Liagorothamnion mucoides gen. et sp. nov. (Ceramiaceae, Rhodophyta) from the Caribbean Sea

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A new genus and species, Liagorothamnion mucoides Huisman, Ballantine & Wynne (Ceramiaceae, Rhodophyta), is described from the Caribbean Sea. Thalli are mucilaginous and filamentous and generally have one indeterminate lateral branch and 1–4 whorl-branchlets per axial cell. Spermatangia are borne on whorls of fertile branchlets on 3–16 successive axial cells. Carpogonial branches are 3–4-celled and borne on a periaxial supporting cell that also bears two or more sterile groups. Lower cells of the carpogonial branch also bear lateral cells. Following presumed fertilization, the carpogonium cuts off short connecting filaments that fuse with the basal cells of whorl-branchlets on the fertile axial cell (which therefore function as auxiliary cells) but not with the supporting cell. Gomimolobes arise from the auxiliary cells and, when mature, are composed entirely of carposporangia. The carposporangia are quadripartite when mature. Tetrasporangia are unknown. The new genus appears to have affinities with the tribe Dohrniielleae but differs from all known genera in a number of unusual features, justifying a new tribe, Liagorothamniaceae, to accommodate it. In contrast to virtually all members of the Ceramiaceae, the supporting cell of the carpogonial branch of Liagorothamnion bears two sterile cell groups, which appear to provide nutrition for the postfertilization processes. This feature is found, however, in members of the other families included in the Ceramiales (Rhodomelaceae, Delesseieraceae, Daisyaceae) and could indicate that Liagorothamnion represents the primitive condition for this character in the Ceramiaceae.

INTRODUCTION

The marine benthic algae of the Caribbean Sea have been the subject of many studies, perhaps most notably those of W.R. Taylor, which culminated in the publication of his landmark Marine algae of the eastern tropical and subtropical coasts of the Americas (Taylor 1960). Within the region, the island of Puerto Rico is located on the northern boundary of the Caribbean Sea in the western Atlantic. Ballantine & Aponte (1997) have reviewed Puerto Rico's phycological history and presented a checklist of the marine benthic algae recorded from the island. Its algal flora is diverse and arguably the best known for any islands in the region due to over a century of active collection and study. Nevertheless, an ongoing study of Puerto Rico by the second author and his associates continues to uncover new species and species records, although principally from offshore, deep-water habitats (see Ballantine & Aponte 1997). It was therefore surprising when an unusual red alga was discovered in a what had been thought to be a well-known, near-shore, shallow-water habitat in southwestern Puerto Rico. That alga is described here as the new genus and species Liagorothamnion mucoides; it represents a new tribe of Ceramiaceae, the Liagorothamniaceae.

MATERIAL AND METHODS

Specimens were both dried as herbarium material and preserved in 10% formalin–seawater. Herbarium sheets and microscope slides have been deposited in MSM, MICH and MURU. Material for microscopical examination was stained in a mixture of 1 g aniline blue powder, 70 ml Karo®, 30 ml distilled water and 5 ml acetic acid. Material for nuclear studies was stained using Wittmann's aceto-iron-haematoxylin–chloral hydrate technique (Wittmann 1965) following the procedures of Hommersand & Fredericq (1988). Line drawings were prepared using a camera lucida mounted on a Leitz microscope, while macrophotographs and photomicrographs were made using Kodak Technical Pan black and white film. Herbarium abbreviations follow Holmgren et al. (1990).

RESULTS

Liagorothamnion Huisman, D.L. Ballantine & M.J. Wynne, gen. nov.


