THE GENUS PTILOTHAMNION (CERAMIACEAE, RHODOPHYTA) IN SOUTH AFRICA, WITH THE DESCRIPTION OF P. GOUKAMMAE SPEC. NOV.

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SUMMARY

The genus Ptilothamnion Thur. in Le Jolis is represented in South Africa by three, or possibly four species: P. codicolum, P. polysporum, P. goukammae spec. nov., and reportedly P. subsimplex, all recorded after 1983. An earlier record of P. pluma is probably erroneous.

The new species differs from known representatives of the genus by producing strictly one involucral filament from the hypogenous cell and additionally one from the subhypogenous cell. Ptilothamnion is a widespread genus, but rarely with more than two species in any given regional flora. A critical comparison of the c. 12 species shows that very few characters are shared by all of them.

Key words: Ceramiaceae, Ptilothamnion, Spermothamnioneae, South Africa, taxonomy.

INTRODUCTION

The first unequivocal record of the genus Ptilothamnion in South Africa is comparatively recent: it is true that Stephenson (1948) recorded P. pluma (Dillwyn) Thur. from East London, but it was reported to be growing in a vegetation of Bostrychia mixta Hook. & Harv. (= Stictosiphonia intricata (Bory) P.C. Silva) and ‘Gelidium heterocladum’ (a species never formally described). Stictosiphonia intricata is a high intertidal/supralittoral species and in South Africa it has often been found mixed with Gymnothamnion elegans (Schousb. ex C. Agardh) J. Agardh, a species in vegetative morphology rather similar to Ptilothamnion pluma [the two species appear to have been confused before – see comment of Feldmann-Mazoyer, 1941]. Ptilothamnion pluma, type species of the genus, is known from the subtidal or sublittoral fringe, and we consider that it has not been found outside the warm temperate Eastern North Atlantic Ocean (cf. Maggs & Hommersand, 1993). This makes P. polysporum E.M. Woll., described as a new species from the Eastern Cape Province (Wollaston, 1984), the earliest positive South African record of the genus. Bolton & Stegenga (1987) mentioned P. subsimplex Gordon-Mills from the Transkei coast, but since cell sizes of this

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species are rather similar to those of *P. polysporum*, and only carposporophytic specimens were found, it would be difficult to prove that it was any different from the latter species (the two can be distinguished by the asexual sporangia, *P. subsimplex* having tetrarosporangia, *P. polysporum* producing polysporangia). Recently, Stegenga et al. (2000) reported *P. codicolum* (Dawson) I.A. Abbott from the South African south coast, a species hitherto only known from Pacific Mexico and adjacent California.

New collections, made in the Goukamma Nature Reserve on the South African south coast, revealed the presence of yet another species of *Ptilothamnion* that could not be identified with previously described taxa. Also, we found new material of *P. polysporum* and *P. codicolum*, which allowed us to make a critical comparison of vegetative and reproductive structures of the South African and other species.

**MATERIAL AND METHODS**

A general collection of seaweeds was made in the intertidal and sublittoral fringe of the Goukamma Nature Reserve, Western Cape Province, South Africa (Fig. 1, sites 1 and 2), 12–15 October 2000. Immediately after collection material was fixed in 5% formaldehyde in seawater. Individual plants of the small filamentous algae were stained in FCF fast green and whole mounts embedded in corn syrup.

Drawings were made with a camera lucida on a Leitz Diaplan microscope. The type of the new species is in the Bolus Herbarium of the University of Cape Town (BOL), and additional slides are in the collection of the Phycology section of the Botany Department of the same Institution, while duplicates of the isotype have been deposited in L.

![Fig. 1. Map of southern South Africa, with localities mentioned in the text: 1 = Goukamma, Oyster-beds; 2 = Goukamma, Walker Point; 3 = Tsitsikamma, Scot's Hut; 4 = Tsitsikamma, Storms River; 5 = East London; 6 = Double Mouth; 7 = Kei Mouth; 8 = Hluleka. PE = Port Elizabeth.](image-url)
RESULTS

Ptilothamnion goulkammae Stegenga, J.J. Bolton & R.J. Anderson, spec. nov. — Fig. 2, 3

Plantae caespitosae base endophytica. Filamenta emergentes ad 2.5 mm alta et 25–35 μm diametro. Tetrasporangia sessiles seriebus adaxialibus in filamentis lateralis. Capi
tula spermatangiales terminales ovoidea ad cylindrica. Cystocarpi filamentis involu
growing on/in Galaxaura obtusata (Ellis et Sol.) J.V. Lamour., leg. SANPAD expedition 2000. Isotypus: slides EC 1136 and 1137 in the slide collection of the Botany Department (Phycology Section) of the University of Cape Town, slides EC 1138 and 1139 in L.

