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*, Spermothamnieae, 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 speci-
mens 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
tetrasporangia, *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 Afri-
can 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
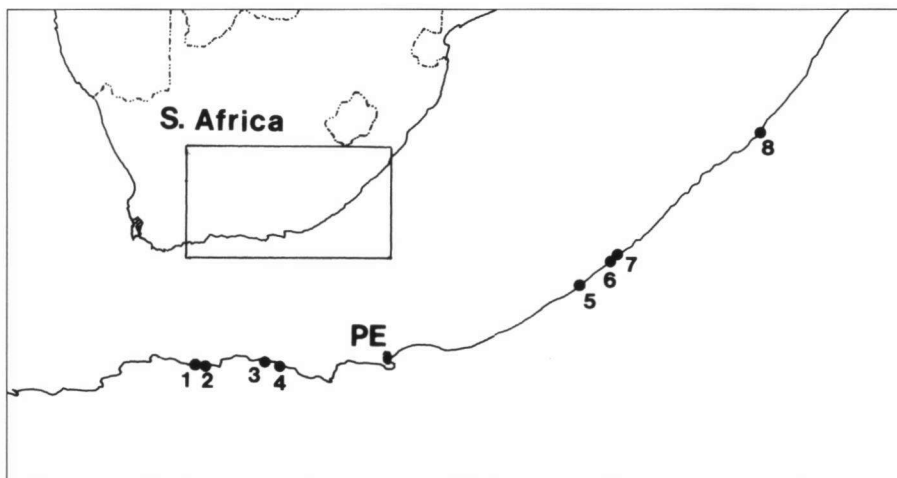deposited in L.

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.

RESULTS

Ptilothamnion goukammae 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 lateralibus. Capi-
> tula spermatangiales terminales ovoidea ad cylindrica. Cystocarpi filamentis involu-
> cralibis e cellulis hypogenis et subhypogenis ante fecundatione effectis. Carposporangia
> simultanea. — Holotypus in BOL, no. G052, 15-X-2000, Oesterbank (= oysterbeds) of
> the Goukamma Nature Reserve, Western Cape Province, R.S.A. (34° 04' S, 22° 56' E),
> material 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-
phytic 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, branch-
ing in apical sections of the erect filaments. *Tetrasporangia* (Fig. 2a, b) formed in ad-
axial 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. Occa-
sionally, 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 con-
nected 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 carpogonial filament.
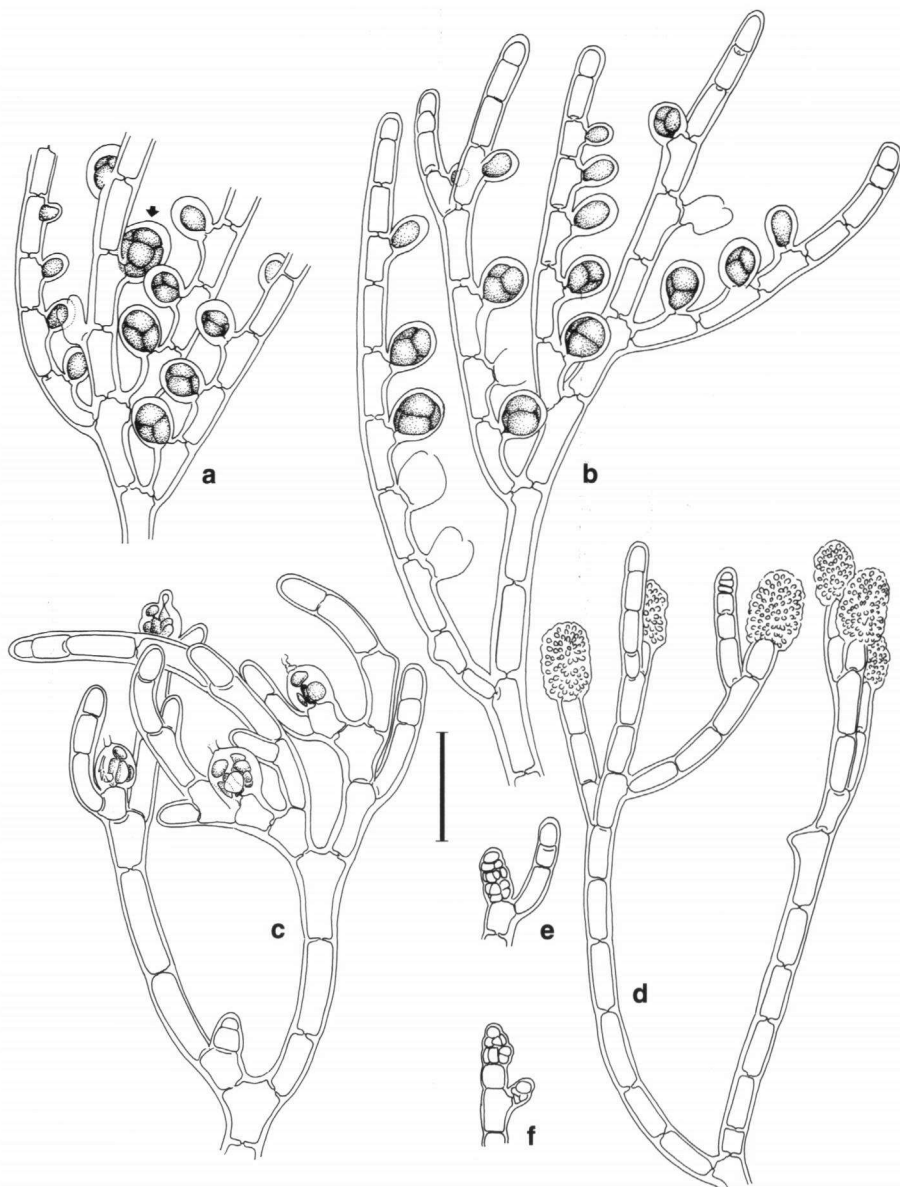*Carpogonial filament* 4-celled, the carpogonium with a short club-shaped trichogyne.

