

NOTES ON CERAMIACEAE (RHODOPHYTA) FROM
THE EASTERN CAPE PROVINCE, SOUTH AFRICA. II

Zonariophila semiendophytica nov. gen., nov. spec.,
a minute epi/endophyte of *Zonaria subarticulata* (Lamour.) Papenf.

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SUMMARY

Zonariophila semiendophytica is described as a new genus and species from the coast of the East Cape, South Africa. It is characterized by a single large elongate basal cell immersed in the thallus of *Zonaria subarticulata* (Lamour.) Papenf.; this laterally compressed cell gives rise, on both edges, to several short (up to 2.5 mm), uncorticated, erect, sparingly branched filaments. The position and structure of the procarp (the subapical cell in a determinate female fertile filament bears two sterile pericentral cells and one fertile pericentral cell, the latter with one sterile cell and a four-celled carposogonial filament), and the development of a single involucrel filament from the hypogenous cell, put this genus in the immediate vicinity of *Pleonosporium*, and placement in the tribe Compsothamnieae is proposed.

INTRODUCTION

The South African coast is fairly rich in species belonging to the family Ceramiaceae. After the appearance of the South African checklist (Seagrief, 1984), several new species and new records were published (e.g. Stegenga, 1986, 1988). Stegenga & Bolton (1992) listed 85 species for the coastal area between the Orange River mouth and Transkei (the former Cape Province), a coastline c. 1800 km long with a marine climate best described as cool to warm temperate, and, apart from a few sheltered bays, fully exposed to ocean swell. Stegenga & Bolton (l.c.) showed that the highest diversity of the family was found in the East Cape, and especially in the area around Port Alfred (33° 36' S, 26° 53' E), with 65 species recorded.

A number of Ceramiaceae have extremely small dimensions; in many cases these species grow on other algae; they often have endophytic basal parts and they are restricted to one or a few host genera, although they do not appear to be parasitic. Apparently, this phenomenon has developed in several tribes; for instance, in South Africa representatives are found of:

- Spermiothamnieae: *Lomathamnion capense* Stegenga, on *Codium*, and *L. humile* (Kützinger) Stegenga, on *Phyllymenia* and *Grateloupia*.
- Ceramiaceae: *Syringocolax macrolepharis* Reinsch, on Gelidiaceae.
- Heterothamnieae: *Laurenciophila minima* Stegenga, on *Laurencia*.
- Callithamnieae: *Callithamnion* sp. ined., on *Codium* (Stegenga, unpublished observation – a species with emergent parts only c. 200 µm high).

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The present paper draws attention to yet another minute semi-endophyte, growing exclusively on *Zonaria subarticulata* (Dictyotales, Phaeophyta). We will demonstrate that this species belongs in the tribe Compsothamnieae (s.l.) and is close to *Pleonosporium*; since it has some morphological peculiarities, however, it is best described as a new genus.

MATERIAL AND METHODS

Material was collected in the Port Alfred–Riet River area, between Sharks Bay (33° 36' S, 26° 53' E) and Kleinemonde (33° 32' S, 27° 3' E), during the year 1987 (locations listed below). This coastal area is characterized by long sandy beaches interspersed with small rocky promontories; the marine climate is warm temperate, the average monthly water temperature fluctuating between 16 and 21°C through the year.

After preservation in 5% formaldehyde in seawater, some plants were dissected out from the host, stained in FCF fast green and embedded in corn syrup. Drawings were made with the aid of a camera lucida.

Voucher specimens (Sa-numbers) and the type-slides are in the Rhodes University Herbarium (RUH), Grahamstown, RSA. Other permanent slides (EC-numbers) are stored in the Botany Department, University of Cape Town, RSA.

Collections: Port Alfred, Sharks Bay, 17-III-1987, from low tide level and in drift (Sa 1132, EC 98, 99, 100, 123, 124, 130); idem, 3-XII-1987, in drift; Three Sisters, 28-IV-1987, in low intertidal pool (Sa 1274); idem, 11-VIII-1987, in large shaded rockpool (Sa 1637, EC 319); Kleinemonde, 27-III-1987, in drift (EC 138). In all cases plants grew on/in *Zonaria subarticulata*. Slides EC 99 (male and female) and EC 98 (tetrasporangial) are designated as holotype and isotype, respectively.

