

# *Aglaothamnion rigidulum* nov. spec. (Rhodophyta, Ceramiaceae) from South Africa

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## Abstract

*Aglaothamnion rigidulum* is described as a new species from southern Kwazulu-Natal, South Africa. The main distinguishing characters are the robust nature of the filaments, the dense cortication in the lower part of the thallus, the alternating distichous branching pattern and the unbranched determinate laterals which curve upwards and overtop the apical cell. In addition to a detailed description of the vegetative anatomy and reproductive structures, attention is drawn to unusual changes of the branching pattern associated with the formation of procarps near the apices of indeterminate axes, and the subsequent formation of an involucrem protecting the developing gonimoblast. The plane of branching changes by 90° at the fertile axial cell, and the determinate laterals 2–3 cells below and above the fertile axial cell are strongly incurved and branch once or twice subdichotomously, thereby forming a protective involucrem enclosing the developing gonimoblast from all sides. This aspect of the morphology has not been well documented in either *Aglaothamnion* or *Callithamnion*, but may well occur in several other species belonging to the Callithamnieae.

**Keywords:** *Aglaothamnion*; *Callithamnion*; Ceramiaceae; Rhodophyta; South Africa.

## Introduction

Of all South African Rhodophyta, the Ceramiaceae has probably received most attention recently. Despite the vast body of literature devoted to this group, new records, species and even genera are being reported on a regular basis (e.g., Stegenga et al. 1997, 2000, 2002, De Clerck et al. 2002a,b). Furthermore, several publications mention specimens which unfortunately could not be assigned to an existing species with certainty due to fragmentary or sterile material. Wollaston (1984) while reporting on the Ceramiaceae collected by Papenfuss and Scagel in the framework of the International Indian Ocean Expedition in 1962 reported no less than seven

*Callithamnion*-like taxa which could not be identified to species level. One of those species, "*Callithamnion* sp. 4", is described here as a new species of *Aglaothamnion* based on recent collections from Palm Beach (Ugu district) in southern Kwazulu-Natal, South Africa.

## Materials and methods

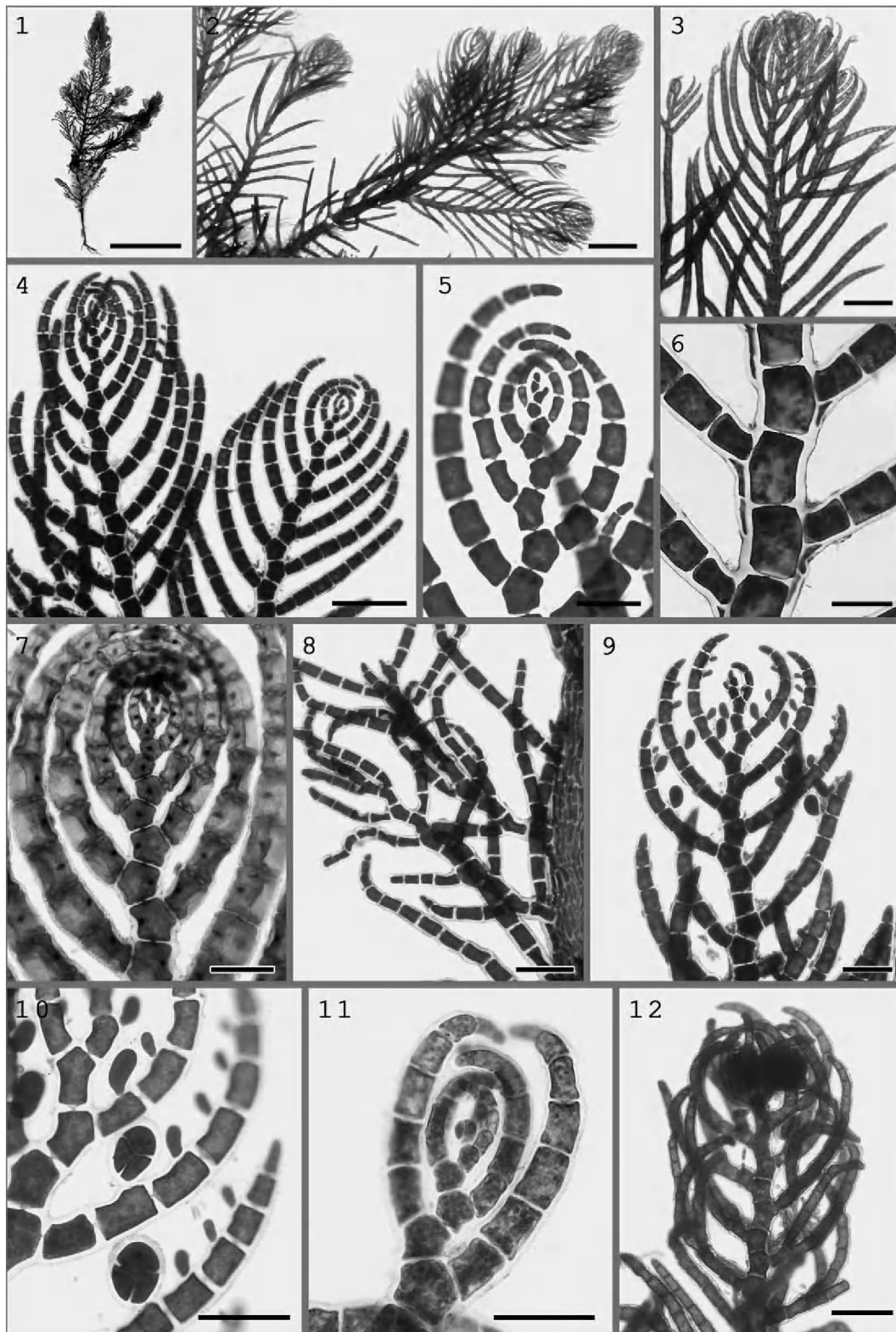
Specimens of the newly described species were collected in the framework of a Belgian – South African research project aimed at describing and interpreting the biogeographical patterns of the marine benthic algal flora along the South African east coast (Bolton et al. 2001, 2004). Material was photographed *in situ*, preserved in 5% formaldehyde in seawater and sorted in the laboratory. Whole-mount material was stained either with aniline-blue and mounted in Karo<sup>®</sup> syrup, or stained with Wittmann's aceto-iron-hematoxylin-chloral-hydrate and mounted in Hoyer medium as described in Hommersand et al. (1992). Photographs were taken with an Olympus DP50 digital camera mounted on an Olympus BX51 compound microscope (Olympus, Melville, USA) or Leica Wild M10 stereo microscope (Wetzlar, Germany).

