rami determinati initiati). Cellula apicalis axium indeterminatorum crescentium per septa obliqua alternantia dividens et illa axium indeterminatorum quiescentium et axium determinatorum per septa transversa dividens. Rhizoidea filamentosa e cellulis infimis et subinfimis ramorum principalium initiata, deorsum crescentia, ramificantia et axes principales laxo corticantia.

Organa reproductionis in ramis indeterminatis modificatis, in axibus indeterminatis vel circa basim axium determinatorum insertis, portata. Sporangia polyedrice divisa. Spermatangia in capitula laxa formata. Procarpia circa apicem (infra cellulam apicalem 2–4 cellulis) ramorum fertilium portata, cellula pericentrali primum formata (lateralis) cellulam supportantem facienti, illa secunde formata (transversali) cellulam maternam cellulae auxiliaris secundae facienti; cellulae fusionis carens, gonimoblastus ex uno vel utrisque cellularum auxiliarum evolutus; cellulae gonimoblasti maximum partem in carposporangia evolutae; carposporangia binucleata; filamenta involucralis e cellulis vegetativis axium fertilium infra procarpiam prodientia. Axis fertilis parum per evolutionem carposporophytarum elongatascens.

Species typica: *A. polysporum* sp. nov.

Ceramiceae with alternate-distichous primary branching; determinate branches simple, indeterminate branches primary (initiated at apex) or secondary (initiated by main axes to form incomplete or complete whorls of 1–4 branches or by basal cell of determinate branch). Apical cell of active indeterminate axes dividing by alternating oblique septa, apical cell of quiescent indeterminate axes and determinate axes dividing by transverse septa. Rhizoidal filaments initiated by lowermost cell or two cells of major branches, growing downward, branching, and loosely corticating main axes. Reproductive organs borne on modified indeterminate branches inserted on indeterminate axes or near base of determinate axes. Sporangia polyhedrally divided. Spermatangia formed in loose heads. Procarps borne near apex (2–4 cells below apical cell) of fertile branch or branchlet, the first-formed (lateral) pericentral cell serving as the supporting cell, the second-formed (transverse) pericentral cell serving as the mother cell of a second auxiliary cell; supporting cell giving rise to a 4-celled carpogonial branch and a sterile cell. Fusion cell absent; gonimoblast developing from one or both auxiliary cells; most cells of gonimoblast developing into carposporangia; carposporangia binucleate; involucral filaments produced by vegetative cells of fertile axis below procarp; fertile axis elongating slightly during carposporophyte development.

Type species: *A. polysporum* sp. nov.

### *ANTARCTICOTHAMNION POLYSPORUM* SP. NOV.

#### DIAGNOSIS

Thallus rubiginosus, flaccidus, ad 6 cm alt.; axis principalis plus minusve percurrent, cellulis maximis  $150 \times 500 \mu\text{m}$ . Rami determinati subulati, ad  $130 \mu\text{m}$  diam. in media; rami indeterminati semper secundario in axibus principalibus efferentes. Sporangia ad maturitatem ad  $120 \mu\text{m}$  diam., 12–24 sporas continentia. Spermatangia subglobosa,  $4\text{--}5 \mu\text{m}$  diam., nucleo distali et vacuolam proximalem continentia. Gonimolobi magnitudinibus divergentibus, carposporangiis ad  $50\text{--}60 \mu\text{m}$  diam.

Holotypus: planta sterilis ad insulam Elephantorum in insulis dictis "South Shetland" d. 15 m. Jan. a. 1974 lecta (Moe 130, UC 1446016).

Thallus dull red, flaccid, to 6 cm tall; main axis more or less percurrent, the largest cells  $150 \times 500 \mu\text{m}$ . Determinate branches subulate, to  $130 \mu\text{m}$  diam. in middle; indeterminate branches always produced secondarily on main axes. Sporangia to  $120 \mu\text{m}$  diam. at maturity, containing 12–24 spores. Spermatangia subspherical,  $4\text{--}5 \mu\text{m}$  diam., containing a distal nucleus and a proximal vacuole. Gonimolobes of different sizes, carposporangia to  $50\text{--}60 \mu\text{m}$  diam.

Holotype: sterile plant from Elephant I., South Shetland Is., collected 15 Jan. 1974 (Moe 130, UC 1446016).

### *ANTARCTICOTHAMNIEAE* TRIB. NOV.

#### DIAGNOSIS

Ceramiceae cum ramificatione principalia disticha-alterna; rami determinati simplices, rami indeterminati primarii (ad apicem initiati) vel secundarii (ex axibus principalibus initiati) verticilli 1–4 ramosi facientes vel e cellula basili rami determinati initiati). Apex indeterminatus per septa obliqua alternantia dividens. Organa reproductionis in ramis indeterminatis

modificatis portata. Procarpia circa apicem, sed non semper in cellula subapicali, rami fertilis portata, cellula pericentrali primum formata (lateralis) cellulam supportantem facienti, illa secunde formata (transversalis) cellulam maternam cellulae auxiliaris secundae facienti. Cellula-fusionis carens; gonimoblastus ex uno vel utrisque cellularum auxiliarum evolutus; cellulae gonimoblasti maximum partem in carposporangia evolutae.

Genus typicum: *Antarcticothamnion* gen. nov.

Ceramiaceae with alternate-distichous primary branching, determinate branches simple, indeterminate branches primary (initiated at apex) or secondary (initiated by main axes to form incomplete or complete whorls of 1–4 branches or by basal cell of determinate branch). Main axes loosely corticated by downgrowing rhizoidal filaments initiated by lowermost cells of major branches. Reproductive organs borne on modified indeterminate branches inserted on indeterminate axes or near base of determinate axes. Procarps borne near apex, but not always on subapical cell, of fertile branch or branchlet, the first-formed (lateral) pericentral cell serving as the supporting cell, the second-formed (transverse) pericentral cell serving as the mother cell of a second auxiliary cell. Fusion cell absent; gonimoblast developing from one or both auxiliary cells; most cells of gonimoblast developing into carposporangia.

Type genus: *Antarcticothamnion* gen. nov.

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