RESULTS

Zonariophila semiendophytica, nov. gen., nov. spec.

Plantae minusculae, cum basi unicellularia endophytico. Cellulae basales elongatae, truncatae necnon lateraliter compressae, cum pluribus filamentis erectis bilateraliter emergentibus ex hospite. Axes erecti usque ad 2.5 mm alto, incurvati; filamentorum diameter crescens ab 60 µm proximaliter usque ad 160 µm distaliter, cellulae 2–3 plo longiores quam latiores. Axes erecti cum uno solo vel duobus lateralibus oppositis per segmentum, lateralia interdum ramosa. Tetrasporangia sessilia in cellulis systematum spissorum ramificationis, c. 90 × 80 µm, divisa tetradrice. Spermatangia conjuncta in stichidiis; stichidia cylindrica, c. 180 × 90 µm, cum axi centrali tricellularia. Filamenta feminea fertilia tricellulari, in positione laterali. Carposporophytum globulare, c. 600 µm diametro, circumcinctum filamento involucri singulari et pluribus lateralibus incurvatis. — Holotypus in RUH lamina vitrea no. Stegenga EC 99 (masculini et feminei), isotypus in RUH lamina vitrea no. Stegenga EC 98 (tetrasporophytici), lecti 17-III-1987, Port Alfred, Sharks Bay, crescentes semi-endophytice in *Zonaria subarticulata* (Lamour.) Papenf., materia in litus ejecta.

Plants are small, consisting of a single endophytic cell and several short emergent multicellular filaments (Fig. 1–3, 11).

The basal cell is elongated horizontally, truncate apically and tapering basally, and laterally compressed: up to 2 mm in length by 200–260 µm in height by 40–100 µm