Macroscopically, plants can only be detected as a low red fur on subapical sections of Galaxaura obtusata and G. diesingiana Zanardini. Plants differentiated into an endo
ychytic part and emergent filaments. Endophytic filaments traversing the intercellular spaces of the medulla of the host; without apparent differentiation of rhizoids or haptera. Endophytic filaments fully provided with chloroplasts, their cells 25–35 μm in diameter and 75–300 μm long, cylindrical or somewhat irregular. Short sections of prostrate filament do occasionally occur outside the substrate species, showing a morphology more typical of the genus, with cells bearing erect filaments and short rhizoids, both issuing more or less from the middle of the cells. Emergent filaments numerous, forming a dense velvety layer up to 2.5 mm tall, the apices often somewhat curved. Branching rather scarce in the proximal sections, more frequent in the distal (and especially the fertile) sections. Erect filaments 25–32.5(–35) μm in diameter, not tapering towards the apex; cells in length varying from 37.5–140 μm, the longer cells in the proximal part, the shortest cell usually associated with reproductive structures on the distal parts; length/diameter 1.5–5. Cells with many small discoid chloroplasts in a parietal layer. Tetrasporic plants with mainly secund, sometimes alternate or opposite, branching in apical sections of the erect filaments. Tetrasporangia (Fig. 2a, b) formed in adaxial rows on the proximal part of the laterals, or also directly on the main filament, sessile, ovoid to nearly globose, 50–62.5 by 45–50 μm, tetrahedrally divided. Occasion ally, octosporangia present, slightly larger than the tetrasporangia. Erect filaments of male plants a few times forked, the spermatangial stands formed apically, while subapical segments may produce a lateral which in turn can form another antheridial stand; erect filaments thus becoming sympodial. Spermatangial heads (Fig. 2d–f) ovoid to short cylindrical, with a 3- (or 4-) celled rachis, at maturity measuring 75–87.5 by 52.5–62.5 μm. Erect axes of female plants producing terminal female fertile filaments. Ramification of the female plant developing as involucral filaments connected with the first-formed fertile filament continuing growth and developing further fertile filaments; the branching system of the plant thereby becoming sympodial (Fig. 2c). Female fertile filament (Fig. 3a–c) consisting of two short cells, the apical cell remaining undivided, the subapical cell with three pericentral cells: two sterile and one supporting cell. Supporting cell bearing a sterile cell and a carposgonial filament. Carposgonial filament 4-celled, the carpogonium with a short club-shaped trichogyne.
Fig. 2. *Ptilothamnion goukammas* Stegenga, J.J. Bolton & R.J. Anderson. a, b. Details of tetrasporangial thalli; note single polysporangium (arrow); c. detail of female thallus with several procarps; d–f. male thallus with terminal spermatangial stands in various stages of development. — Scale bar = 100 µm (a & b: from the isotype, slide EC 1136, Goukamma, 15 Oct. 2000, on *Galaxaura obtusata*; c–f: from Goukamma, 13 Oct. 2000, on *Galaxaura* spec. (EC 1241)).
Fig. 3. *Ptilothamnion goukammae* Stegenga, J.J. Bolton & R.J. Anderson. Developmental stages of procarp and carposporophyte. a, b. Procarp prior to fertilisation; c, d. development of auxiliary cell and diploidisation; e. cutting off of disposal cell; f, g. early development of gonimolobes; h, i. maturation of carposporophytes and further development of involucral filaments. Note presence of involucral filaments before fertilisation (a, b) and development of new fertile filament on mature involucral filament (i). Legend: ap = apical cell of fertile filament; aux = auxiliary cell; con = connecting cell; dis = disposal cell; gi = gonimolobe initial; gl = gonimolobe; hy = hypogenous cell; in = (basal cell of) involucral filament; p = (sterile) pericentral cell; sa = subapical cell of fertile filament; shy = subhypogenous cell; su = supporting cell; su st = sterile cell on supporting cell; tr = trichogyne; 1—4 = cells of carpogonial filament (4 = carpogonium). In d, e and f sterile cell on supporting cell (in similar position as in g) not shown. — Scale bars: a–g = 50 µm; h, i = 100 µm (a–g: from Goukamma, 13 Oct. 2000, on *Galaxaura* spec. (EC 1241); h, i: from the isotype, slide EC 1139, Goukamma, 15 Oct. 2000).
Zonaria subarticulata (EC 912); f, g: from Kei Mouth, 23 Oct. 1999, on (EC 971); h: from Hluleka, June 1983 (slide T 55)).