## Results

### *Aglaothamnion rigidulum* nov. spec. (Figures 1–12)

**Diagnosis** *Ab omnibus speciebus aliis generis differt ramificationibus alternatis-distichis, axilibus infra corticatis rhizoidalis dense, ramulis determinatis simplicibus curvatis cellulae apicale superans. Reproductio asexualis ope tetrasporangium praesentium in seriebus secundis brevibus, adaxialia in ramulis ultimis. Tetrasporangia sessilia, ovata, usque ad 80×90 μm. Procarpia singularibus, in cellulis subapicalibus intercalaribus, axium indeterminatorum portata, cellula axiali fertili efferenti laterale singulum determinatum vegetative et cellulas duas periaxiales perpendiculariter plano lateralis vegetativi abscissas, una cellula periaxiali pro cellula sustinenti fungenti et ramum carpogonialem 4-cellulum ferenti, altera eramosa remanenti et cellulam auxiliarem secundam sub fecundationem carpogonii facienti; cellulae auxiliares gemellae e divisione inaequali cellulae sustinentis et periaxialis fertillis exorientes; gonimoblastus maturus circumcinctus ab involucre bene evoluto e cellulis proximalibus et distalis cellulae axiali fertili oriundo.*

Differing from the other species in the genus by the alternate distichous branching pattern, the dense rhizoidal cortex, the unbranched determinate laterals which curve upwardly and overtop the apical cell. Asexual reproduction by tetrasporangia occurring in short second



**Figures 1–12** *Aglaothamnion rigidulum* nov. spec.

(1) Holotype, GENT KZN-b 2337 (scale: 1 cm). (2, 3) Details of the apical portions of wet preserved specimens (scale Figure 2: 1 mm; Figure 3: 500  $\mu$ m). (4, 5) Axes with a regular alternate distichous branching pattern and determinate laterals overtopping the apical cells. Note distinct zig-zag aspect of the distal axes (scale Figure 3: 250  $\mu$ m; Figure 4: 100  $\mu$ m). (6) Initiation of rhizoidal corticating filaments from the proximal cell of each determinate lateral (scale: 100  $\mu$ m). (7) Apical portion of a thallus stained with haematoxylin, showing the uninucleate nature of the vegetative cells (scale: 100  $\mu$ m). (8) Basal, irregularly branched and contorted laterals (scale: 250  $\mu$ m). (9, 10) Tetrahedrally divided tetrasporangia in second series on the adaxial sides of ultimate branchlets (scale Figure 9: 50  $\mu$ m; Figure 10: 100  $\mu$ m). (11) A single procarp formed near the apex of a young axis (scale: 100  $\mu$ m). (12) A mature bilobed gonimoblast surrounded by dense involucrum (scale: 250  $\mu$ m).

