



The genus *Phymatolithon* (Hapalidiaceae, Corallinales, Rhodophyta) in South Africa, including species previously ascribed to *Leptophytum*



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ABSTRACT

Of the genera within the coralline algal subfamily Melobesioideae, the genera *Leptophytum* Adey and *Phymatolithon* Foslie have probably been the most contentious in recent years. In recent publications, the name *Leptophytum* was used in quotation marks because South African taxa ascribed to this genus had not been formally transferred to another genus or reduced to synonymy. The status and generic disposition of those species (*L. acervatum*, *L. ferox*, *L. foveatum*) have remained unresolved ever since Düwel and Wegeberg (1996) determined from a study of relevant types and other specimens that *Leptophytum* Adey was a heterotypic synonym of *Phymatolithon* Foslie. Based on our study of numerous recently collected specimens and of published data on the relevant types, we have concluded that each of the above species previously ascribed to *Leptophytum* represents a distinct species of *Phymatolithon*, and that four species (incl. *P. repandum*) of *Phymatolithon* are currently known to occur in South Africa.

Here we present detailed illustrated accounts of each of the four species, including: new data on male and female/carposporangial conceptacles; ecological and morphological/anatomical comparisons; and a review of the information on the various features used previously to separate *Leptophytum* and *Phymatolithon*. Southern African species ascribed to the genus *Phymatolithon* may be separated from one another in the field by their growth forms, the substrata on which they are generally found, and the colour of living thalli. A key for identifying southern African specimens in the field is included. Our data support the conclusion that the characters upon which *Leptophytum* is based are unreliable for generic delimitation from *Phymatolithon*.

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1. Introduction

This paper contains an account of South African representatives of the coralline red algal genus *Phymatolithon* (Hapalidiaceae, Corallinales, Rhodophyta), including three species based on South African types that had previously been referred to the genus *Leptophytum*. The status and generic disposition of those species (*L. acervatum*, *L. ferox*, *L. foveatum*) have remained unresolved ever since Düwel and Wegeberg (1996) determined from a study of relevant types and other specimens that *Leptophytum* Adey was a heterotypic synonym of *Phymatolithon* Foslie. The complex nomenclatural history of *Leptophytum* has been reviewed by Woelkerling (1988: 217–218), Düwel and Wegeberg (1996), Woelkerling et al. (2002) and Teichert et al. (2013: footnote 1), and comments on this genus from the Nomenclature Committee for Algae appear in Compère (2004) and in Prud'homme Van Reine (2011).

Based on our study of numerous recently collected specimens and of published data on the relevant types, we have concluded that each of the above species hitherto ascribed to *Leptophytum* represents a distinct species of *Phymatolithon*, and that four species of *Phymatolithon* are currently known to occur in South Africa. Detailed illustrated accounts

of each species are presented, including data on synonymy and types, etymology, specimens examined, distribution, habit, and vegetative and reproductive anatomy. New data on male and female/carposporangial conceptacles are provided; ecological and morphological/anatomical comparisons of the four species are summarised; various features used previously to separate *Leptophytum* and *Phymatolithon* are reviewed; and a key for identifying South African specimens in the field is included.

2. Materials & methods

Field collections were made from the high to low intertidal and shallow subtidal zones of Southern Africa from Namibia, South Africa and Mozambique (Inhaca Island). Thalli were examined as far as possible when fresh; otherwise they were air-dried or fixed in neutralized 10% commercial formalin seawater (4% formaldehyde) and stored in a 70% ethanol: 10% glycerol: 20% distilled water solution.

Specimens for microscopy were prepared following Maneveldt and Van der Merwe (2012). For scanning electron microscopy, air-dried material was fractured using forceps, diagonal cutters, or a small hammer and chisel. Fractures perpendicular to a leading edge was used to determine internal anatomy. The fractured pieces were mounted on stubs, using adhesive tabs (Agar Scientific, 66a Cambridge Rd., Stanstead, Essex CM24 8DA, UK), stored in a desiccator for at least

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24 h prior to examination, coated with carbon in a single cycle for 2 s in an EMITECH K950X Carbon evaporator, and examined with a LEO 1450 scanning electron microscope (SEM) at an accelerating voltage of 20 kV.

For light microscopy, formalin preserved specimens were first decalcified in 10% nitric acid. Thereafter, specimens were immersed in 70%, 90% and 100% ethanol solutions respectively for a minimum of 60 min each in order to displace any water and acid in the specimens. Thereafter, each specimen was removed from the 100% ethanol and allowed to air dry for no more than a few seconds. Specimens were then immersed in Leica Histo-resin filtration medium for several hours (3–6) until completely infiltrated. A hardening solution was then added to the infiltration medium and the specimens orientated in this final solution until set. Gelling of the hardener usually occurred within 30–45 min; for more rapid hardening, specimens were placed immediately in an oven at 60 °C for approximately 10–20 min.