Zonaria subarticulata Ptilothamnion cf. subsimplex E.M. Gordon, procarp, showing two connecting cells cut off from the fertilised carpogonium. Legend as in Fig. 3. — Scale bars: a = 100 µm; b–g = 50 µm (a–e: from Double Mouth, 25 Oct. 1999, on Zonaria subarticulata (EC 912); f, g: from Kei Mouth, 23 Oct. 1999, on Zonaria subarticulata (EC 971); h: from Hluleka, June 1983 (slide T 55)).

Fig. 4a–g. Ptilothamnion codicolum (E.Y. Dawson) I.A. Abbott. a. Habit of male thallus; b–e. developmental stages of terminal spermatangial stands; f, g. details of female thalli with procarps at the base of emergent filaments. — Fig. 4h. Ptilothamnion cf. subsimplex E.M. Gordon, procarp, showing two connecting cells cut off from the fertilised carpogonium. Legend as in Fig. 3. — Scale bars: a = 100 µm; b–g = 50 µm (a–e: from Double Mouth, 25 Oct. 1999, on Zonaria subarticulata (EC 912); f, g: from Kei Mouth, 23 Oct. 1999, on Zonaria subarticulata (EC 971); h: from Hluleka, June 1983 (slide T 55)).
After fertilisation, the supporting cell cuts off an auxiliary cell which is presumably diploidised by the carpogonium via a connecting cell (Fig. 3d). The auxiliary cell then immediately functions as a gonimoblast initial, first cutting off a disposal cell, then two or three gonimolobes that mature in succession (Fig. 3e–g). Virtually all cells of the gonimolobes turning into carposporangia simultaneously. Mature gonimolobes (Fig. 3h, i) roundish, c. 180 μm in diameter, individual carpospores c. 25 μm. The hypogenous cell, below the subapical cell of the fertile filament, not much different from the vegetative cells, albeit somewhat shorter, producing, prior to fertilisation, a single involucral filament. In addition, the subhypogenous cell giving off an involucral filament, alternating in position with the filament from the hypogenous cell (Fig. 3a–h). Quite often, also the cell below the subhypogenous cell producing an involucral filament, usually on the same side as the one from the subhypogenous cell (Fig. 3i). Involute filaments each developing one to three laterals, enclosing the maturing gonimolobes. Involucral filaments, also those of ‘successful’ carposporophytes, often developing further terminal fertile filaments.

Other material — Goukamma Coastal Reserve, central section of the Oysterbeds (34° 03’ S, 22° 54’ E), growing on Galaxaura obtusata and G. diesingiana, collected 15-X-2000 by the SANPAD expedition, BOL no. G176, slides EC 1228, 1241, 1269).

Ecology — Plants have been found only as epi/endophytes of Galaxaura species, the substrate growing in deep intertidal pools eroded out in the comparatively soft aeolian sandstone that constitutes the Oesterbank. Whereas the lower intertidal vegetation here mainly consists of a few mm to a few cm thick sand-binding turf of many caespitose species (mainly red algae), these pools often harbour larger individuals of species like Zonaria subarticulata (J.V. Lamour.) Papenf., Sargassum heterophyllum (Turner) C. Agardh, the above-mentioned Galaxaura species, and some articulated corallines. The substrate species sometimes also bore Ptilothamnion polysporum, but usually on more proximal parts of the thallus (P. goukammae was always subterminal), and filaments of P. polysporum do not become endophytic; P. polysporum also appears to have a wider choice of substrates (see below), whereas P. goukammae is probably substrate-specific.