Fig. 2. *Ptilothamnion goukammae* 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)).
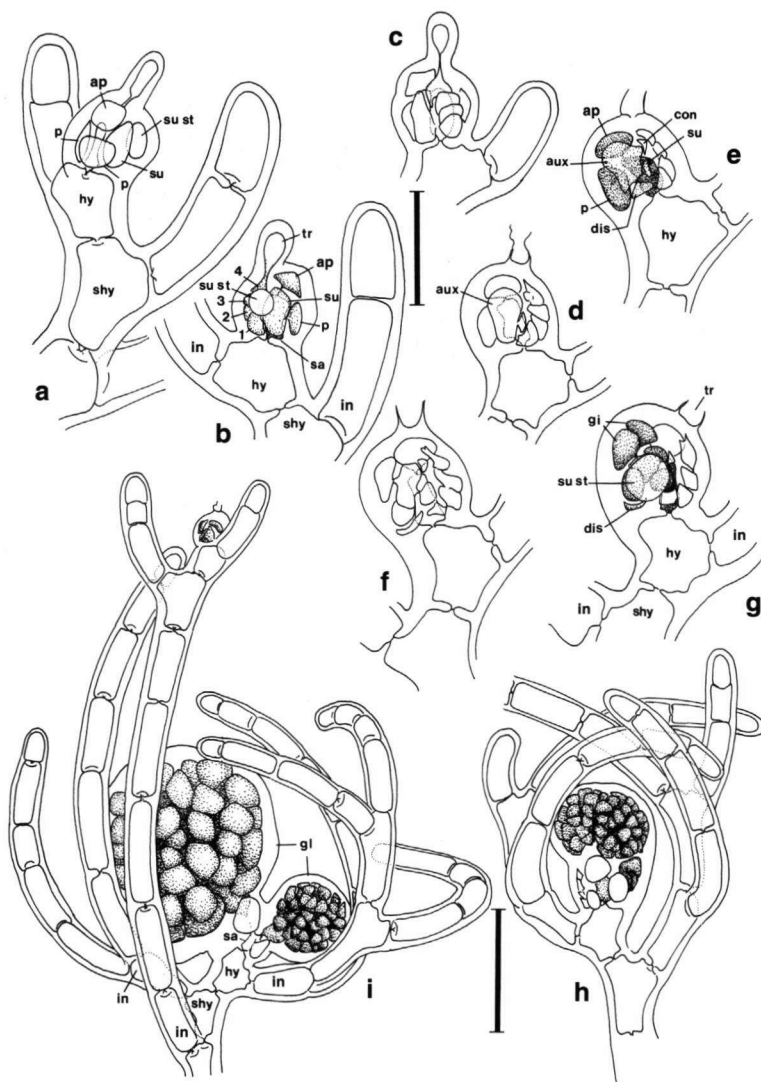
Fig. 3. *Ptilothamnion goukammae* Stegenga, J.J. Bolton & R.J. Anderson. Developmental stages of procarp and carposporophyte. a, b. Procarp prior to fertilisation; c, d. development of auxiliary cell and diploidisation; e. cutting off of disposal cell; f, g. early development of gonimolobes; h, i. maturation 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).