Specimens were then sectioned at 8–10 µm thickness using a Bright 5030 microtome. Individual cut sections were removed from the microtome blade using a fine sable hair brush and transferred to a slide covered with distilled water. In this way, multiple sections were orientated on a single slide. Slides were then left to air dry for at least 24 h. Once dried, slides bearing sections were stained with toluidine blue (0.25 g borax/100 ml and 0.06 g toluidine blue/100 ml) that was previously filtered to prevent dye crystal formation, again left to air dry, and later covered with cover slips using DPX Mountant for microscopy (BDH Laboratory Supplies, England).

In cell measurements, length denotes the distance between primary pit connections, and diameter the maximum width of the cell lumen at right angles to this. Conceptacle measurements follow Adey and Adey (1973). Thallus anatomical terminology follows Chamberlain (1990).

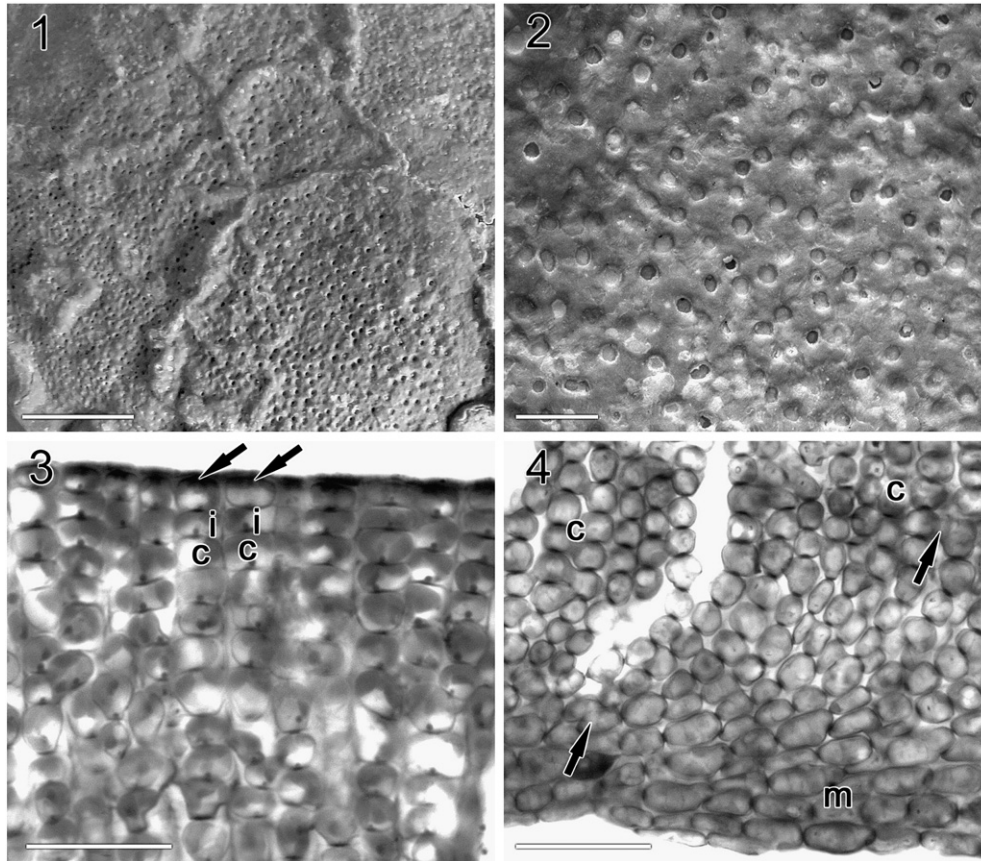
Morphological (growth forms) terminology follows Woelkerling et al. (1993). Typification data follow Woelkerling (1993). Herbarium abbreviations follow Thiers (2013, continuously updated).

Collection data are presented firstly according to geographic location from north to south along the South African west coast and then from west to east, followed by date of collection within a region, and finally by collection number on a particular day.

3. Generic concept and species accounts

3.1. *Phymatolithon* Foslie

Phymatolithon, as delimited by Harvey et al. (2003), is the only known genus in the family Hapalidiaceae (subfamily Melobesioideae): 1) possessing subepithallial initials that are as short as or shorter than the cells immediately subtending them; and 2) producing both branched (dendroid) and unbranched (simple) spermatangial filaments in male conceptacles. Two other genera of Melobesioideae (*Kvaleya*; *Mastophoropsis*) also have subepithallial initials that are as short as or shorter than subtending cells, but these genera produce only unbranched spermatangial filaments in their male conceptacles. Furthermore, *Kvaleya* differs in possessing haustoria (which are lacking in *Phymatolithon* and *Mastophoropsis*), while *Mastophoropsis* is arborescent and flabelliform, a growth-form that is absent in *Phymatolithon* and *Kvaleya*. Harvey et al. (2003: 676) provide a synoptic description of the genus, and Harvey et al. (2003: 653, Table 2) summarise diagnostic characters and character states separating all nine currently recognized extant genera of Melobesioideae.