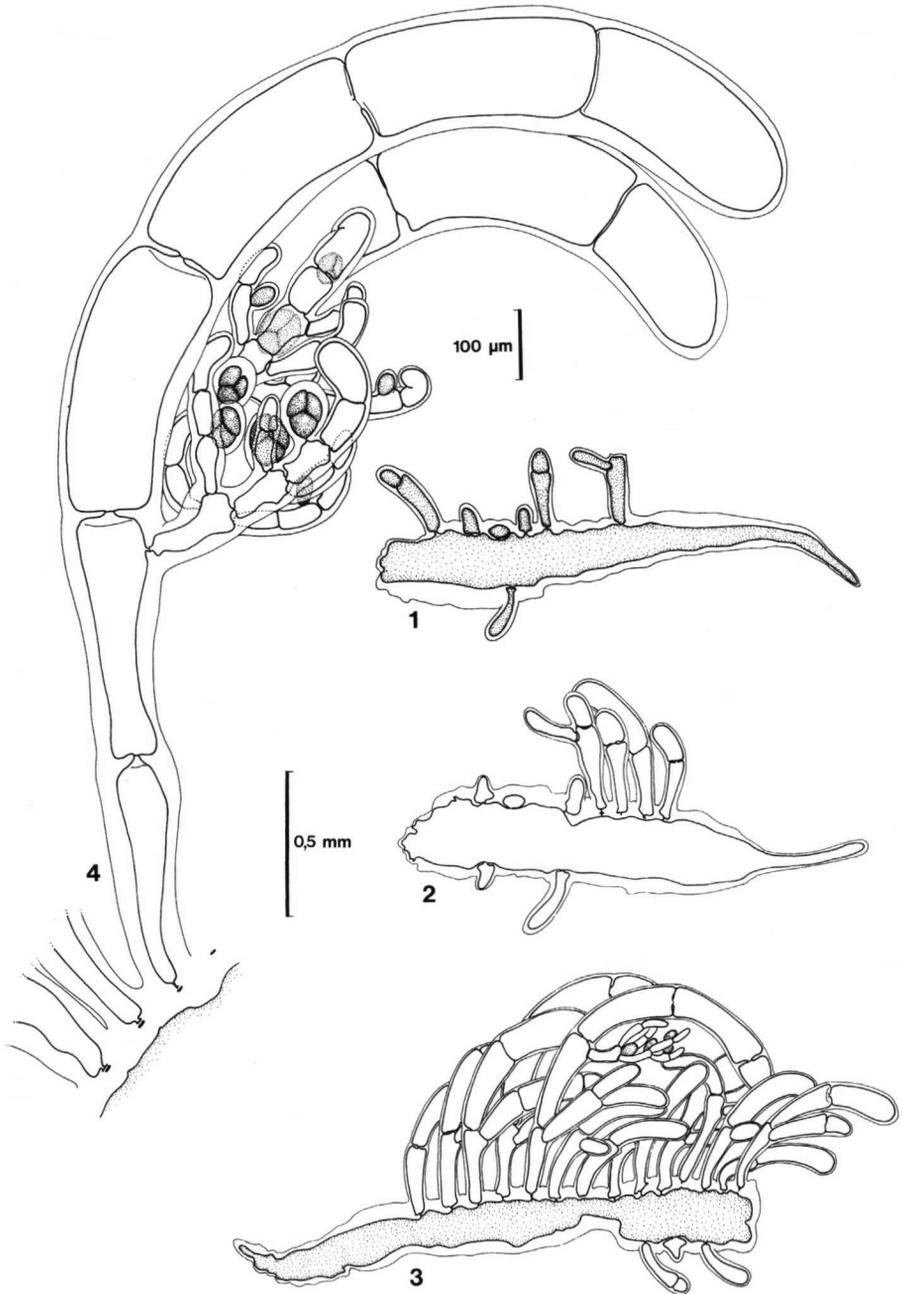


Fig. 1–3. Habit of juvenile plants (isolated from the substratum), showing large basal cell and young emergent filaments. — Fig. 4. Mature erect axis with tetrasporiferous branchlets; from the isotype (EC 98).