series, adaxial on the ultimate branchlets. Tetrasporangia sessile, ovate,  $80 \times 90 \mu\text{m}$ . Procarps single, borne subapically on intercalary cells of indeterminate axes, fertile axial cell producing a single determinate vegetative lateral and two periaxial cells cut off perpendicularly to the plane of the vegetative lateral, one periaxial cell functioning as the supporting cell and bearing a four-celled carpogonial branch, the other remaining unbranched and giving rise to a second auxiliary cell upon fertilization of the carpogonium; paired auxiliary cells formed by unequal division of the supporting cell and fertile periaxial cell; mature gonimoblasts enveloped by a well-developed involucrem derived from cells proximal as well as cells distal to the fertile axial cell.

**Holotype** Palm Beach ( $30^{\circ}59'00''\text{S}$ ,  $30^{\circ}16'00''\text{E}$ ), KwaZulu-Natal, South Africa: 11.xi.2003, *leg. De Clerck O., Schils T., Verbruggen H. and Demeulenare E.*, KZN-b 2337, growing in pools of the lower intertidal (Figure 1). Holotype deposited in GENT; isotype slide material in BOL.

**Additional collection** Palm Beach ( $30^{\circ}59'00''\text{S}$ ,  $30^{\circ}16'00''\text{E}$ ), KwaZulu-Natal, South Africa: 10.xi.2003, *leg. De Clerck O., Schils T., Verbruggen H. and Demeulenare E.*, KZN-b 2334, epiphytic on *Inkyuleea beckeri* (Schmitz ex Mazza) Choi, Saunders et Kraft, collected from the drift.

**Etymology** The epithet *rigidulum* refers to the stiff nature of the determinate laterals.

### Description

The thallus is rather rigid and stiff, up to 3 cm high, attached at the base by multicellular rhizoids. Fronds consist of repeatedly and irregularly pseudodichotomously branched indeterminate axes that bear distichously arranged determinate laterals (Figures 2, 3). At irregular intervals, the plane of branching shifts approximately  $90^{\circ}$ , thereby maintaining the regular distichous pattern of the determinate laterals. Such an abrupt change in branching pattern often coincides with the formation of indeterminate axes or female reproductive structures. Near the base of the thallus, the initial regular distichous pattern is sometimes less easy to observe. Basal determinate laterals are often irregularly contorted and much branched (Figure 8). Freshly collected thalli are reddish in color with a marked bluish-grey iridescence. The middle and proximal parts of the thallus were completely covered by large numbers of diatoms (*Toxarium* sp., *Cocconeis* spp., *Amphora* spp.).

Axes are completely filamentous. Growth of indeterminate axes takes place by oblique divisions of the apical cells, with the high sides of successive axial cells alternately offset in a  $1/2$  divergence (Figures 4, 5). This results in a marked zig-zag arrangement of the axial cells in the apical parts of the thallus. Mature axial cells, ca. 25 cells below the apex, are nearly isodiametric or slightly longer than broad ( $80\text{--}100 \mu\text{m} \times 90\text{--}110 \mu\text{m}$ ; L/B: 1–1.2). Proximal axial cells retain the same shape but the diam-

eter increases to  $250 \mu\text{m}$ . Indeterminate laterals form at short intervals (2–8 cells) along parent axes by direct conversion of determinate laterals. Approximately 20 cells below the apex of principal axes, basal cells of determinate laterals each form a single branched corticating filament, growing downwards in the axial cell wall (Figure 6). At first, the rhizoidal filaments grow in the plane of branching, parallel to the lateral edges of the axial cells. Only when a second or a third corticating filament is formed, do branches of corticating filaments spread across the axial cell itself. No differentiation was observed between an inner and outer cortical tissue. The degree to which indeterminate axes were corticated varied. Axes of higher order often showed little or no cortication, while their parent axes were fully corticated. Determinate laterals are formed by protrusions of the axial cells, 1–2 cells down from the apical cell, in an alternating distichous manner ( $1/2$  spiral) and remain completely uncorticated. The laterals, reaching 10–16 cells ( $200\text{--}600 \mu\text{m}$  in length) are inserted at an angle of  $40\text{--}55^{\circ}$  to the parent axis and curve distinctly upwardly, overtopping the apical cell when young. Most typically, determinate laterals remain unbranched, but occasionally they may branch once (rarely twice). The apical cell of the determinate laterals is broadly rounded to somewhat conical. Deciduous hairs terminating the ultimate cells were observed only in close proximity to the apex. All vegetative cells are uninucleate (Figure 7).