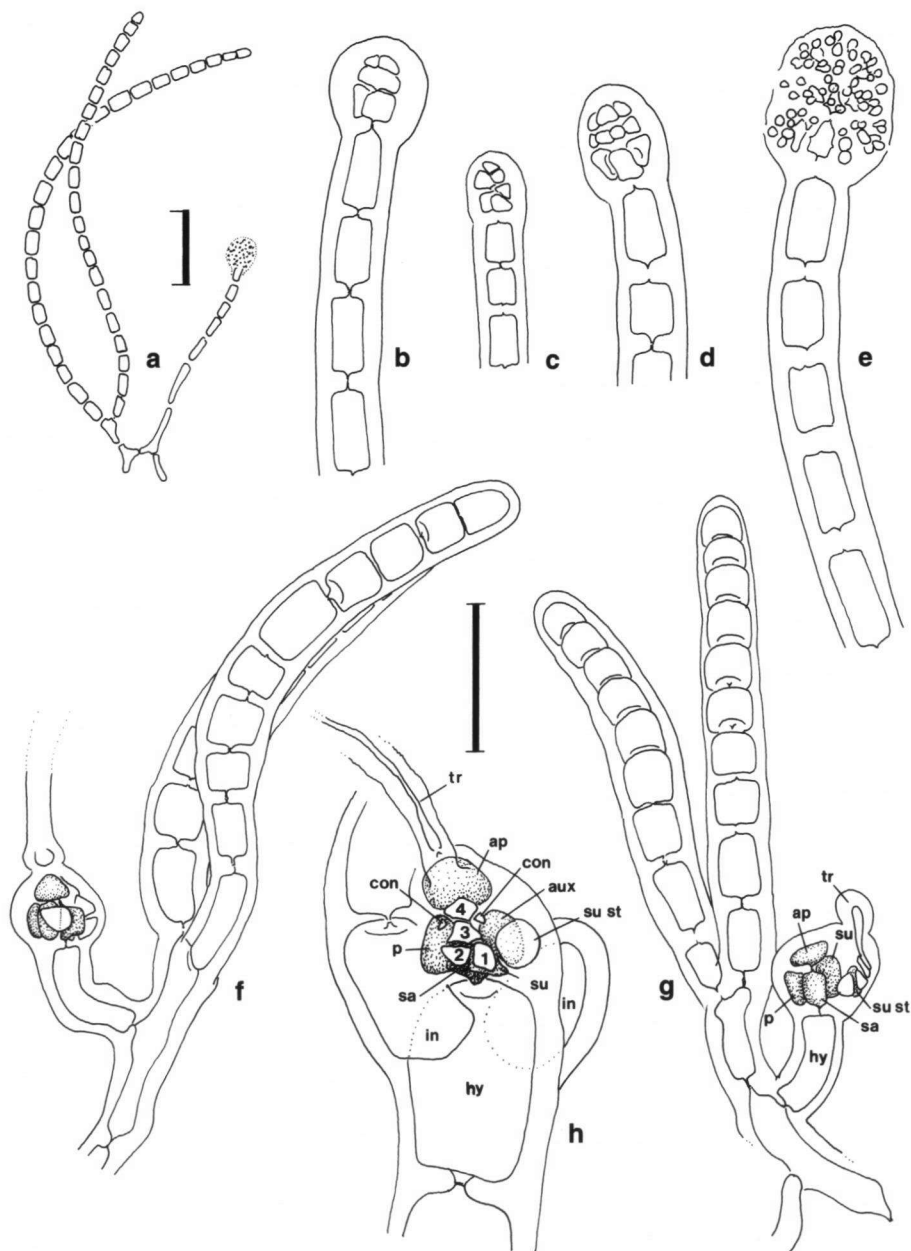
Fig. 4a–g. *Ptilothamnion codicolum* (E.Y. Dawson) I.A. Abbott. a. Habit of male thallus; b–e. developmental stages of terminal spermatangial stands; f, g. details of female thalli with procarps at the base of emergent filaments. — Fig. 4h. *Ptilothamnion* cf. *subsimplex* E.M. Gordon, procarp, showing 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). *Involucral 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