Figs. 1–4. Morphology and vegetative anatomy of *P. acervatum* (UWC 10/129). 1.) View of several abutting individual thalli. Note the pitted nature of the thallus. Scale bar = 5 mm. 2.) Magnified view of the thallus showing sunken conceptacles giving the thallus its pitted appearance. Scale bar = 2 mm. 3.) Vertical section of the dorsal region of the thallus showing subepithallial initials (i), the first cortical cells (c) and a single layer of epithallial cells (arrows). Scale bar = 20 µm. 4.) Vertical section of the ventral region of the thallus showing medullary filaments (m) running more or less parallel to the substrate and giving rise to upward curving cortical filaments (c). Note the cell fusions (arrows) between cells of adjoining filaments. Scale bar = 15 µm.

Like all members of the Corallinales, *Phymatolithon* bears tetra/bisporangia in conceptacles and produce tetra/bisporangia that are zonately divided. Like all members of the Hapalidiaceae, thalli are entirely non-geniculate and tetra/bisporangia are produced in multiporate conceptacles that bear apical pore plugs. Also, like all members of the Melobesioideae, contiguous vegetative filaments are joined by cell fusions and the multiporate conceptacle roofs are composed of cells rather than a calcified sieve-like matrix.

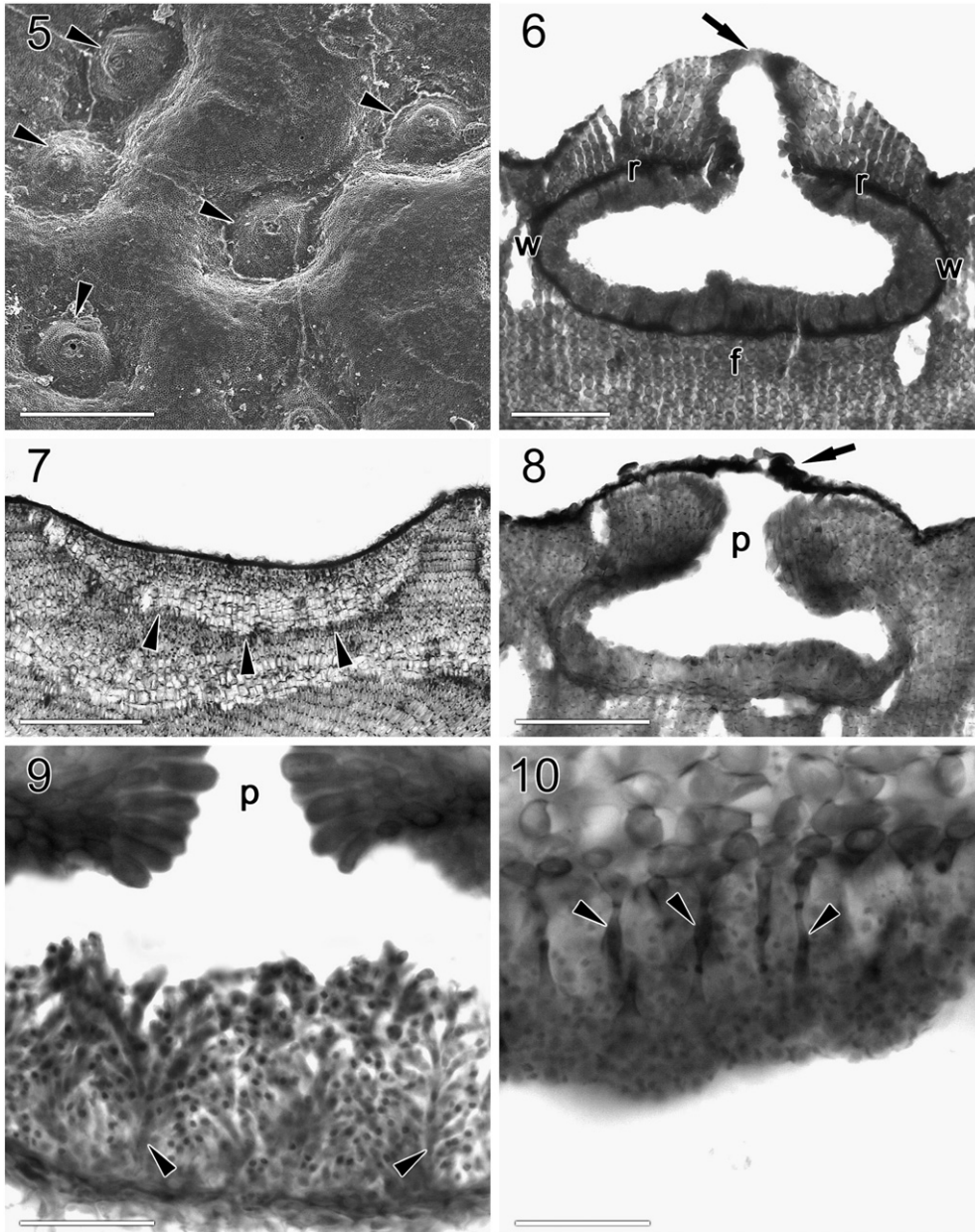
Phymatolithon is typified by *P. calcareum* (Pallas) W.H.Adey & D.L.McKibbin. Spencer et al. (2009: 253) recently updated the nomenclature of that name; an account of the type is provided by Woelkerling and Irvine (1986).