Notes — For systematic relationships, see the general discussion.

The most peculiar characteristic of P. goukammae (making it unique within the genus) is the consistent development of single involucral filaments from the hypogenous and subhypogenous cells.

ADDITIONAL OBSERVATIONS ON OTHER SOUTH AFRICAN SPECIES OF PTILOTHAMNION

Ptilothamnion codicolum (E. Y. Dawson) I. A. Abbott — Fig. 4a–g

Recorded previously from Tsitsikamma, South Africa, by Stegenga et al. (2000), who described only polysporic plants, similar to the type from Pacific Mexico (Dawson, 1962); Abbott (1971) described sexual plants from California, which were characterised by longer cells than those reported in the type description. In material collected recently in the Kei Mouth–Haga Haga area, c. 50 km east of East London, R.S.A., we found this species again, as before growing in the felty rhizoidal basal portions of Zonaria
subarticulata. This time both male and a few female plants were present: In vegetative morphology and cell dimensions these plants were completely similar to asexual thalli. Spermatangial heads (Fig. 4a–e) develop singly at the apex of erect filaments. They have a 3-celled rachis and at maturity are more or less ovoid, measuring c. 50 by 45 μm.

Procarps (Fig. 4f, g) developing on top of a single cell issuing from the proximal part of emergent filament. Female fertile filament 2-celled, the hypogenous cell being much longer than the apical and subapical cell. Subapical cell with only two pericentral cells: one sterile, the other a supporting cell; supporting cell with a sterile cell and a carpogonial filament. Carpogonial filament 4-celled, the carpogonium with a relatively long trichogyne. No post-fertilisation developments seen, so it is not known whether involucral filaments develop after fertilisation.

Collections — In addition to the material from Tsitsikamma (Stegenga et al., 2000), we now have records from: Kei Mouth, 23-X-1999, in felty foot of Zonaria subarticulata, male specimens (EC 971, 972); Double Mouth, 25-X-1999, on/in Zonaria subarticulata, female specimens (EC 896, 912); Goukamma, Walker Point, on/in Zonaria subarticulata, 12-X-2000, polysporangial (EC 1193).

Note — There are some differences from the Californian material described by Abbott (1971): The spermatangial heads are single and terminal, rather than “terminating one-celled secund or opposite laterals”; on the other hand, the position of the female fertile filaments is the same as in the Californian material, and Abbott (1971) also indicates a post-fertilisation development of involucral filaments, their number given as “one-two”, the illustration suggesting that these arise from the hypogenous cell. A more precise comparison of the female structure is impossible for lack of detail on the procarp construction in Abbott’s (1971) description and the absence of mature carposporophytes in our material.

Ptilothamnion polysporum Gordon-Mills & E.M. Woll. — Fig. 5

For a general description, see Wollaston (1984) and Stegenga et al. (1997). Material we collected from the Goukamma Reserve provided some interesting additional observations on the morphology: Especially in epilithic plants, which were larger than epiphytic specimens (up to 15 mm tall – epiphytic plants from the same location rarely over 4 mm tall), polysporangia were developed in regular adaxial rows on the secundly branched thallus apices (Fig. 5b, c); sexual reproductive structures were not found on epilithic plants. On the epiphytic plants sexual structures were frequent: spermatangial heads ovoid to elongate, sessile, often organised in alternating positions on the (monopodial) erect axes (Fig. 5a). Fertile female plants branch sympodially, as involucral filaments developed in connection with the first-formed procarp may produce further procarps (Fig. 5d). The carposporophytes are surrounded by two branched involucral filaments that originate from the hypogenous cell (Fig. 5e).