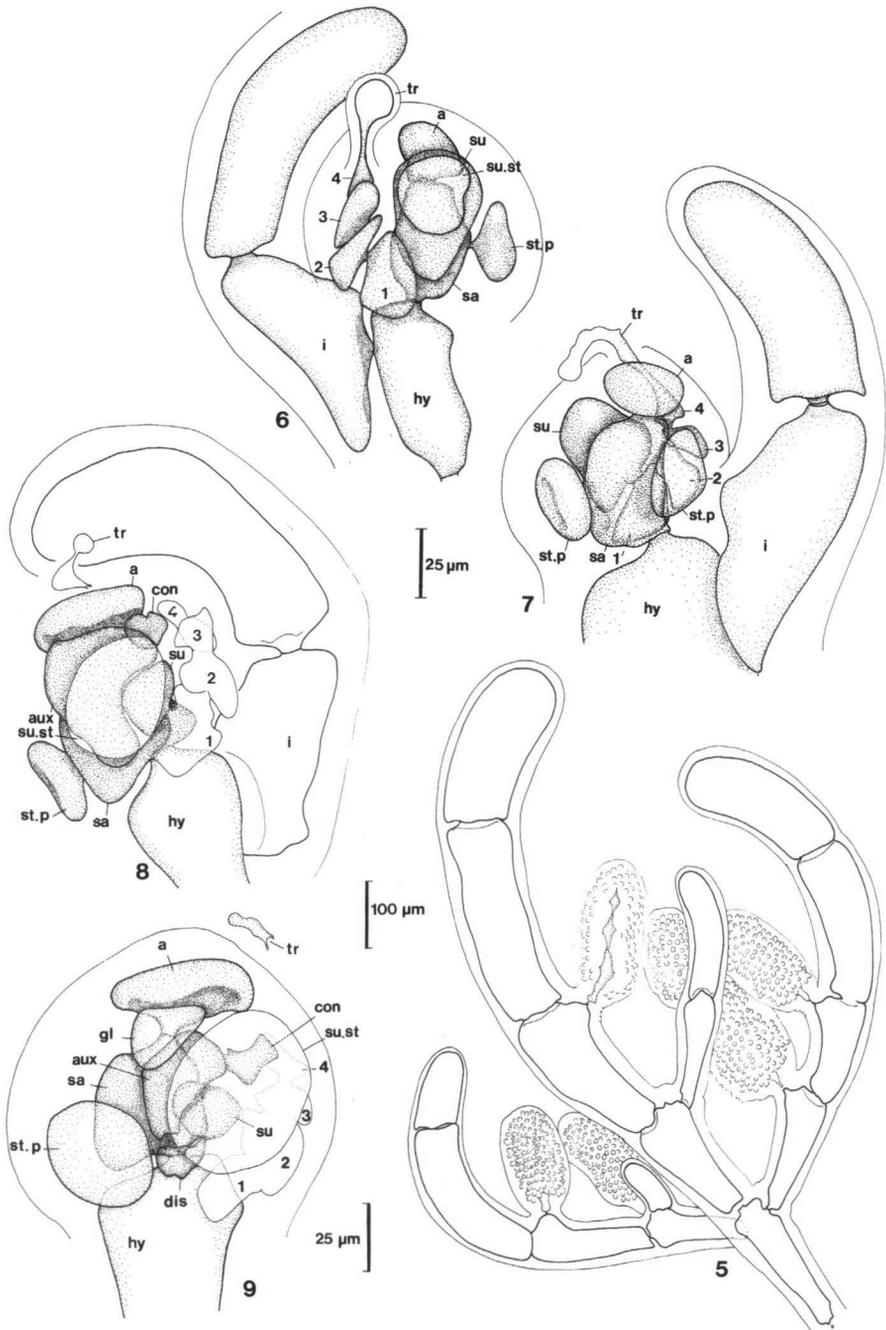


Fig. 5. Erect branch with spermatangial heads. — Fig. 6 & 7. Full-grown procarps prior to fertilization. — Fig. 8. Procarp just after fertilization; the auxiliary cell has been cut off from the supporting cell and has probably already been diploidized via the connecting cell. — Fig. 9. The auxiliary cell has cut off the disposal cell at the bottom and the first gonimolobe initial at the top; all material from the holotype (EC 99). — Legend (Fig. 6–9): a = apical cell of fertile filament; aux = →

in width. The longitudinal axis of the basal cell runs parallel to the length axis of the host *Zonaria*, while the 'sharp' edges of the flattened cell protrude between the host's epidermal cell rows and are flush with its surface; usually, the truncate apex is directed towards the apex of the host. Erect filaments originate from both exposed edges of the basal cell, arising in no specific (e.g. acropetal) order, but often more abundant on one (the dorsal) side than on the other. This is probably a response to the somewhat decumbent habit of *Zonaria* in the field. Filaments are ecorticate, incurved towards the apex of the basal cell; they are up to 2.5 mm and till seven cells long, increasing in diameter from 60 μm proximally to 160 μm distally, with rounded apical cell. Vegetative cells are cylindrical or slightly swollen, 2 to 3 times longer than broad. Erect axes are branched from a few proximal segments only, with one single or two opposite laterals per segment, the laterals occasionally rebranching in the same manner.

Tetrasporangia (Fig. 4) are sessile on the inside of cells of condensed branch systems in the position of ordinary laterals; cells of such systems are much narrower and shorter than those of vegetative laterals, and as these systems branch frequently they may produce dense fascicles. Mature tetrasporangia are tetrahedrally divided and measure c. 90 \times 80 μm .

Sexual plants are dioecious. Spermatangial capitula (Fig. 5) are produced singly or in short rows on the inside of incurved axes and laterals, not more than one capitulum per cell. Spermatangial heads are ovoid to subcylindrical, measuring up to 180 \times 90 μm , with a three-celled central axis each cell of which produces a whorl of cells bearing the spermatangial mother cells.