Le Gall et al. (2010: 305, Table 1) list characters that distinguish the Corallinales from the other two orders (Rhodogorgonales,

Sporolithales) of the subclass Corallinophycidae and Le Gall and Saunders (2007: 1129) provide the characterisation of Corallinophycidae. A synoptic description of the Hapalidiaceae and further data on included subfamilies occurs in Harvey et al. (2003: 648–649).

3.2. Identification key of southern African species of *Phymatolithon* based on diagnostic characters

- 1 Thalli encrusting (smooth) only 2
- Thalli mostly warty to lumpy to fruticose 3
- 2 Thalli mostly epilithic on pebbles and small boulders, surface with a pitted appearance ... *Phymatolithon acervatum*



Figs. 5–10. Spermatangial (male) anatomy of *P. acervatum*. 5.) SEM of the thallus surface showing conceptacles with raised roofs (arrowheads) sunken in depressions (UWC 10/129). Scale bar = 500 μm . 6.) Vertical section through a conceptacle showing spermatangial systems distributed across the floor (f), walls (w) and roof (r) of the conceptacle chamber. The pore opening is occluded by a mucilage plug (arrow) (UWC 10/129). Scale bar = 50 μm . 7.) Vertical section through a conceptacle primordium showing adventitious development from a group of vegetative cells (arrowheads) within the thallus (UWC 10/129). Scale bar = 150 μm . 8.) Vertical section through an immature conceptacle. Note the remains of the protective layer of epithallial and cortical cells (arrow) (UWC 10/129). Scale bar = 70 μm . 9.) Magnified view of the centre of the conceptacle chamber floor showing branched (arrowheads) spermatangial systems interspersed amongst unbranched spermatangial systems. The pore canal (p) is lined by cells that project into the canal as papillae (UWC 10/129). Scale bar = 25 μm . 10.) Magnified view of the roof of the conceptacle chamber showing a cluster of branched spermatangial systems (arrowheads) (UWC 08/26). Scale bar = 20 μm .

- 3 Thalli producing secondary mouth-like margins, gonimoblast filaments peripherally arranged in carposporangial conceptacle chambers *Phymatolithon ferox*
- Thalli without conspicuous secondary margins, gonimoblast filaments peripherally arranged or scattered across the floor in carposporangial conceptacle chambers *Phymatolithon repandum*