Collections — In addition to material mentioned in Wollaston (1984) and Stegenga et al. (1997), we now have records from the following localities: East Cape Province: Tsitsikamma Coastal Park, near Storms River Mouth, 14 April 1994, polysporangial, in algal turf (EC 716); idem, 15 Oct. 1997, polysporangial (EC 578); idem, 17 Oct. 1997, female specimens, on corallines and hydroids ((EC 600, 602, 614); idem, near

Note — Especially in the Goukamma Reserve, P. polysporum was frequently found on Galaxaura spp., together with P. goukammae. Ptilothamnion polysporum occupies

Fig. 5. Ptilothamnion polysporum Gordon-Mills & E.M. Woll. a. Male thallus with alternating spermatangial stands; b, c. details of thallus, with polysporangia; d. apex of female thallus with several procarps; e. mature carposporophyte. Note: polysporangial plants from epilithic material, other specimens epiphytic. — Scale bars: a, b, d, e = 100 µm; c = 50 µm (a: from Goukamma, 15 Oct. 2000, on Galaxaura spec. (EC 1140); b, c: from Goukamma, 15 Oct. 2000, epilithic (EC 1152); d, e: from Goukamma, 13 Oct. 2000, on Galaxaura obtusata (EC 1227)).
<table>
<thead>
<tr>
<th>species [basionym]</th>
<th>height of thallus</th>
<th>erect filament diameter (µm)</th>
<th>cell l/d</th>
<th>branching</th>
<th>sporangia – type</th>
<th>sporangia – position</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. cladophorae</em> (Yamada &amp; Tanaka) Feldmann-Mazoyer [Spermothamnion cladophorae Yamada &amp; Tanaka]</td>
<td>1-3 mm</td>
<td>c. 18</td>
<td>1.5-3.5 ×</td>
<td>rarely 1 or 2 laterals</td>
<td>tetra, rarely poly</td>
<td>sessile, + secund</td>
</tr>
<tr>
<td><em>P. codicolum</em> (E.Y. Dawson) I.A. Abbott [Pleosporium codicolum E.Y. Dawson]</td>
<td>0.5-0.8 mm (3-5 mm)</td>
<td>c. 30</td>
<td>1-1.5 × [2.5 ×]</td>
<td>subdichotomous, simple or irregular</td>
<td>poly (12-18)</td>
<td>pedicellate, near base of axes</td>
</tr>
<tr>
<td><em>P. occidentale</em> Searles &amp; Schneider</td>
<td>to 1 mm</td>
<td>18-29</td>
<td>to 4 × in figure</td>
<td>simple or few laterals</td>
<td>tetra</td>
<td>pedicellate, 1-2 on branchlet</td>
</tr>
<tr>
<td><em>P. plumula</em> (Dillwyn) Thur. in Le Jolis [Conferva plumula Dillwyn]</td>
<td>to 8 mm</td>
<td>22-32(-40 basally)</td>
<td>1-1.3(-2) ×, slightly longer basally</td>
<td>regular pinnate, opposite</td>
<td>tetra (and octo)</td>
<td>terminal and lateral on axes and branchlets</td>
</tr>
<tr>
<td><em>P. polysporum</em> Gordon-Mills &amp; E.M. Woll.</td>
<td>to 8 mm</td>
<td>30-50</td>
<td>2-5 ×</td>
<td>simple or sparingly branched</td>
<td>poly (12-18)</td>
<td>sessile on upper thallus</td>
</tr>
<tr>
<td><em>P. pusillum</em> (Okamura &amp; Segawa) Itono [Spermothamnion pusillum Okamura &amp; Segawa]</td>
<td>1.5 mm</td>
<td>18-20</td>
<td>2 ×</td>
<td>simple or few laterals</td>
<td>tetra</td>
<td>pedicellate, secund on filaments</td>
</tr>
<tr>
<td><em>P. richardsii</em> Skuja</td>
<td>0.5-1 mm (14-)17-29</td>
<td>c. 1 ×</td>
<td>pinnate, alternate</td>
<td>mono</td>
<td>sessile on branchlets</td>
<td></td>
</tr>
<tr>
<td><em>P. rupicolum</em> Gordon-Mills</td>
<td>to 30 mm (35-)40-60</td>
<td>1.5-4.5 ×</td>
<td>irregular, scarce</td>
<td>tetra</td>
<td>pedicellate, lateral on erect axes</td>
<td></td>
</tr>
<tr>
<td><em>P. schmitzii</em> Heydrich</td>
<td>0.5-1(-2) mm</td>
<td>16-20</td>
<td>0.5-1 ×</td>
<td>simple or few laterals</td>
<td>tetra</td>
<td>pedicellate</td>
</tr>
<tr>
<td><em>P. speluncarum</em> (Collins &amp; Hervey) Ballentine &amp; Wynne [Rhodochorton speluncarum Collins &amp; Hervey]</td>