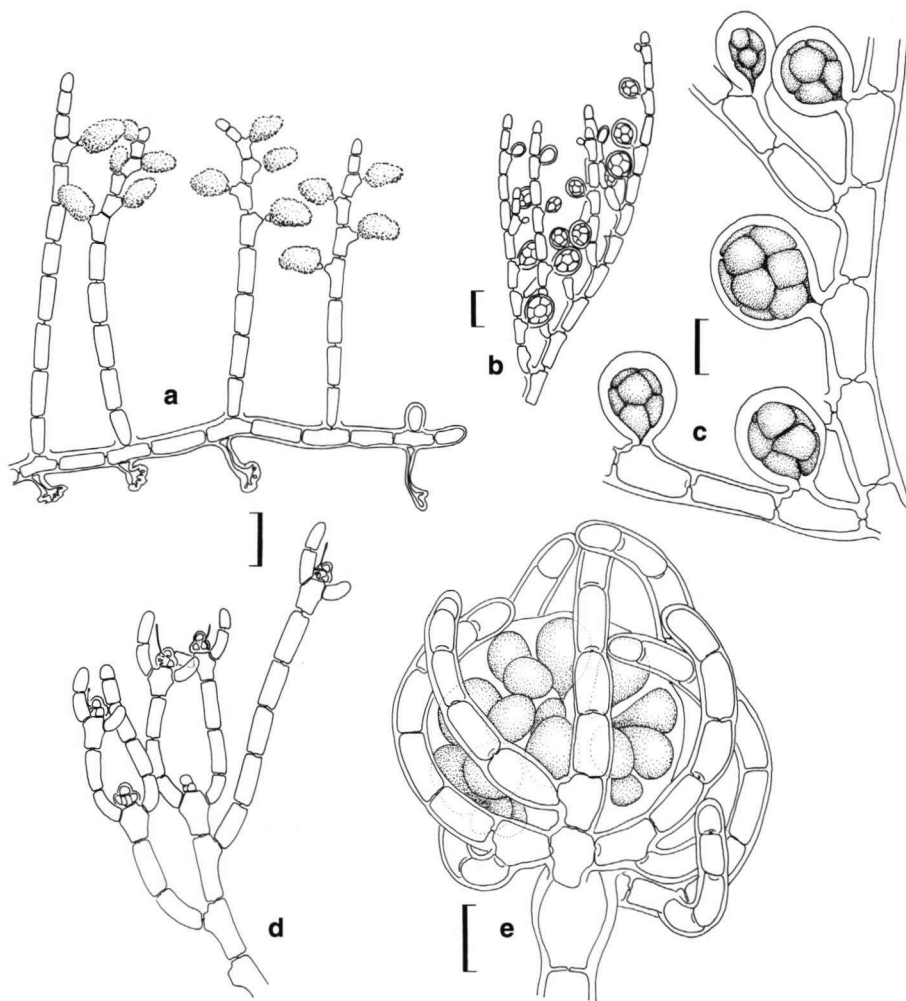
Fig. 5. *Ptilothamnion polysporum* Gordon-Mills & E.M. Woll. a. Male thallus with alternating spermatangial stands; b, c. details of thallus, with polysporangia; d. apex of female thallus with several procarps; e. mature carposporophyte. Note: polysporangial plants from epilithic material, other specimens 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)).