Female fertile axes are formed in the position of a lateral; they are three-celled, consisting of apical cell, subapical (= fertile axial) cell, and hypogenous cell. The subapical cell cuts off three pericentral cells: two sterile cells and one supporting cell, the latter cutting off a sterile cell and a four-celled carpogonial filament. The carpogonium bears a short bulbous trichogyne (Fig. 6, 7). After fertilization, the supporting cell cuts off a large auxiliary cell that is diploidized via a connecting cell (presumably cut off from the fertilized carpogonium – this could not be established unequivocally from our material – Fig. 8). The auxiliary cell then first cuts off a disposal cell and subsequently gives rise to (usually three) gonimolobes in quick succession (Fig. 9, 10). The gonimolobes form a globular carposporophyte about 600 μm in diameter (Fig. 12). Virtually all cells of the gonimolobes develop into carposporangia simultaneously; individual carpospores are about 50 μm in diameter. No significant cell fusions have been observed in the carposporophyte, but during its development the apical cell of the fertile filament, one of the sterile pericentral cells, and the sterile cell on the supporting cell undergo significant enlargement (compare Fig. 6 and 10). Prior to fertilization a single two-celled involucrel filament is produced from the hypogenous cell (Fig. 6–8, 10); additional incurved filaments, developing from segments below the fertile axis, complete the formation of a loose involucre (Fig. 12).

auxiliary cell; con = connecting cell; dis = disposal cell; gl = gonimolobe; hy = hypogenous cell; i = involucrel filament; sa = subapical cell of fertile filament; st.p = sterile pericentral cell; su = supporting cell; su.st. = sterile cell on supporting cell; tr = trichogyne; 1, 2, 3, 4 = cells of carpogonial filament (4 = carpogonium). — Note that the supporting cell may develop either to the right (Fig. 6) or to the left (Fig. 7, 8) of the involucrel filament.

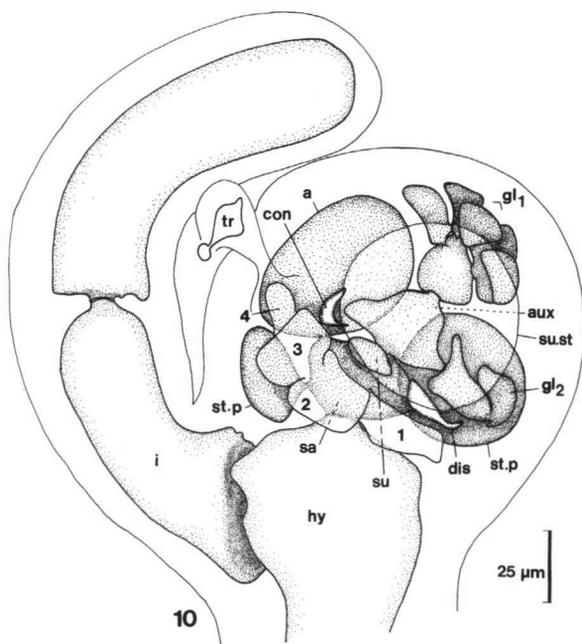


Fig. 10. Juvenile carposporophyte, showing two developing gonimolobes (gl_1 , gl_2); from the holotype (EC 99). Legend as in Fig. 6–9.

DISCUSSION

Zonariophila semiendophytica shows an interesting adaptation to its substratum: the height of the basal cell in mature plants equals the thickness of the blade of *Zonaria*, so that on both sides the cortical layers are pierced; emergent filaments are produced over the entire length of the exposed part of the basal cell. The basal cell reaches almost its full size before the first emergent filaments are initiated. Probably, germination of spores takes place on the surface of the host, as suggested by the curved-up 'tail' visible in some plants (Fig. 11); subsequently the developing basal cell forces itself in between the longitudinal medullary cell rows of *Zonaria*, almost always in an acropetal direction.