<td>to 15 mm</td>
<td>27-35</td>
<td>c. 2.5 × in figure</td>
<td>irregular, alternate or secund</td>
<td>tetra (+ poly and mono)</td>
<td>sessile, solitary or in short rows</td>
</tr>
<tr>
<td><em>P. sphaericum</em> (Crouan &amp; Crouan) Maggs &amp; Hommersand [Callithamnion sphaericum Crouan &amp; Crouan]</td>
<td>to 25 mm</td>
<td>60 apically, 40-85 basally</td>
<td>0.7-1.5 × (1-4 × basally)</td>
<td>irregular, sparse</td>
<td>poly (8-16)</td>
<td>sessile, lateral near apices</td>
</tr>
<tr>
<td><em>P. subsimplex</em> Gordon-Mills</td>
<td>2 mm</td>
<td>30-60</td>
<td>1-3.5 ×</td>
<td>simple or sparingly branched</td>
<td>tetra</td>
<td>sessile, more or less secund</td>
</tr>
<tr>
<td><em>P. goukammae</em> spec. nov.</td>
<td>to 2.5 mm</td>
<td>25-32.5(35)</td>
<td>1.5-5 ×</td>
<td>simple, branching when fertile</td>
<td>tetra (octo)</td>
<td>sessile, adaxial on laterals</td>
</tr>
<tr>
<td>species [basionym]</td>
<td>sporangia – size (µm)</td>
<td>involucre development</td>
<td>involucre – number</td>
<td>substrate</td>
<td>type loc., distribution</td>
<td>reference</td>
</tr>
<tr>
<td>--------------------</td>
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<tr>
<td><em>P. cladophorae</em> (Yamada &amp; Tanaka) Feldmann-Mazoyer [<em>Spermothamnion cladophorae</em> Yamada &amp; Tanaka]</td>
<td>55 × 47, ovoid</td>
<td>pre</td>
<td>2</td>
<td><em>Cladophora</em></td>
<td>Taiwan, S. Japan</td>
<td>Yamada &amp; Tanaka, 1934</td>
</tr>
<tr>
<td><em>P. codicolum</em> (E.Y. Dawson) I.A. Abbott [<em>Pleurospermum codicolum</em> E.Y. Dawson]</td>
<td>90(–100), globose</td>
<td>[post]</td>
<td>[1–2]</td>
<td><em>Codium</em>, ‘other algae’, <em>Zonaria</em></td>
<td>Pac. Mexico, California, S. Africa</td>
<td>Dawson, 1962; Abbott, 1971; this paper</td>
</tr>
<tr>
<td><em>P. occidentale</em> Searles &amp; Schneider</td>
<td>34–54 × 27–45, ovoid</td>
<td>pre</td>
<td>1–2</td>
<td>?</td>
<td>Southeast USA</td>
<td>Searles &amp; Schneider, 1989</td>
</tr>
<tr>
<td><em>P. pluma</em> (Dillwyn) Thur. in Le Jolis [<em>Conerva pluma</em> Dillwyn]</td>
<td>60–74 × 52–70 (octo 84–96 × 60–70)</td>
<td>pre</td>
<td>2</td>
<td><em>Laminaria</em> and epilithic</td>
<td>British Isles, E. N. Atlantic, W. Mediterranean</td>
<td>Maggs &amp; Hommersand, 1993</td>
</tr>
<tr>
<td><em>P. polysporum</em> Gordon-Mills &amp; E.M. Woll.</td>
<td>to 100, globose</td>
<td>pre</td>
<td>2</td>
<td>‘epiphytic’</td>
<td>S. Africa, W. Australia</td>
<td>Wollaston, 1984; this paper</td>
</tr>
<tr>
<td><em>P. pusillum</em> (Okamura &amp; Segawa) Itono [<em>Spermothamnion pusillum</em> Okamura &amp; Segawa]</td>
<td>50–65, globose</td>
<td>(pre)</td>
<td>2</td>
<td><em>Carpolopsis</em></td>
<td>Prov. Izu, Japan</td>
<td>Segawa, 1936</td>
</tr>
<tr>
<td><em>P. speluncarum</em> (Collins &amp; Hervey) Ballantyne &amp; Wynne [<em>Rhodochorton speluncarum</em> Collins &amp; Hervey]</td>
<td>50 longest diam.</td>
<td>pre</td>
<td>2</td>
<td>epilithic</td>
<td>Bermuda, Puerto Rico</td>
<td>Ballantine &amp; Wynne, 1998</td>
</tr>
<tr>
<td><em>P. subsimplex</em> Gordon-Mills</td>
<td>65, ovoid</td>
<td>pre</td>
<td>2</td>
<td><em>Lenormandia</em></td>
<td>Kangaroo Is., Australia, Tanzania, ? S. Africa</td>
<td>Gordon, 1972; this paper</td>
</tr>
<tr>
<td><em>P. goukammae</em> spec. nov.</td>
<td>50–62.5 × 45–50, ovoid to globose</td>
<td>pre</td>
<td>2 alternating</td>
<td><em>Galaxaura</em></td>
<td>S. Africa, W. Cape Province</td>
<td>this paper</td>
</tr>
</tbody>
</table>
Table 1 (continued)