3.3. Field identification key to the southern African species of *Phymatolithon*

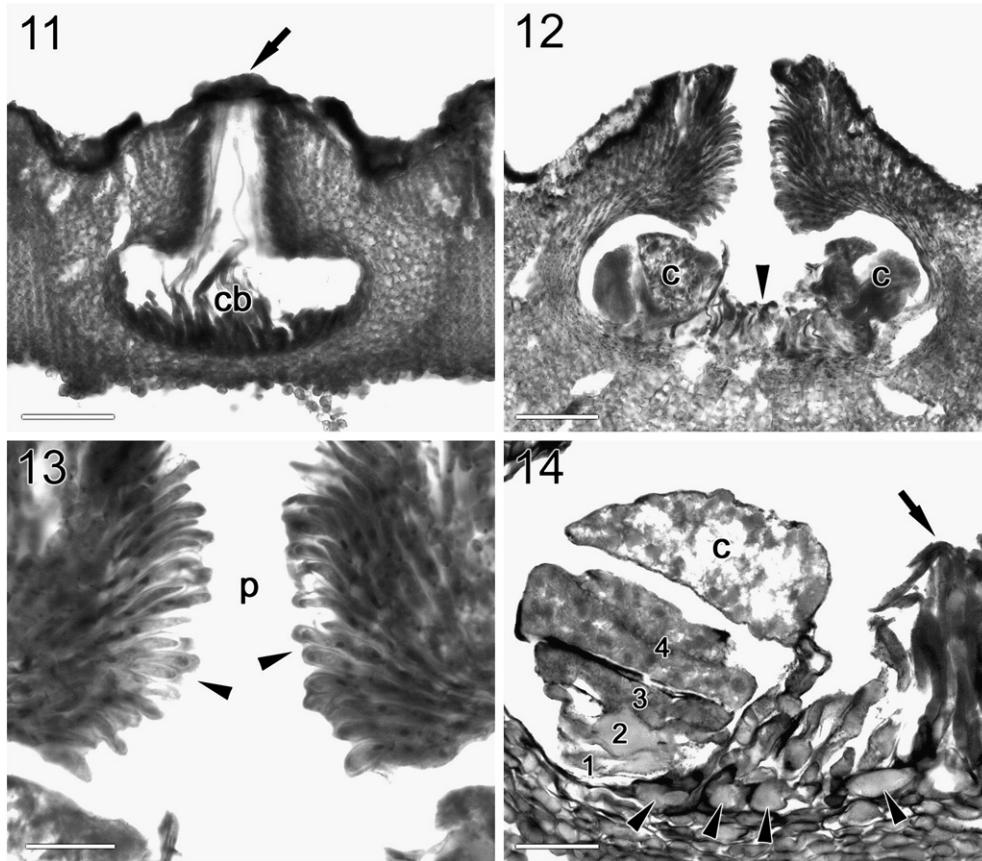
By all accounts, the southern African species now ascribed to the genus *Phymatolithon* may be separated from each other in the field by their growth forms, the substrata on which they are generally found, and the colour of the living specimens. A key (modified from Maneveldt et al., 2008), to the southern African species of *Phymatolithon* is presented below. This key is designed for southern African specimen identification only and the characters used in the key are not necessarily diagnostic of the species to which they pertain.

- 1 Thalli encrusting (smooth) only 2
- Thalli mostly warty to lumpy to fruticose 3
- 2 Thalli mostly epilithic on pebbles and small boulders in intertidal rock pools, living specimens bright pink in colour (Fig. 75), thallus surface matt-like with a pitted appearance (Figs. 1 and 2) *Phymatolithon acervatum*
- Thalli epilithic on the primary bedrock in

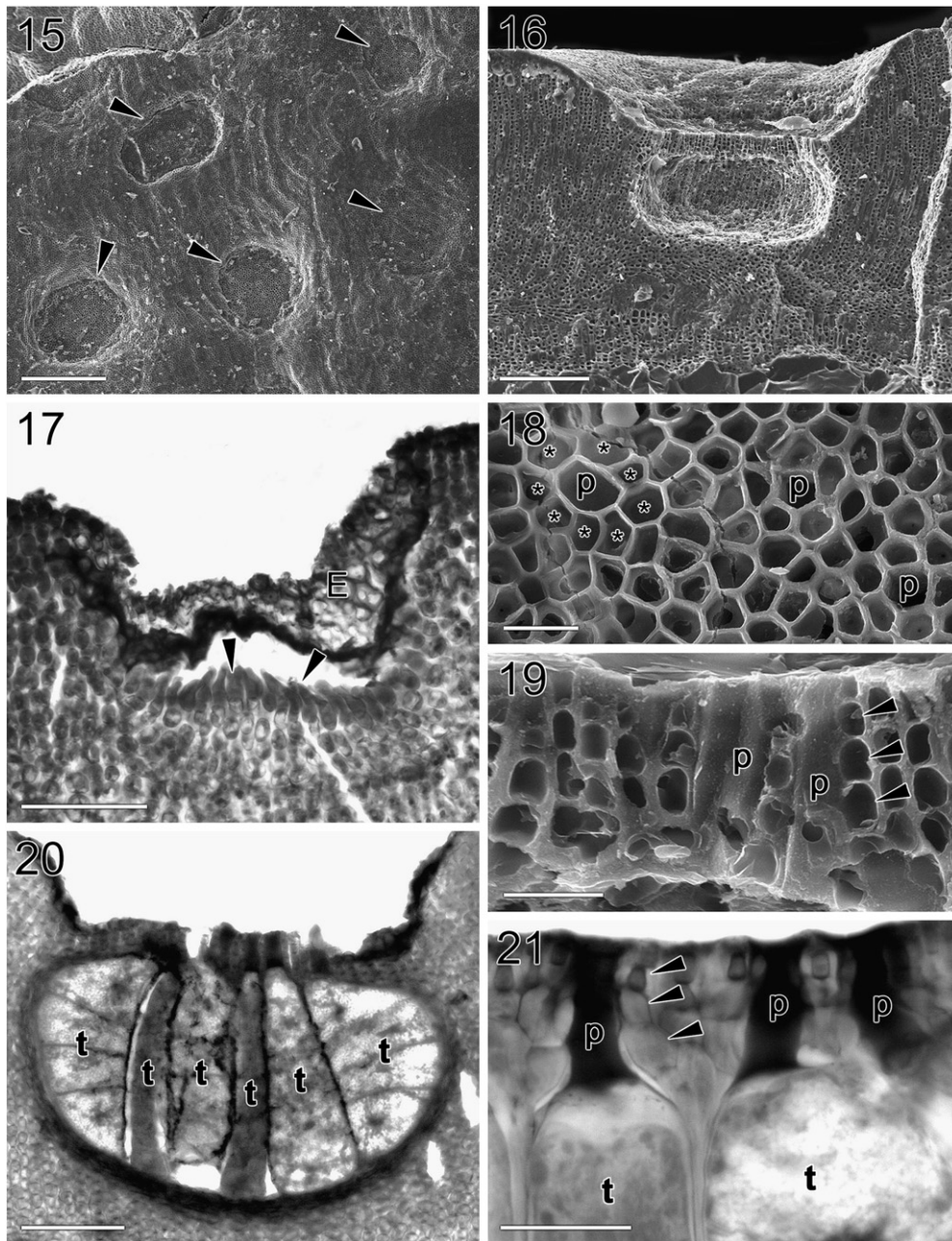
- the low intertidal zone, living specimens brownish-pink in colour (Fig. 77), thallus surface glossy and covered in secondary margins (Fig. 39) giving the thallus an imbricate appearance..... *Phymatolithon foveatum*
- 3 Thalli loosely adherent on the primary bedrock on the exposed intertidal zone and on worm tubes, living specimens mauvish grey (Fig. 76), thalli mostly warty to lumpy and producing numerous secondary margins that form mouth-like structures (Fig. 76) where they meet *Phymatolithon ferox*
- Thalli firmly adherent on the primary bedrock in intertidal rock pools, living specimens variable in colour from dull pinkish to reddish to brownish to purplish brown (Fig. 78), thalli warty to fruticose without conspicuous secondary margins *Phymatolithon repandum*