As was indicated in the introduction, minute cermiacean species with endophytic basal parts exist in various tribes. The same is apparently true for the species where the basal part is restricted to a single specialized cell: *Laurenciophila*, which has a large globose to ovate basal cell, was shown to belong in the Heterothamnieae on the basis of its female reproductive structure (Stegenga, 1988); for another semi-endophyte of *Laurencia*, the Australian *Radiathamnion*, a new tribe Radiathamnieae was erected as it showed a unique combination of morphological and reproductive features (Gordon-Mills & Kraft, 1981), although the authors remarked that the reproductive structures were close to the Antithamnieae and Heterothamnieae.

The new genus *Zonariophila* shows a procarp structure and post-fertilization development that are similar to those of some *Pleonosporium* species: the South African

species *P. filicinum* (Harvey ex J. Agardh) De Toni and *P. paternoster* Stegenga have straight female fertile filaments where the subapical cell bears three pericentral cells (Stegenga, 1986 – to be called ‘group A’ species here); some other species of *Pleonosporium*, e.g. *P. caribaeum* (Børgesen) R.E. Norris and *P. harveyanum* (J. Agardh) De Toni, have fertile axes where the apical cell is deflected and the subapical cell bears only two pericentral cells (Norris, 1985; Stegenga, 1986 – to be called ‘group B’ species here). Kim & Lee (1988) concluded that this difference is sufficient to transfer ‘group A’ species to a separate genus, but Maggs & Hommersand (1993) retain both types in *Pleonosporium*. Traditionally, *Pleonosporium* has been included in the tribe Compsothamnieae (Kylin, 1956), as it still is by Maggs & Hommersand (1993). Gordon-Mills & Wollaston (1990) and Wollaston (1990) considered recognition of the Spongoclonieae [comprising *Pleonosporium* (incl. *Mesothamnion*) and *Spongoclonium*] on the basis of formation of pericentral cells strictly on the subapical cell of the fertile filament whereas the remaining Compsothamnieae (*Antarcticothamnion*, *Compsothamnion*, *Compsothamnionella*) have the fertile axial cell at the 3rd to 6th position below the apical cell of the fertile filament; at the same time they (Gordon-Mills & Wollaston, 1990) left the position of *Dasythamniella*, *Lophothamnion* and *Haloplegma* undecided for lack of relevant knowledge. Since in this case the recog-

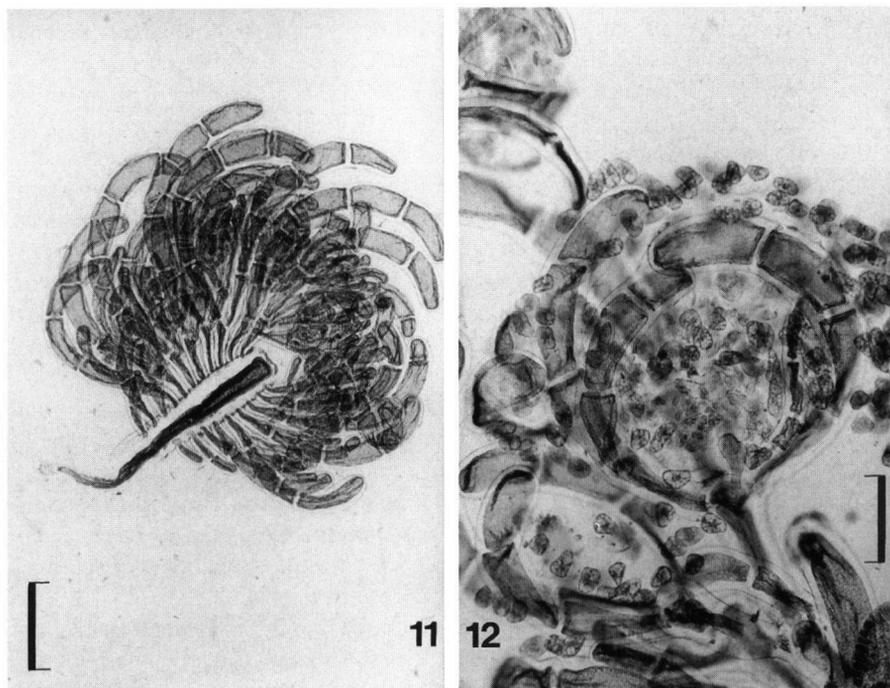


Fig. 11. Habit of full-grown plant (note the curved-up ‘tail’ of basal cell); scale bar = 0.5 mm. — Fig. 12. Mature carposporophyte, partly disintegrated into loose carpospores; also showing curved involucre branches of subhypogenous origin; scale bar = 200 μ m.