Thallus filamentosus, erect, from a discoid holdfast, generally with one indeterminate lateral branch and one to four whorl-branchlets per axial cell. Vegetative cells mostly unimunicate, with ribbon-like rhodoplasts. Spermatangial branches much divided, in whorls on
successive axial cells. Carpogonial branch three- to four-celled, borne on a supporting cell on an intercalary axial cell, strongly curved, with a lateral cell borne on the basal cell. Supporting cell with two to three sterile groups. Basal cells of whorl-branchlets on the fertile axial cell (but not the supporting cell) functioning as auxiliary cells. Carposporophytes globular, with gonimolobes comprised almost entirely of carposporangia. Carposporangia quadrpartite.

**TYPE SPECIES:** _L. mucoides._

**Liagorrhaminion mucoides** Huisman, D.L. Ballantine & M.J. Wynne, *sp. nov.*

Figs 1–19


**ETYMOLOGY:** The generic name is derived from *Liagora* (reflecting its superficial resemblance in the field to that genus) and *thamnion* (= shrub, bush). The specific epithet refers to the mucilaginous habit.

**TYPE SPECIMENS AND LOCALITY:** Media Luna Reef, 5 November 1996 (leg. Austin Bowden-Kerby, = DLB 5243). Holotype (Fig. 1) in MIC; isotypes in MSM, MURU, US.

**DISTRIBUTION:** Known only from the type locality. In addition to the type collection, two further specimens have been collected: (1) leg. AB-K, 27 November 1998, = DLB 5296 (MSM); and (2) leg. DLB, 5 February 2000, = DLB 5402 (MSM).

**HABITAT:** Specimens were collected from a shallow-water rhodolith bed (Ballantine *et al.* 2000) in a back reef environment, growing at a depth of 1.0 m. Algae were attached to coral rubble.

**HABIT AND VEGETATIVE STRUCTURE:** Plants are filamentous and erect, growing to 8 cm in height with the largest axes up to 1.0 mm diameter, and arise from a discoid holdfast. They are mucilaginous and appear calcified, owing to the accumulation of detritus in the mucilage, although some calcification could be autogenous. Cells of the primary axial filaments are 5–10 μm in diameter; they are equidimensional or broader than long near the apices, gradually becoming longer than broad (L/W 2–3) approximately 10 cells from the apex (Fig. 6). Mature axial cells have diameters > 200 μm. The apices of primary axial filaments are sparsely branched, the lateral branches not arising until some 7–20 cells from the apex (Fig. 6). Lateral branches arise in a distal position on the cell bearing them and are either indeterminate or determinate (= whorl-branchlets). Each axial cell generally bears one indeterminate lateral branch and one to four whorl-branchlets (Fig. 7). Indeterminate lateral branches are born in a distal position, with successive branches arising in an irregularly alternate or seemingly random pattern. The branching pattern and cell morphology of the indeterminate lateral branches are similar to those of the primary axes, except that the basal cell of these branches is shorter than the more distal cells (Fig. 7). Whorl-branchlets (Fig. 7) arise in a seemingly random pattern and many axial cells bear whorl-branchlets of varying lengths. Whorl-branchlets are generally simple, 1–15 cells long, and their constituent cells are smaller than those of the indeterminate lateral branches (Fig. 7). The basal cells of whorl-branchlets are often subcylindrical. Cells of whorl-branchlets are 4–7 μm in diameter and equidimensional near the apices, becoming longer than broad as they mature. In older portions of the thallus, the axes are secondarily corticated by rhizoidal filaments, which arise from the basal cells of lateral branches (Figs 2–4), or rarely from the proximal portion of the axial cell. Vegetative cells are mostly uninucleate, occasionally becoming binucleate in older cells (Fig. 5). The rhodoplasts are elongate, becoming ribbon-like and branched in larger cells (Figs 2, 7).

**SPERMATANGIA:** Spermangial branches are formed in whorls on successive branch cells, generally extending over 3–16 cells (Fig. 9). Spermangial branch initials arise in whorls of two or three near the distal end of the vegetative cell bearing them. Each branch initial bears numerous spermangial mother cells or spermangia directly (Fig. 8). An additional whorl is often borne in a more proximal position (with branch initials slightly offset in relation to the distal whorl). The spermangia are 2–4 μm in diameter.