Tetrasporangia,  $80 \times 90 \mu\text{m}$ , develop in series on the adaxial side of determinate laterals near the apices (Figures 9, 10). Only a single and sessile sporangium is formed per cell. Gametophytes are most probably dioecious. Procarps are borne near the apices of the indeterminate axes (Figure 11). Carpogonial branches forming series along a single axis were not observed. Instead, carpogonial branches appear to be solitary, some 5–6 cells below the apex. The structure of the procarp was typically that of the Callithamnieae, with a fertile axial cell bearing two opposite fertile periaxial cells oriented at an angle of  $90^{\circ}$  to the plane of vegetative branching. The first formed periaxial cell will act as the supporting cell of a 4-celled carpogonial branch. The complete sequence in which the respective cells are formed was not observed. The mature carpogonial branch has a zig-zag configuration. Following presumed fertilization, the supporting cell and fertile periaxial cells divide unevenly to produce a distal auxiliary cell and a basal cell each. The gonimoblasts are typically paired, with two rounded gonimolobes. All gonimoblast cells mature into angular carposporangia,  $45\text{--}60 \mu\text{m}$  in diameter. The development of a procarp near the apex of an indeterminate lateral coincides with some morphological “adaptations” of the vegetative system. The plane of branching changes by  $90^{\circ}$  at the fertile axial cell, and the determinate laterals 2–3 cells below and above the fertile axial cell are strongly incurved and branch once or twice subdichotomously, thereby forming a protective involucrem enclosing the developing gonimoblast from all sides (Figure 12). No additional laterals are formed on the cells proximal and distal to the fertile axial cell. After the initiation of gonimoblast development, growth of the indeterminate axes ceases, resulting in a subapical gonimoblast. Spermatangia were not observed.

## Discussion

The vegetative morphology as well as the structure and placement of the procarp, and the development of the gonimoblast, clearly link the newly described species to the tribe Callithamnieae as defined by Schmitz and Hauptfleisch (1897). The latter tribe currently encompasses 5 or 6 genera, of which *Aglaothamnion* and *Callithamnion* are the most widespread. The distinction between *Aglaothamnion* and *Callithamnion* is entirely based on the uninucleate versus multinucleate nature of the vegetative cells, respectively (Feldmann-Mazoyer 1941). Separation of the two genera on the basis of the number of nuclei per cell, however, is not accepted unanimously (e.g., Stegenga 1986, 1988, Stegenga et al. 1997, Womersley and Wollaston 1998). A recent phylogeny based on *rbcL* sequence data suggests, be it with very moderate bootstrap support, that the multinucleate condition (*Callithamnion*) evolved only once in the Callithamnieae, thereby strengthening the argument for two separate genera *Callithamnion* and *Aglaothamnion* (McIvor et al. 2002). It is worth noting that, although *Callithamnion* is a monophyletic genus, *Aglaothamnion* represents a paraphyletic clade (see McIvor et al. 2002: fig. 8). We tend to follow the latter authors in their taxonomic opinion. The new species, being characterized by uninucleate vegetative cells, would hence belong to *Aglaothamnion* rather than *Callithamnion sensu stricto*.

The morphology of the procarp in *Aglaothamnion rigidulum* is identical to those observed in both *Aglaothamnion* and *Callithamnion* (e.g., Dixon and Price 1981, O'Kelly and Baca 1984, Hommersand 1997). However, the newly described species never produces more than a single procarp per axis. This condition is somewhat atypical in the Callithamnieae where procarps are usually formed at intervals along an indeterminate axis (Kylin 1956, Hommersand 1963). Also, in *Sciurothamnion*, a genus linked to the Callithamnieae but differing by decussate branching, procarps are formed at intervals along the main axes (De Clerck et al. 2002b). In *Euptilota* on the other hand, Hommersand et al. (2004) noticed a clear tendency towards apicalization of the procarp. In *E. molle* (Wollaston) De Clerck procarps occupy the same position as in *Callithamnion* and *Seirospora*. In *E. formosissima* (Montagne) Kützing only a single subterminal procarp is formed. Procarp position in the other *Euptilota* species seems to be intermediate between the two aforementioned conditions.