dition of the tribe Spongoconieae apparently also rests on the presence of a deflected apical cell in the female fertile filament, we feel that inclusion of *Zonariophila* (and 'group A' *Pleonosporium* species) in this tribe would be questionable, even though the fertile axial cell is strictly subapical in these species. The recognition of a tribe Pleonosporieae in a narrow sense as implied by e.g. Kim & Lee (1988) would not bring a solution to our problem either, as this tribe is (presumably) based on *Pleonosporium borrieri* (J.E. Smith) Nägeli, a species that probably has the same cell configuration in the female reproductive structure as the Spongoconieae (i.e. 'group B' *Pleonosporium* species). We therefore conclude that *Zonariophila* is, for the time being, best kept in the Compsothamnieae (s.l.).

Other genera than those mentioned by Gordon-Mills & Wollaston (1990) are sometimes associated with the Compsothamnieae: *Tanakaella* (Moe & Silva, 1979), *Gymnophycus* (Huisman & Kraft, 1983), *Mazoyerella* (Gordon-Mills & Womersley, 1974), and *Deucalion* (Huisman & Kraft, 1982). Only in *Deucalion* does the female reproductive structure come close to that of *Zonariophila*: these genera share the possession of three pericentral cells on the (subapical) fertile axial cell, and the development of involucre filaments both from the hypogenous and subhypogenous cells. *Gymnophycus* lacks an involucre altogether, and it has a large fusion cell, while *Tanakaella* and *Mazoyerella* have involucre filaments developed from sterile cells within the procarp.

Deucalion is a robust alga, and it is therefore not unlike the previously mentioned *Pleonosporium filicinum* and *P. paternoster*, differing mainly by the largely secund branching pattern of its laterals; indeed, Huisman & Kraft (1982) remark that the single most important difference between *Deucalion* and *Pleonosporium* is the structure of the procarp. This difference would be completely lost in a broad concept of *Pleonosporium* as e.g. in Maggs & Hommersand (1993).

The function of the 'disposal cell', namely the disposal of the superfluous (haploid) nuclei from the developing carposporophyte, has been clarified by Huisman & Kraft (1992). The presence of disposal cells (also termed rest cells – Stegenga, 1986) has been demonstrated in some Compsothamnieae and Spermothamnieae, and also in the genera *Guiryella* (Huisman & Kraft, 1992) and *Anotrichium* (at least *A. furcellatum* (J. Agardh) Baldock – Stegenga, 1988), both with uncertain tribal affinities. The taxonomic significance of the presence of a disposal cell is unknown at present.

A regular alternate/distichous branching pattern, sometimes cited as one of the characteristics of the Compsothamnieae, is not found in *Zonariophila*, but here thalli are perhaps too much reduced to allow a good comparison of vegetative structures. The occurrence of asexual sporangia in rather compact branch systems is found in other genera of the tribe, e.g. *Spongoconium* (Wollaston, 1990) and *Pleonosporium* [e.g. *P. ramulosum* (J. Agardh) De Toni – Stegenga, 1986]. Morphology of spermatangial heads is fairly similar throughout the Compsothamnieae.

Although our species exactly resembles 'group A' *Pleonosporium* and *Deucalion* in reproductive morphology, we believe that the specialized vegetative morphology warrants the recognition of a new genus. The occurrence of tetrasporangia in *Zonariophila*, and of polysporangia in *Deucalion* and 'group A' species of *Pleonosporium* is a further difference. 'Group B' of *Pleonosporium* is now regarded as including both species with polysporangia and tetrasporangia (e.g. Norris, 1985).