**TETRASPORANGIA:** Unknown.

**CARPOGONIAL BRANCH AND CARPOSOROPHYTE:** Carpogonial branches are borne on supporting cells on intercalary axial cells (= fertile axial cells) (Figs 10, 12, 13). The supporting cell arises in a position similar to that of whorl-branchlets, on an axial cell some six cells from the apex. The production of the carpogonial branch does not affect the continued growth of the vegetative filament. On axial cells bearing a supporting cell, one or two additional, short whorl-branchlets are produced, proximal to the normal whorl-branchlets and supporting cell. In addition, the whorl-branchlets on the fertile axial cell often branch, in contrast to the simple whorl-branchlets found on vegetative axial cells. As the carpogonial branch matures, the supporting cell and lower cell(s) of the carpogonial branch produce additional sterile groups — generally one (but occasionally two) two-celled branches and a single lateral cell on the supporting cell, and a single lateral cell borne on the basal cell of the carpogonial branch (Fig. 14). This pattern is not consistent, however, and one branch (Fig. 15) was observed with a supporting cell bearing three branches (one three-celled with a two-celled lateral on its basal cell, one one-celled, and one two-celled), and a carpogonial branch was seen whose basal cell bore two branches (one one-celled and one two-celled) and whose next cell bore a single-celled lateral. This proliferation of sterile groups does not appear to be a consequence of the procarp returning to a vegetative state if fertilization does not take place: the branches described above all had elongate trichogynes and were presumably viable.

The mature carpogonial branch is three or four cells long, strongly curved, with an elongate trichogyn (Figs 10, 13–15). Following presumed fertilization, the supporting cell, carpogonial branch and associated sterile groups become hyaline. The precise details of transfer of the diploid nucleus
Figs 1–5. *Liagorothamnion mucoides* (all DLB 5243).

**Fig. 1.** The holotype specimen.
**Fig. 2.** Axial filament showing the origin of corticating filaments (arrows) from the basal cells of lateral branches.
**Fig. 3.** Mature, corticated axial filament.
**Fig. 4.** Section of mature axis showing cells of the large central filament and corticating filaments.
**Fig. 5.** Material stained to show nuclei. Note both uninucleate and binucleate cells.

were difficult to observe, owing to the crowded nature of the carpogonial branch cluster, but it appears that connecting cells or short filaments arise from the carpogonium and fuse with the basal cells of the whorl-branchlets borne on the fertile axial cell (Figs 16, 17), but not with the supporting cell itself. *De novo* auxiliary cells are not produced; the basal cells act in that role. In more mature stages, the basal cells (= auxiliary cells) can be observed with elongate projections directed towards the position of the carpogonial branch. Most whorl-branchlets on the fertile axial cell are involved, such that the single fertilization results in the diploidization of three or four auxiliary cells. Some apparent fusions between cells of the carpogonial branch and those of the sterile groups were observed, possibly indicating a nutritive function for the latter (Fig. 16). Gonimoblast initials are formed from the projections arising from the auxiliary cells (Fig. 18). As the distal cells of the whorl-branchlets are persistent, each basal cell ultimately bears both gonimolobes and a whorl-branchlet (Fig. 18). Mature carposporophytes (Fig. 11) are globular, 150–360 μm in diameter, and composed of three or four gonimolobes, each comprised almost entirely of carposporangia and being slightly diffuse in appearance. Carposporangia are subspherical and 10–12 μm in diameter. Immature carposporangia are undivided, but when mature they are quadripartite (Fig. 19). The divided nature of the carposporangia is best observed in fresh material, as preservation and mounting in Karo® solution tends to destroy the arrangement of the spores.
DISCUSSION