Notes:
1) Itono (1977) mentions Cladophoropsis and Dasyphila as substrates.
2) Data in [ ] according to Abbott (1971), who was the first to observe sexual reproductive structures in this species— for more, and partly aberrant, data see the present paper.
3) Ptilothamnion pluma presently includes P. micropterum (Mont.) Bornet in Sauvageau (1897) and P. lucifugum Cotton (1912) — e.g. Maggs & Hommersand, 1993; Feldmann-Mazoyer, 1941.
4) Carpospores mature successively, in centripetal direction.
5) Segawa (1936) notes a „likeness to Spermothamnion cladophorae Yamada et Tanaka”, the pedicellate sporangia being a diagnostic character.
6) Assigned to Ptilothamnion on the basis of vegetative characters (see above); the authors included Anfractutofilum umbracolens Cribb in this species. The presence of monosporangia is otherwise unknown in the genus, with the possible exception of P. speluncarum (see note 9).
7) Tetrasporangia (and, incidentally, also antheridial stands) occur in branched clusters on the erect axes. This species is further aberrant as the fertile axial cell bears only two instead of three pericentral cells (see also P. codicolum— this paper). The fertilised carpogonium produces two connecting cells - the latter character was also observed in South African material of ‘P. subsimplex’ (this paper).
8) A description by Womersley (1998 — data in [ ] ) mentions much longer cells in the erect axes: 2.5–4.5 times as long as broad; this author also gives more detail on female reproductive structures: carpospores in gonimolobes mature simultaneously.
9) It is uncertain whether reported monosporangia are immature stages of tetra- and polysporangia.
10) Included in Ptilothamnion on the basis of vegetative characters, especially median position of erect axes and rhizoids on cells of the prostrate system.
11) Maturation of carpospores within gonimolobes is successive, in centripetal direction.

the proximal regions of the host and does not develop endophytic filaments, whereas P. goukammae is situated just below the apices of the host and develops an extensive endophytic growth of prostrate filaments. Also at Goukamma, P. polysporum was found as part of an epilithic sand binding turf, in which case plants became larger than epiphytic specimens.

Ptilothamnion ‘subsimplex’ Gordon-Mills — Fig. 4h

This species was reported from Hluleka, Transkei (now East Cape Province), South Africa (Bolton & Stegenga, 1987). As already mentioned in the introduction, the female specimens would be able to distinguish from P. polysporum. We mention this material again as the development of the post-fertilisation structure clearly shows the presence of two connecting cells from the fertilised carpogonium, otherwise rarely observed in the genus (see P. rupicolum). This is to not say that P. subsimplex differs in this respect from P. polysporum, adequate observations on the latter species are simply lacking.

No new South African material has been found that could unequivocally be attributed to P. subsimplex.
GENERAL DISCUSSION

Although the genus *Ptilothamnion* has been recognised for quite some time (Thuret, 1863), about half of the now distinguished species were described under other generic names (see Table 1). A combination of characters distinguishes this genus from other members of the tribe Spermothamnieae:

- The production of erect filaments and rhizoids from about the middle of the cells of the prostrate axes.
- Female fertile filaments terminal and consisting of only two specialised cells (apical and subapical cell), the hypogenous and subhypogenous cells being similar in size to vegetative cells. Some authors have given cell numbers in the fertile filament as high as 4–6 (Gordon-Mills, 1977), but the actual configuration is much the same as in other species.
- The production of, as a rule, two involucral filaments from the hypogenous cell, often initiated before fertilisation, sometimes post fertilisation.