From the material we have seen so far, it appears that *Zonariophila semiendophytica* has a very restricted geographical distribution. Despite an intensive search in our own and herbarium collections of *Zonaria*, we have not found this epi/endophyte outside the c. 15 km between Port Alfred and Kleinemonde. *Zonaria subarticulata*, on the other hand, is more or less abundant between False Bay and Mozambique; in the East Cape it is often a prominent member of the algal communities of the subtidal and sublittoral fringe. *Zonariophila* has not been found on other species of *Zonaria* in the same area either, notably *Zonaria harveyana* (Pappe ex Kützting) Areschoug, or on other Dictyotales.

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REFERENCES

- Gordon-Mills, E.M., & G.T. Kraft. 1981. The morphology of *Radiathamnion speleotis* gen. et sp. nov., representing a new tribe in the Ceramiaceae (Rhodophyta) from southern Australia. *Phycologia* 20: 122–130.
- Gordon-Mills, E.M., & E.M. Wollaston. 1990. *Compsothamnionella huismanii* sp. nov. (Ceramiaceae, Rhodophyta) from southern Australia. *Botanica marina* 33: 9–17.
- Gordon-Mills, E.M., & H.B.S. Womersley. 1974. The morphology and life history of *Mazoyerella* gen. nov. (*M. arachnoidea* (Harvey) comb. nov.) Rhodophyta Ceramiaceae from southern Australia. *Br. Phycol. J.* 9: 127–137.
- Huisman, J.M., & G.T. Kraft. 1982. *Deucalion* gen. nov. and *Anisoschizus* gen. nov. (Ceramiaceae, Ceramiales), two new propagule-forming red algae from southern Australia. *J. Phycol.* 18: 177–192.
- Huisman, J.M., & G.T. Kraft. 1983. *Gymnophycus*, a new genus of Ceramiaceae (Rhodophyta) from eastern Australia. *Phycologia* 22: 285–294.
- Huisman, J.M., & G.T. Kraft. 1992. Disposal of auxiliary cell haploid nuclei during post-fertilization development in *Guiryella repens* gen. et sp. nov. (Ceramiaceae, Rhodophyta). *Phycologia* 31: 127–137.
- Kim, H.-S., & I.K. Lee. 1988. Morphology and reproduction of two species of *Pleonosporium Naegeli* (Ceramiaceae, Rhodophyta) in Korea. *Korean J. Phycol.* 2: 95–109.
- Kylin, H. 1956. *Die Gattungen der Rhodophyceen*. Gleerup, Lund. 673 pp.
- Maggs, C.A., & M.H. Hommersand. 1993. *Seaweeds of the British Isles 1. Rhodophyta 3A. Ceramiales*. HMSO, London. 444 pp.
- Moe, R.L., & P.C. Silva. 1979. Morphological and taxonomic studies on Antarctic Ceramiaceae (Rhodophyceae) 1. *Antarcticothamnion polysporum* gen. et sp. nov. *Br. phycol. J.* 14: 385–405.
- Norris, R.E. 1985. Studies on *Pleonosporium* and *Mesothamnion* (Ceramiaceae, Rhodophyta) with a description of a new species from Natal. *Br. Phycol. J.* 20: 59–68.
- Seagrief, S.C. 1984. A catalogue of South African green, brown and red marine algae. *Mem. Bot. Survey South Africa* 47: 1–72.
- Stegenga, H. 1986. The Ceramiaceae (excl. Ceramium) (Rhodophyta) of the south west Cape Province, South Africa. *Bibl. Phycol.* 74. 149 pp.

- Stegenga, H. 1988. Notes on Ceramiaceae (Rhodophyta) from the eastern Cape Province, South Africa I. New records and remarks on morphology. *Blumea* 33: 371–393.
- Stegenga, H., & J. J. Bolton. 1992. Ceramiaceae (Rhodophyta) of the Cape Province, South Africa: Distribution in relation to concepts of marine provinces. *Botanica marina* 35: 99–107.
- Wollaston, E.M. 1990. Recognition of the genera *Spongoclonium* Sonder and *Lasiothalia* Harvey (Ceramiaceae, Rhodophyta) in southern Australia. *Botanica marina* 33: 19–30.