It is not immediately apparent to which family or order of the red algae *Liagorothamnion* should be assigned. Its filamentous habit suggests the Ceramiaceae of the Ceramiidae, but similar morphologies are also found in the family Naccariaceae [a family generally placed in the Bonnemainioziales but included in the Gigartinales by Abbott (1999, p. 120)]. The genus *Reticulocaulis* I.A. Abbott of the Naccariaceae has a filamentous habit with whorl branches, is strongly mucilaginous and has a carpogonophore composed almost entirely of sporangia (Abbott 1985). Superficially, these features would appear to indicate a close relationship between *Liagorothamnion* and the Naccariaceae. If we ignore what we believe to be ceramioaceous reproduction in *Liagorothamnion* (which could be open to interpretation), the genus still does not sit comfortably in the Naccariaceae. Members of that family have a vegetative construction that includes distinctive inflated corticating filaments, forming a pseudoparenchyma surrounding the primary axial filament. The primary axial filament remains narrow. While *Liagorothamnion* has corticating filaments, they do not become markedly inflated, and it is the axial filament that increases in girth with maturity. In addition, *Liagorothamnion* differs from the Naccariaceae in forming whorled spermatangia, as opposed to the terminal clusters found in genera such as *Reticulocaulis* (Abbott 1985). When postfertilization development is considered, *Liagorothamnion* seems even further removed. Members of the Naccariaceae do not possess auxiliary cells, and the gonimoblast develops directly from the carpogonium, after fusion with the hypogynous cell (Abbott 1985; Womersley 1996, p. 354). In *Liagorothamnion*, however, the basal cells of whorl branches function as auxiliary cells.

Another family with some superficial similarities to *Liagorothamnion* is the Gloiosiphonaceae (Gigartinales). Its members are also uniaxial (with whorl-branches) and mucilaginous but differ from *Liagorothamnion* in their spermatangia, which are borne in terminal clusters, and in producing auxiliary cells that terminate special auxiliary-cell branches borne on the supporting cell of the carpogonial branch (Abbott 1999, p. 110). Both features are fundamentally different from those found in *Liagorothamnion*.

We conclude that *Liagorothamnion* displays greatest affinities with the Ceramiaceae of the Ceramiidae, with which it shares a filamentous construction, a procarpal arrangement of the carpogonial branch and similar postfertilization develop-
ment. However, the suite of unique features found in *Liagorothamnion* unquestionably sets the new genus apart from all known Ceramiaceae. None of the Ceramiaceae have been described as regularly producing more than one sterile group on the supporting cell, most have distinct auxiliary cells (in virtually all, the supporting cell acts as the auxiliary mother cell or as the auxiliary cell where no *de novo* cell is produced), and none produce quadripartite carposporangia. Given that some of these features are regarded as defining the order Ceramiaceae, it is reasonable to question whether *Liagorothamnion* should be placed in the Ceramiaceae at all. In fact, the postfertilization development observed in the genus is not compatible with the Ceramiaceae *sensu stricto*, whose defining features include the production of auxiliary cells after fertilization (Maggs & Hømmersand 1993, p. 2). This feature has often been compromised, however, with many taxa apparently lacking auxiliary cells (see discussion below).

Given the unusual nature of the reproductive morphology of *Liagorothamnion* and given too that the affinities of the genus are not readily apparent, we feel that each of its characteristics warrants individual attention. Below, we discuss the various features separately and what implications, if any, they suggest regarding possible relationships.

### Habit

A mucilaginous habit is unusual in the Ceramiaceae, but it is found in genera such as *Crouania* J. Agardh (Wollaston 1968, p. 233). It is generally not accorded any taxonomic significance.