3.4. *Phymatolithon acervatum* (Foslie) Adey, 1970: 28

(Figs. 1-21 and 75)
 Basionym: *Lithothamnion acervatum* Foslie, 1907: 4.
 Synonyms: *Leptophytum acervatum* (Foslie) Y.M.Chamberlain and Keats, 1994: 111.
 Lectotype: TRH, B1-1607. Natal, South Africa, A. Weber Van Bosse. Foslie slide 702; Printz, 1929, pl. 1, fig. 15 (as *Lithothamnion*).
 Syntype: TRH, B1-1608. Knysna, Cape Province, South Africa A. Weber Van Bosse. Foslie slide 704; Printz, 1929, pl. 1, fig. 14.



Figs. 11–14. Female anatomy of *P. acervatum*. 11.) Vertical section through a carogonial conceptacle showing carogonial branches (cb) distributed across the conceptacle chamber floor. The pore opening is occluded by a mucilage plug (arrow) (UWC 10/129). Scale bar = 50 µm. 12.) Vertical section through a carposporangial conceptacle showing peripherally arranged gonimoblast filaments terminating in carpospores (C). The central region of the conceptacle chamber floor bears unfertilised carogonial branches (arrowhead) (UWC 08/14). Scale bar = 50 µm. 13.) Vertical section through the pore of a carposporangial conceptacle showing pore canal cells (arrowheads) projecting into the pore canal (p) as papillae (UWC 08/14). Scale bar = 20 µm. 14.) Magnified view of the floor of a carposporangial conceptacle showing a discontinuous fusion cell (arrowheads) bearing a peripherally arranged gonimoblast filament (1–4) terminating in a carpospore (C). The central region of the conceptacle chamber floor bears unfertilised carogonial branches (arrow) (UWC 08/26). Scale bar = 20 µm.



Figs. 15–21. Tetrasporangial anatomy of *P. acervatum* (UWC 10/129). 15.) SEM of the thallus surface showing conceptacles (arrowheads) sunken in depressions. Scale bar = 200 μm . 16.) Fracture of the thallus under SEM showing a conceptacle sunken in a depression. Scale bar = 100 μm . 17.) Vertical section through a sunken conceptacle primordium showing adventitious development from a group of tetrasporangial initials (arrowheads) deep within the thallus. Note the protective layer of epithallial and cortical cells (E). Scale bar = 50 μm . 18.) SEM of a conceptacle pore plate showing multiple pores (p) surrounded by rosette cells (*). Scale bar = 10 μm . 19.) Fracture through a conceptacle pore plate under SEM showing multiple pore canals (p) and the cells lining a pore canal (arrowheads). Scale bar = 10 μm . 20.) Vertical section through a sunken conceptacle showing tetrasporangia (t) distributed across the chamber floor. Scale bar = 50 μm . 21.) Magnified view of the outer surface of a conceptacle showing tetrasporangia (t) bearing apical pore plugs (p) in the pore plate. The cells lining the pore canal (arrowheads) become more elongate as they progress towards the conceptacle chamber. Scale = 20 μm .