The development of the procarp in *Aglaothamnion rigidulum* coincides with a shift in the vegetative branching pattern of the fertile axial cell. As discussed in Hommersand et al. (2004), the two opposite fertile periaxial cells are positioned at a 90° angle relative to the plane of vegetative branching in the Callithamnieae. This is also the case in *A. rigidulum*, although the determinate lateral produced by the fertile axial cell is already 90° offset to the plane of vegetative branching of the proximal axial cells. The shift in branching pattern enables the formation of an involucre which extends in three dimensions and encloses the developing gonimoblast. The involucre branchlets are derived directly from the vegetative determinate laterals of the fertile segment and the one cell

proximal and distal to the fertile axial cell (which branch once or twice). Contrary to the pattern in *Euptilota* and *Sciurothamnion*, no additional involucre branches are formed from the cells of the fertile axes. Although involucre filaments are reported for at least *Aglaothamnion*, *Callithamnion*, *Hirsutithalia* and *Seirospora* (Maggs and Hommersand 1993, Womersley and Wollaston 1998), the lack of detail in the description of reproductive structures in many species does not allow a detailed comparison on the development of involucre branches in those genera. There is clear evidence, however, that at least in some species of *Seirospora* and two species of *Hirsutithalia*, additional involucre filaments are formed from the hypogenous cell (Feldmann-Mazoyer 1941, Aponte and Ballantine 1995, Womersley and Wollaston 1998).

A literature search revealed very few taxa with similar vegetative and reproductive morphology. The alternate distichous branching pattern, combined with predominantly simple determinate laterals and a closely adherent rhizoidal cortex appears to be rather unique in the Callithamnieae. The new species most closely resembles *Aglaothamnion hookeri* (Dillwyn) Maggs et Hommersand and, to a lesser extent, *A. tripinnatum* (C. Agardh) Feldmann-Mazoyer. Both species are originally described from the warm temperate northeast Atlantic Ocean, but have subsequently been reported from the Mediterranean Basin, the African coasts (including South Africa) and a few localities in the Indian Ocean (Guiry and Nic Donncha 2004). Both species are clearly distinguished from *A. rigidulum* by a series of vegetative characters. The branching pattern of *A. tripinnatum* is regularly distichous but the determinate laterals are alternately distichously branched (Maggs and Hommersand 1993). In *A. rigidulum*, determinate laterals are generally unbranched. Furthermore, *A. tripinnatum* thalli from the South African coasts are minute, reaching a height of barely 5 mm (Stegenga 1988). *Aglaothamnion rigidulum* resembles *A. hookeri* in many aspects. Comparing both species in detail is hampered by the wide variation in overall size and pattern and density of branching of the latter (Dixon and Price 1981, Maggs and Hommersand 1993). Apart from the overall dimensions of the thallus, both species share a predominant alternate-distichous branching pattern, but in *A. hookeri* parts of the thallus are spirally branched (1/4 divergence). In *A. rigidulum*, deviations from the regular 1/2 divergence are limited to some axial cells, thereby simply altering the plane of branching but not the branching pattern (alternate-distichous) itself. Further differences relate to the morphology of the laterals, which are straight and often branched up to 3 orders in *A. hookeri* compared to upwardly curved and usually unbranched in *A. rigidulum*. The upwardly curved determinate laterals conspicuously overtop the growing tip of the axis. Overtopping of the apex is also reported for *A. hookeri*, but only in combination with a spiral branching pattern. In parts of the thallus exhibiting a distichous branching pattern, the apex is not concealed by the laterals. Despite close similarities between the South African and Australian seaweed floras (Norris and Aken 1985, Hommersand 1986), *A. rigidulum* seems similar to only a single Australian Callithamnieae species, *C. pinnatum* Womersley. The latter species, characterized by

**Table 1** *Aglaothamnion* and *Callithamnion* species reported from South Africa with indication of their distribution and main bibliographic references.