### Vegetative structure

The production of lax whorl-branchlets in an irregular pattern, with the periaxial cells shorter than the contiguous cells, is similar to what is found in members of the Dohriellae as defined by Athanasiadis [1996, including some members of the Heterothamnaceae as defined by Wollaston (1968)]. As presently constituted, the Dohriellae includes five genera—Dohriella Funk, Callithamnium Feldmann-Mazoyer, Antithamnionella Lyle, Trithamnion Wollaston and Acrothamniosis Athanasiadis & Kraft. Of those genera, *Acrothamniosis* has a distinctive branching pattern with two opposite major whorl-branchlets. It also differs from *Liagorothamnion* in producing gland cells (as do most members of the Dohriellae, with the exception of some species of *Callithamniumella, Dohriella* and *Antithamnionella*), although Athanasiadis (1996) does not consider this feature to be of generic importance. *Trithamnion* also displays an apparently uniform pattern of whorl-branchlet initiation unlike that of *Liagorothamnion*. In addition, both *Acrothamniosis* and *Trithamnion* have branched whorl-branchlets, unlike the mostly simple branches in *Liagorothamnion*. The genus *Callithamniumella* is widespread, but unfortunately its sexual reproduction is incompletely known. It differs from *Liagorothamnion* in its decumbent habit and the production of only a single lateral branch.
Figs 12–18. Liagoretammion mucoides (all DLB 5243).  Abbreviations: aux, auxiliary cell; ca, carposporangia; con, connecting filament; con.r, connecting filament remnants; fa, fertile axial cell; gi, gonimoblast initial; su, supporting cell; wb, whorl-branchlet; wb+, whorl-branchlet with basal cell functioning as an auxiliary cell.

Fig. 12. Developing carpogonial branch. Arrows indicate sterile cells borne laterally on the supporting cell and basal cell of the carpogonial branch.

Fig. 13. Developing carpogonial branch with elongate trichogyne.

Fig. 14. Carpogonial branch. The supporting cell bears two sterile groups, with a single sterile cell arising from the basal cell of the carpogonial branch.

Fig. 15. Much-branched carpogonial branch cluster, with sterile groups arising on the supporting cell and the two lower cells of the carpogonial branch.

Fig. 16. Postfertilization stage (apparently) with a divided connecting filament arising from the carpogonium. There appears to be a fusion between the carpogonium and one of the sterile cells (arrowhead).

Fig. 17. Immature carposporophyte, with a gonimolobe arising from the auxiliary cell. The remnants of the supporting cell, carpogonial branch, associated sterile cells and branched connecting filament are evident.

Fig. 18. Gonimolobe composed entirely of immature (undivided) carposporangia. Note the remnants of the whorl-branchlet (wb+) remaining attached to the auxiliary cell.
per axial cell. Of the Dohriellae, *Liagorothamnion* appears most similar to *Dohriella*, a genus characterized by the production of one to three papilliform cells (= unicellular branchlets) per axial cell (L’Hardy-Halos 1966; Stegenga & Vroman 1987, p. 411, fig. 37; Schneider & Searles 1997, p. 20, fig. 23). While these cells do not occur consistently in *Liagorothamnion*, it is likely that they are homologous to the whorl-branchlets of the new genus. The type species of *Dohriella* (*D. neapolitana* Funk) differs from *Liagorothamnion* in producing gland cells, but a second species, *D. antillarum* (W.R. Taylor) Feldmann-Mazoyer, does not, further reinforcing the possible connection between the genus and *Liagorothamnion*.

### Sterile cell groups

The production of several sterile cell groups on the supporting cell is unlike what occurs in most members of the Ceramiaceae. Hommersand (1963) recorded more than one group for *Reinboldiella schmitziana* (Reinbold) De Toni (p. 211, fig. 16h) and *Microcladia coulteri* Harvey (p. 219, fig. 20i) but suggested that they arose only when the development of the gonimoblast has been inhibited, possibly due to the proximity of a fertilized procarp. In many Ceramiaceae, unfertilized or inhibited procarps can revert to a vegetative state. In *Liagorothamnion*, however, the sterile groups are evident when trichogynes are present and also during postfertilization events; thus, their production as a response to the carpogonium being unfertilized or inhibited is unlikely.