Adey (1970: 28, as *Phymatolithon*) referred to the above specimens as cotypes. Woelkerling (1993: 16) did not distinguish between the two specimens and designated them jointly as holotypes although the labels show the specimens to come from Natal and Knysna respectively. Chamberlain and Keats (1994: 112) subsequently designated the Natal specimen as lectotype and the Knysna specimen as syntype.

Etymology: *acervatum*, heaped up, crowded together. Foslie (1907) did not explain the origin of the epithet. According to Chamberlain and Keats (1994: 112) this may refer to the raised mounds of thallus surrounding the sunken conceptacles or to the presence of crowded thalli on small stones.

3.4.1. Specimens examined

In total, forty three (43) specimens were examined, these currently representing our entire collection for this taxon.

South Africa. Northern Cape Province: Groenriviermond, epilithic on pebbles and small boulders tide pools (17.vii.1993, D.W. Keats, UWC 93/172).

South Africa. Western Cape Province: Yzerfontein, epilithic on low shore bedrock, and epizoic on low shore limpet (*Scutellastra argenvillei* and *S. cochlear*) shells (18.ii.1992, D.W. Keats, UWC 92/73); Robben Island, epilithic on bedrock at depths of 9–12 m (17.xi.1993, D.W. Keats, UWC 93/228; 24.ii.1994, D.W. Keats, UWC 94/24); Cape Point, epilithic on pebbles and small boulders in low shore tide pools

Table 1A comparison of the habit and vegetative features of the four species of *Phymatolithon* now known to exist in South Africa compared against those of previously published records. ND = no data.

Character	<i>P. acervatum</i> (this study)	<i>L. acervatum</i> (Chamberlain and Keats, 1994)	<i>P. ferox</i> (this study)	<i>L. ferox</i> (Chamberlain and Keats, 1994)	<i>P. foveatum</i> (this study)	<i>L. foveatum</i> (Chamberlain and Keats, 1994)	<i>P. repandum</i> (this study)
Substrate	Mostly epilithic on pebbles and small boulders	Epilithic on pebbles and small boulders	Epilithic on rock, epizoic on worm tubes	Epilithic on rock, epizoic on worm tubes	Epilithic on rock, epizoic worm tubes and mollusk shells	Epilithic on rock, epizoic worm tubes and mollusk shells	Epilithic on rock
Growth form	Encrusting	Encrusting	Encrusting to warty to lumpy	Encrusting to protuberant (= warty/lumpy)	Encrusting	Encrusting	Encrusting to warty to lumpy to fruticose
Thallus thickness	To 500 µm	To 500 µm	To 500 µm, protuberances to 10 mm	To 500 µm, protuberances to 10 mm	To 500 µm	To 500 µm	To 1860 µm, protuberances to 3 mm
Thallus construction	Monomerous and plumose	Monomerous and non-coaxial (= plumose)	Monomerous and plumose	Monomerous and non-coaxial (= plumose)	Monomerous and plumose	Monomerous and non-coaxial (= plumose)	Monomerous and mostly plumose; some coaxial areas occur
Medullary cell length	4–15 µm	4–14 µm	10–22 µm	9–22 µm	10–33 µm	15–50 µm	7–42 µm
Medullary cell diameter	4–7 µm	4–6 µm	2–9 µm	3–9 µm	5–10 µm	4–9 µm	5–11 µm
Cortical cell length	5–10 µm	4–6 µm	5–10 µm	2–10 µm	4–13 µm	4–10 µm	6–16 µm
Cortical cell diameter	4–7 µm	4–6 µm	4–7 µm	2–5 µm	2–10 µm	4–5 µm	4–9 µm
Subepithallial cell length	3–5 µm	ND	4–5 µm	ND	2–7 µm	ND	4–7 µm
Subepithallial cell diameter	4–6 µm	ND	5–6 µm	ND	2–9 µm	ND	4–8 µm
Epithallial cell length	2–6 µm	2–4 µm	4–5 µm	2–4 µm	2–4 µm	2–4 µm	4–5 µm
Epithallial cell diameter	3–6(10) µm	4–6 µm	4–7 µm	4–5 µm	4–7 µm	4–8 µm	5–6 µm
Trichocytes	None observed	ND	None observed	ND	Solitary	ND	None observed
Trichocyte length	–	–	–	–	12–22 µm	–	–
Trichocyte diameter	–	–	–	–	5–7 µm	–	–

Table 2

A comparison of the reproductive features of the four species of *Phymatolithon* now known to exist in South Africa compared against those of previously published records. ND = no data.