Scot's Hut, female specimens, on *Phloiocaulon squamulosum* (Suhr) Geyl.; West Cape Province: Goukamma Nature Reserve, Walker Point, 12 Oct. 2000; Goukamma, Oesterbank, 13 Oct. 2000, polysporangial, male and female, on *Galaxaura* spp. and *Zonaria subarticulata* (EC 1227, 1249, 1267); idem, 15 Oct. 2000, polysporangial, male and female, on *Galaxaura diesingiana* and *G. obtusata*, and also (larger plants) epilithic.

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

Table 1. Comparison of known species of *Ptilothamnion*.

species [basionym]	height of thallus	erect filament diameter (μm)	cell l/d	branching	sporangia – type	sporangia – position
P. cladophorae (Yamada & Tanaka) Feldmann-Mazoyer [*Spermothamnion cladophorae* Yamada & Tanaka]	1–3 mm	c. 18	1.5–3.5 ×	rarely 1 or 2 laterals	tetra, rarely poly	sessile, + secund
P. codicolum (E. Y. Dawson) I.A. Abbott [*Pleonosporium codicolum* E. Y. Dawson]	0.5–0.8 mm [3(–5) mm]	c. 30 [(20–)26–32]	1–1.5 × [2.5 ×]	subdichotomous, simple or irregular	poly (12–18)	pedicellate, near base of axes
P. occidentale Searles & Schneider	to 1 mm	18–29	to 4 × in figure	simple or few laterals	tetra	pedicellate, 1–2 on branchlet
P. pluma (Dillwyn) Thur. in Le Jolis [*Conferva pluma* Dillwyn]	to 8 mm	22–32(–40 basally)	1–1.3(–2) ×, slightly longer basally	regular pinnate, opposite	tetra (and octo)	terminal and lateral on axes and branchlets
P. polysporum Gordon-Mills & E.M. Woll.	to 8 mm	30–50	2–5 ×	simple or sparingly branched	poly (12–18)	sessile on upper thallus
P. pusillum (Okamura & Segawa) Itono [*Spermothamnion pusillum* Okamura & Segawa]	1.5 mm	18–20	2 ×	simple or few laterals	tetra	pedicellate, secund on filaments
P. richardsii Skuja	0.5–1 mm	(14–)17–29	c. 1 ×	pinnate, alternate	mono	sessile on branchlets
P. rupicolum Gordon-Mills	to 30 mm	(35–)40–60	1.5–4.5 ×	irregular, scarce	tetra	pedicellate, lateral on erect axes
P. schmitzii Heydrich	0.5–1(–2) mm	16–20	0.5–1 ×	simple or few laterals	tetra	pedicellate
P. speluncarum (Collins & Hervey) Ballantine & Wynne [*Rhodochorton speluncarum* Collins & Hervey]	to 15 mm	27–35	c. 2.5 × in figure	irregular, alternate or secund	tetra (+ poly and mono)	sessile, solitary or in short rows
P. sphaericum (Crouan & Crouan) Maggs & Hommersand [*Callithamnion sphaericum* Crouan & Crouan]	to 25 mm	60 apically, 40–85 basally	0.7–1.5 × (1–4 × basally)	irregular, sparse	poly (8–16)	sessile, lateral near apices
P. subsimplex Gordon-Mills	2 mm	30–60	1–3.5 ×	simple or sparingly branched	tetra	sessile, more or less secund
P. goukammae spec. nov.	to 2.5 mm	25–32.5(35)	1.5–5 ×	simple, branching when fertile	tetra (octo)	sessile, adaxial on laterals