The sterile groups in *Liagorothamnion* do not mimic the whorl-branchlets, which might be expected if they are the result of the reduction of vegetative branches. It would appear that they are homologous to nutritive cells, as occurs in a number of red algae. Hommersand & Fredericq (1990) regarded the sterile groups in *Polysiphonia* (Rhodomelaceae) as nutritive, and it appears that those of *Liagorothamnion* act in a similar fashion. The sterile groups in *Liagorothamnion* are initially pigmented, but become hyaline as postfertilization events progress, again suggesting a nutritive role.

More than one sterile cell group occurs on the supporting cells in the other families of the order (Rhodomelaceae, Delesseriaceae, Dasyaceae), and so this probably represents the pleisomorphic (or relict) condition. What is perhaps more unusual is the production of sterile cells on additional cells of the carpogonial branch. This condition has not been reported for the Ceramiaceae, and its significance is unknown.

### Auxiliary cells

The lack of *de novo* auxiliary cells is an unusual condition for the Ceramiaceae, but it is not unknown. Genera that have been reported to lack auxiliary cells include *Antithamnionella* (Dixon 1964, as *Antithamnion*), Griffithsia C. Agardh (Dixon 1964; Baldock 1976), *Mediethamnion* Pujals (Brauner 1979), and *Radiathamnion* Gordon-Mills & Kraft (1981), all otherwise seeming to be normal members of the family. In all cases cited above, the supporting cell of the carpogonial branch functions as the auxiliary cell. In *Liagorothamnion*, however, it is the basal cells of whorl-branches that act as auxiliary cells, the supporting cell playing no role in postfertilization development. A somewhat comparable situation has been reported for *Campylium reductum* Baardseth (1941, p. 91–92, fig. 47), in which a *de novo* auxiliary cell arises from the basal cell of a second pericentral (= periaxial) cell, the supporting cell remaining undivided. More typical of species of the Callithamniaceae is the production of two auxiliary cells, one from each of the supporting and second periaxial cells [as described for *Aglaothamnion halliae* (Collins) Aponte, D.L. Ballantine & J.N. Norris by Hommersand (1997) and for *A. boergesenii* (Aponte & D.L. Ballantine) L’Hardy-Halos & Ruinen in Aponte, D.L. Ballantine & J.N. Norris by Aponte & Ballantine (1990)]. Baardseth also observed what appeared to be two connecting cells arising from the carpogonium and therefore interpreted the process in *C. reductum* as being ‘derived by reduction from the normal type of gonimoblast’ (Baardseth 1941, p. 92). *De novo* auxiliary cells are lacking in a number of tribes of Ceramiaceae and this therefore appears to be a secondary loss that has occurred on several occasions.

### Carposporophyte

The procarp and carposporophyte of *Liagorothamnion* are borne on an axial cell of a filament that continues vegetative growth, unimpeded by the production of the carposporophyte. This type of development is similar to that found in some members of the Antithamniaceae, Scagelieae, Pterothamniaceae, Delesseriopsaeae, Dohriellae and Callithamniaceae. Athanasiadis (1996, p. 27) regarded this type of development as primitive in the family; persisting in a number of tribes. Of the aforementioned tribes, *Liagorothamnion* appears closest to the Dohriellae based on features other than those of the carposporophyte (see Vegetative structure above). Unimpeded growth of the carposporophyte-bearing axis, however, is only rarely reported for the Dohriellae, although the situation in *Dohriella* (the genus with the greatest similarity to *Liagorothamnion*) is somewhat unclear. Athanasiadis (1996, p. 90) described ‘carposporophyte development suppressing the growth of the bearing fertile axis, and apical growth continu-
ing sympodially from a lateral axis borne below the carposporophyte. This process appears to be known only in *D. antillarum var. brasiliensis* A.B. Joly & Ugadim (Joly & Oliveira Filho 1971) and, in part, in *D. neopolitana* (L’Hardy-Halos 1966). In the former, the fertile axial cells are described as being ‘well below the ultimate segments of the main axis’ (Joly & Oliveira Filho 1971, p. 365). No description of the position of the mature carposporophyte was given, but an illustration (their fig. 3) suggests it to be terminal, possibly with sympodial growth as described by Athanasiadis (1996). L’Hardy-Halos (1966) illustrated only carpogonial branches, which appear to be subterminal in position. It would seem that procarps can arise in series on intercalary cells, but that carposporophyte development either displaces the vegetative axis or suppresses its growth. This is unlike the situation in *Liagorothamnion*, in which the gonimolobes arise from the basal cells of whorl-branchlets, and the carposporophyte effectively encircles the fertile axial cell.