However, even in the hitherto described species, these characters are not universal:

- Plants without clear differentiation of prostrate and erect filaments and rhizoids are found in *P. codicolum*. In *P. goukammae* they are only observed in (rarely) emergent prostrate filaments, but indistinct in endophytic filaments.
- This character seems to hold for all species, but sexual reproductive structures are not known in *P. sphaericum* and the freshwater species *P. richardsii*.
- A number of 3 or 4 involucral filaments was quoted for *P. rupicolum* (Gordon-Mills, 1977), 1 involucral filament is mentioned as the occasional state of affairs in more than one species (Table 1). The configuration of the involucral filaments in *P. goukammae*, i.e. the consistent production of single filaments from both hypogenous and subhypogenous cells in alternating position, appears to be unique in the genus.

Other remarkable variations in the genus include:

- The number of pericentral cells of the fertile axial cell: normally three, but two in *P. rupicolum* and *P. codicolum*. Reduction of the basic number of three pericentral cells is found in at least one other genus of the Spermothamnieae: *Lomathamnion* (Gordon, 1972).
- The development of carpospores, being simultaneous in some species, but successive in others. The former situation is clearly the case in *P. goukammae*, the latter in *P. polysporum*. A similar variation has also been suggested for the genus *Lomathamnion* (Stegenga et al., 1997), and the inclusion of 'terminal carposporangia' in the tribal diagnosis (Womersley, 1998) may have to be revised.
- The asexual sporangia, being either tetrasporangia or polysporangia. This happens in many red algal genera and is not considered a character of taxonomic significance at genus level. Within the Spermothamnieae, again, *Lomathamnion* is the other genus with representatives of both types, although octosporangia have also been described for *Spermothamnion repens* (Dillwyn) Rosenv. (Maggs & Hommersand, 1993).
Among the variations found (see above), the presence in Ptilothamnion of two types of carpospore development (i.e. simultaneous and successive) seems the most significant. Womersley (1998) still mentioned terminal carposporangia (i.e. successive development) as a character of the tribe Spermothamnioideae, although apparently he was fully aware of the simultaneous development of these structures in (Australian) P. schmitzii and P. subsimplex. All the other genera in the tribe, with the exception of one species of Lomathamnion, have terminal carposporangia.

Other variations in the genus can often be explained by reduction, for instance: the loss of rhizoids in P. codicolum and P. goukammae; the presence of only two pericentral cells in P. codicolum and P. rupicolum; loss of function of the second fertile pericentral cell – the presence, in some species of Ptilothamnion, of two connecting cells suggest relationships with those genera that have two fertile pericentral cells (Gordoniella, Interthamnion, Spermothamnion, Tiffaniella). These reductions may parallel developments in Lomathamnion, for instance L. epicodii Gordon still has regular development of rhizoids – issuing from the middle of the cell! – the other species of Lomathamnion are without rhizoids. In short, Ptilothamnion (and Lomathamnion) may represent the product of reductional developments in several spermothamnoid algae, and not constitute a natural group. The reductional trends may be connected with the very small size of most species, loss of rhizoids is probably functionally related to a semi-endophytic habit.

The distribution of the genus Ptilothamnion is worldwide (Table 1), with no apparent ‘hot spots’ of diversity, except that most species have been described from (warm) temperate localities. Local floras rarely have more than two species of the genus (three in South Africa) and representation is about equal in northern and southern hemispheres. There is little indication that there is any pattern in the geographical distribution in connection with the morphological traits and their variations described above.

ACKNOWLEDGEMENTS

Material for this study was collected during a seaweed identification course in the framework of a SANPAD program (South Africa – Netherlands Programme on Alternatives in Development). Facilities provided by the University of Cape Town and the Seaweed Unit of Marine and Coastal Management are gratefully acknowledged, as well as funding to JJB from the National Research Foundation and the Department of Education and Tourism.

We thank Dr. G.M. Lokhorst (NHN – Leiden) for critically reading the manuscript and Dr. H.P. Nooteboom (NHN – Leiden) for the Latin rendering of the diagnosis.

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