Table 1 *(continued)*

species [basionym]	sporangia – size (μm)	involucre development	involucre – number	substrate	type loc., distribution	reference	notes
P. cladophorae (Yamada & Tanaka) Feldmann-Mazoyer [*Spermothamnion cladophorae* Yamada & Tanaka]	55 × 47, ovoid	pre	2	*Cladophora*	Taiwan, S. Japan	Yamada & Tanaka, 1934	1
P. codicolum (E.Y. Dawson) I.A. Abbott [*Pleonosporium codicolum* E.Y. Dawson]	90(–100), globose	[post]	[1–2]	*Codium*, 'other algae', *Zonaria*	Pac. Mexico, California, S. Africa	Dawson, 1962; Abbott, 1971; this paper	2
P. occidentale Searles & Schneider	34–54 × 27–45, ovoid	pre	1–2	?	Southeast USA	Searles & Schneider, 1989	
P. pluma (Dillwyn) Thur. in Le Jolis [*Conferva pluma* Dillwyn]	60–74 × 52–70 (octo 84–96 × 60–70)	pre	2	*Laminaria* and epilithic	British Isles, E. N. Atlantic, W. Mediterranean	Maggs & Hommersand, 1993	3
P. polysporum Gordon-Mills & E.M. Woll.	to 100, globose	pre	2	'epiphytic'	S. Africa, W. Australia	Wollaston, 1984; this paper	4
P. pusillum (Okamura & Segawa) Itono [*Spermothamnion pusillum* Okamura & Segawa]	50–65, globose	(pre)	2	*Carpopeltis*	Prov. Izu, Japan	Segawa, 1936	5
P. richardsii Skuja	13–17 × 9–11	sexual plants unknown		? epilithic, freshwater	British Guyana, Australia	Entwisle & Foard, 1999	6
P. rupicolum Gordon-Mills	50, globose	pre and post	3–4	epilithic	New Zealand	Gordon-Mills, 1977	7
P. schmitzii Heydrich	not stated [40–45]	not stated [post]	1 [2]	*Zonaria*	New Zealand, S. Australia	Heydrich, 1893; Womersley, 1998	8
P. speluncarum (Collins & Hervey) Ballantine & Wynne [*Rhodochorton speluncarum* Collins & Hervey]	50 longest diam.	pre	2	epilithic	Bermuda, Puerto Rico	Ballantine & Wynne, 1998	9
P. sphaericum (Crouan & Crouan) Maggs & Hommersand [*Callithamnion sphaericum* Crouan & Crouan]	75–120, spherical	sexual plants unknown		epilithic	Atl. France, British Isles	Maggs & Hommersand, 1993	10
P. subsimplex Gordon-Mills	65, ovoid	pre	2	*Lenormandia*	Kangaroo Is., Australia, Tanzania, ? S. Africa	Gordon, 1972; this paper	11
P. goukammae spec. nov.	50–62.5 × 45–50, ovoid to globose	pre	2 alternating	*Galaxaura*	S. Africa, W. Cape Province	this paper	

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 difficult 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 not to 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 Spermothamnieae, 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 spermothamnioid 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.

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