Another genus of the Dohrnieleae with some affinity to *Liagorothamnion* is *Callithamniella*, but unfortunately post-fertilization events in *Callithamniella* are unknown. Stegenga (1988) described and illustrated the carpogonial branches in *C. tingitana* (Schousboe ex Bornet) Feldmann-Mazoyer (as *C. capensis* Simons, see Athanasiadis 1996, p. 89), which are borne in series on axial cells and could potentially produce carpogonial spores sequentially and not inhibit the vegetative growth. The procarp morphology of *Callithamniella*, however, includes only a single sterile cell borne on the supporting cell (Stegenga 1988, p. 378, fig. 40), unlike the multiple sterile groups found in *Liagorothamnion*.

### Quadripartite carposporangia

Divided carposporangia, in which the individual spores are arranged in a cruciate or tetrahedral pattern, occur in several orders of red algae. These sporangia are generally referred to as ‘carpotetrasporangia’ (see Guiry 1990b), a term that suggests a functional role similar to that of tetrasporangia (i.e. with meiosis occurring in their formation and germination to produce the gametophytes). That this is not always the case was shown by Guiry (1990a), who cultured the carpotetrasporangia of *Liagora harveyana* Zeh and found them to grow into an independent filamentous sporophyte stage that produced tetrads. As a consequence, Guiry questioned the generally accepted belief that carpotetrasporangia functionally replaced tetrads and suggested that they are simply divided carpogonia. He adopted the term ‘quadripartite carpogonia’. The role of these divided carpogonia remains a subject of debate (see Guiry 1990b), and they are variously reported as (1) carpotetrasporangia, in which meiosis occurs and which functionally replace the tetrads (and tetrasporophyte) (e.g. Bodard 1971); (2) quadripartite carpogonia, a general term used in a descriptive rather than functional sense (but implying sporangia derived by mitosis) (e.g. Guiry 1990a); or (3) normal carpogonia germinating in situ. It is unlikely that the divided spores in *Liagorothamnion* are carpogonia that have germinated in situ, as spores in the Ceramiaceae typically germinate in a bipolar fashion and therefore would not produce tetrads. It is possible that the divided carpogonia in *Liagorothamnion* represent carpotetrasporangia. If this is the case, it would account for the absence of tetrasporangial specimens, since the carpotetrasporangia would presumably regenerate the gametophyte generation directly. However, since we have no evidence of meiosis, nor any life history information, this must remain speculative. We have therefore chosen to refer to the divided sporangia in *Liagorothamnion* by the more descriptive term ‘quadripartite carpogonia’.