Species	South African distribution		Reference
	Western limit	Eastern limit	
<i>A. byssoides</i> (Arnott ex Harvey) L'Hardy-Halos et Rueness	Kenton On Sea		Stegenga 1988, Stegenga and Bolton 1992 as <i>C. furcellariae</i> J. Agardh
<i>A. cordatum</i> (Børgesen) Feldmann-Mazoyer	Port Alfred	northern Natal	Stegenga 1988, Stegenga and Bolton 1992 as <i>C. cordatum</i> Børgesen
<i>A. hookeri</i> (Dillwyn) Maggs et Hommersand	Namibia	East London	Stegenga 1988, Stegenga and Bolton 1992 and Stegenga et al. 1997 as <i>C. hookeri</i> (Dillwyn) S. Gray
<i>A. tripinnatum</i> (C. Agardh) Feldmann-Mazoyer	Brandfontein	East London	Stegenga 1988, Stegenga and Bolton 1992, and Stegenga et al. 1997 as <i>C. tripinnatum</i> C. Agardh
<i>C. exiguum</i> Stegenga, Bolton et Anderson	Betty's Bay		Stegenga et al. 1997
<i>C. granulatum</i> (Ducluzeau) C. Agardh	Nature's Valley	southern Natal	Bolton and Stegenga 1987, Stegenga 1988, Stegenga and Bolton 1992
<i>C. lasioides</i> Reinsch	Cape Agulhas		Reinsch 1875
<i>C. stuposum</i> Suhr	Swartklip	northern Natal	see Silva et al. 1996, incl. <i>C. variegatum</i> Suhr

uninucleate vegetative cells and therefore in fact belonging to *Aglaothamnion*, shares with *A. rigidulum* a distichous branching pattern, mostly simple determinate branchlets and a closely adherent rhizoidal cortex (Womersley and Wollaston 1998). The pedicellate nature of the tetrasporangia clearly differentiates *C. pinnatum*. Womersley and Wollaston (1998) remark on the similarity between the latter and *A. gallicum* (Nägeli) Halos et Ardré on the basis of a dense rhizoidal cortex and a primarily pinnate branching pattern. The much branched determinate laterals, however, provide a clear diagnostic character differentiating *A. gallicum* from *A. rigidulum*. Furthermore, gonimoblasts lack an involucre in *A. gallicum* (Maggs and Hommersand 1993).

In addition to *Aglaothamnion hookeri* and *A. tripinnatum*, two additional species of *Aglaothamnion* have been reported from South Africa, *A. byssoides* and *A. cordatum* (Table 1). Both of them are easily distinguished by their spirally arranged determinate laterals (1/4 divergence). In addition to the karyological differences which separate *Aglaothamnion rigidulum* from *Callithamnion*, the species is morphologically very different from the five *Callithamnion* species reported from South Africa so far. *Callithamnion granulatum* and *C. stuposum* are both characterized by profusely branched, spirally arranged determinate laterals, while *C. exiguum* is a minute (to 2 mm tall), irregularly branched epiphytic species. *Callithamnion variegatum* Suhr was shown by Athanasiadis (1999), after examination of the type material in KIEL, to belong to *Antithamnionella*. Another obscure species *Callithamnion lasioides* Reinsch (1875), apparently never

reported again since its original description (see Silva et al. 1996), differs markedly by its minute thallus with repeatedly branched laterals.

Much to our initial surprise, the new species resembles to some extent *Euptilota pappeana* Kützinger, a species occurring on the South African west coast. The taxonomic position of the latter species is uncertain at present since Hommersand et al. (2004) excluded it from *Euptilota*, based on a combination of reproductive characters and unpublished molecular evidence. *Aglaothamnion rigidulum* resembles *E. pappeana* in the distinctive alternate distichous branching pattern, the simple determinate branchlets which overtop the apical cell when young and the mode of cortex development. Differences include the robust size of *E. pappeana* (to 20 cm high), the compressed nature of the main axis, the overall extent of cortex formation and the position of the tetrasporangia. Whereas in *A. rigidulum* the single-layered cortex is limited to the main axes, in *E. pappeana* all branches of indeterminate growth become corticated, 2–3 cells thick, even enveloping the proximal cells of determinate laterals. Tetrasporangia are formed on much branched laterals in *E. pappeana*; in *A. rigidulum* the laterals, bearing the tetrasporangia, do not differ from vegetative laterals. Unfortunately, reproductive structures of *E. pappeana* are limited to tetrasporangia, and gametangial thalli have never been observed (Stegenga et al. 1997).

The results and discussion presented here may suggest a close relationship of the newly described *Aglaothamnion* species, with *Euptilota pappeana*. However, because vegetative morphology in the Ceramiaceae is

often highly homoplasious, due to repetitive convergence and parallel evolution between different genealogical lineages, drawing taxonomic conclusions on those data alone would be somewhat premature. Additional studies on the reproductive morphology of *E. pappeana*, combined with molecular systematics should be carried out to investigate the relationships between both taxa.

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