Guiry (1990b, p. 366) recognized two types of carpogonia with divided carpogonia, based on the morphology rather than the function of the spores (i.e. including carpotetrasporangia and quadripartite carpogonia as defined above). In the first, the divided sporangia are ‘formed in sporangia that resemble carpogonia of related species of the same genus’. In the second, the divided sporangia are cut off from gonioblast filaments that spread over the surface of the thallus. Since *Liagorothamnion* represents a new, monospecific genus, we are unable to compare the sporangia of *L. mucoides* with those of related species. Nevertheless, its carpogonia structure is similar to that of many camarialean species, and the gonioblast filaments are not spreading. Thus we believe the sporangia in *Liagorothamnion* to be of the first type mentioned above. Similar structures are otherwise known only in the Liagoraceae (Guiry 1990b), such as *Liagora harveyana* (see Guiry 1990a). Phylogenetically, *Liagorothamnion* has no obvious links to the Liagoraceae, a family whose members have multimassial thalli and in which the carpogonia develops directly from the fertilized carpogonium. Divided carpogonia are also reported for several other taxa that are unrelated, both to *Liagorothamnion* and to each other (summarized in Guiry 1990b, p. 366), and it would appear that the condition has evolved on several occasions. The presence of carpotetrasporangia in *Liagorothamnion* represents another departure from the Ceramiales, since such sporangia are otherwise unknown in the order.

### Spermatangia

In the Ceramiaceae, spermatangia are generally produced in specialized short branches (spermatangial heads), unilaterally on branch cells, or terminally on outer cells (for examples see Hammersand 1963; Wollaston 1968; Huismann & Kraft 1984, 1992; Kraft 1988). The production of spermatangia in whorls on otherwise unmodified successive branch cells is a feature apparently shared only by *Callithamniella* (of the Dohrnieleae) (see Baardseth 1941, fig. 46A). Athanasiadis (1996) described the spermatangia in *Callithamniella* as arising from whorls of unicellular spermatangial mother cells, whereas the comparable structures in *Liagorothamnion* are more profusely branched, the fertile branchlets being several cells in length.

### CONCLUSIONS

*Liagorothamnion*, therefore, possesses a combination of post-fertilization features that is anomalous for a camarialean taxon. An argument could be made that some of these characteristics should exclude the genus from the order *sensu stricto*. When assessed individually, however, they can be readily interpreted as similar to, or modifications of, existing processes. Ironically, the characteristic that is most at odds with place-
ment in the Ceramiales (lack of de novo auxiliary cells) appears to be not infrequent in the order. Given other seemingly indicative characteristics (filamentous habit with whorl-branchlets, basal cell of whorl-branchlets smaller than distal cells, procarpic), we regard Liagorothamnion as a good member of the Ceramiaceae. We do believe, however, that the circumscription of the order should be modified to include taxa in which supporting cells and the basal cells of whorl-branchlets associated with the fertile axial cell can act directly as auxiliary cells (as was done, in part, by Maggs & Hoomersand 1993).

Nevertheless, Liagorothamnion also displays the unusual condition of multiple sterile groups on the supporting cell and a unique arrangement of spermangia. As such, it does not fit comfortably in any existing tribes, and we therefore describe the new tribe Liagorothamnietae to accommodate the genus.

Liagorothamnietae Huisman, D.L. Ballantine & M.J. Wynne, trib. nov.


A new tribe of Ceramiaceae. Thalli irregularly producing whorl-branchlets arising one to four per axial cell. Spermangia on whorls of fertile branchlets borne on successive axial cells. Carposporal branch borne on a perixial supporting cell, which also bears two (or more) sterile cell groups. Basal cells of whorl-branchlets functioning as auxiliary cells. Carposporophyte with several gnomobiotes of carposporangia

TYPE GENUS: Liagorothamnion Huisman, D.L. Ballantine & M.J. Wynne

Hoomersand (1963) regarded the ceramialesan families Delesseriaceae, Rhodomelaceae and Dasyaceae as likely to have arisen independently from different members of the Ceramiaceae. Saunders et al. (1996), however, proposed a phylogenetic scheme based on short subunit (SSU) ribosomal DNA gene sequences, in which these three families represent a monophyletic clade that arose from a single common ancestor within the Ceramiaceae. It is tempting to speculate that Liagorothamnion, with two sterile groups on the supporting cell, might represent the primitive condition of this clade. Whatever the case, Liagorothamnion would be an ideal candidate for sequence studies and might possibly shed some light on the origins of the Ceramiaceae.

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