Character	<i>P. acervatum</i> (this study)	<i>L. acervatum</i> (Chamberlain and Keats, 1994)	<i>P. ferox</i> (this study)	<i>L. ferox</i> (Chamberlain and Keats, 1994)	<i>P. foveatum</i> (this study)	<i>L. foveatum</i> (Chamberlain and Keats, 1994)	<i>P. repandum</i> (this study)
Gametangial thalli	Dioecious	Dioecious	Dioecious	Dioecious	Presumably dioecious	Presumably dioecious	Monoecious or dioecious
Spermatangial thalli							
Conceptacle placement	Sunken in depressions, but with raised roofs	Sunken in depressions, but with raised roofs	Raised above surrounding thallus surface	Raised above surrounding thallus surface	Slightly sunken in depressions, but with raised roofs	ND	Raised above surrounding thallus surface
External conceptacle diameter	370–450 µm	ND	350–600 µm	ND	220–550 µm	ND	320–580 µm
Conceptacle chamber diameter	155–279 µm	156–260 µm	135–250 µm	208–247 µm	159–277 µm	ND	186–314 µm
Conceptacle chamber height	50–118 µm	52–78 µm	47–127 µm	47–117 µm	71–93 µm	ND	71–137 µm
Conceptacle roof thickness	39–76 µm	39–58 µm	37–75 µm	60–73 µm	27–59 µm	ND	27–70 µm
Spermatangial systems	Branched and unbranched on floor, walls and roof	Unbranched on floor, walls and roof; branched at centre of floor	Branched and unbranched on floor, walls and roof	Unbranched on floor, walls and roof; branched at centre of floor	Branched and unbranched on floor; but mostly unbranched on walls and roof	ND	Branched and unbranched on floor, walls and roof
Carpogonial thalli							
Conceptacle placement	Sunken in a depression, but with a raised roof	ND	Raised above surrounding thallus surface	ND	ND	ND	Raised above surrounding thallus surface
External conceptacle diameter	441 µm	ND	400 µm	ND	ND	ND	400–500 µm
Conceptacle chamber diameter	142 µm	ND	154 µm	ND	ND	ND	130–270 µm
Conceptacle chamber height	51 µm	ND	93 µm	ND	ND	ND	54–113 µm
Conceptacle roof thickness	88 µm	ND	118 µm	ND	ND	ND	83–127 µm
Carposporangial thalli							
Conceptacle placement	Sunken in depressions, but with raised roofs	Sunken in depressions, but with raised roofs	Raised above the surrounding thallus	Raised above the surrounding thallus	ND	Sunken in depressions	Raised above surrounding thallus surface
External conceptacle diameter	368–515 µm	ND	400–600 µm	ND	ND	ND	430–640 µm

Conceptacle chamber diameter	180–287 µm	182–286 µm	140–335 µm	143–330 µm	ND	169–286 µm	233–372 µm
Conceptacle chamber height	50–123 µm	52–91 µm	80–206 µm	83–120 µm	ND	78–117 µm	75–159 µm
Conceptacle roof thickness	42–108 µm	47–78 µm	49–100 µm	50–100 µm	ND	65–130 µm	96–115 µm
Type of fusion cell	Discontinuous	Fusion cell absent	Discontinuous	Discontinuous	ND	Scattered (= discontinuous)	Discontinuous
Distribution of gonimoblast filaments	Peripheral	Peripheral	Peripheral	Peripheral	ND	Peripheral	Peripheral or scattered across the floor
No. of cells in gonimoblast filament	4–7	4	4–7	4–5	ND	4–5	3–5
Carospore length	32–47 µm	ND	27–62 µm	ND	ND	ND	25–54 µm
Carospore diameter	44–74 µm	ND	56–78 µm	ND	ND	ND	34–74 µm
Tetrasporangial thalli							
Conceptacle placement	Sunken in depressions	Sunken in depressions	Raised above surrounding thallus	Raised above surrounding thallus	Flush with the surrounding thallus surface to sunken in depressions	Sunken in depressions	Raised above to flush with surrounding thallus surface
External conceptacle diameter	274–490 µm	ND	180–637 µm	ND	290–500 µm	ND	270–600 µm
Conceptacle chamber diameter	115–255 µm	115–208 µm	127–348 µm	130–270 µm	80–289 µm	86–208 µm	191–333 µm
Conceptacle chamber height	50–150 µm	52–143 µm	60–176 µm	60–160 µm	50–115 µm	52–91 µm	88–147 µm
Conceptacle roof thickness	15–25 µm	15–23 (44) µm	20–42 µm	21–34 µm	25–42 µm	26–34 µm	20–27 µm
No. of cell in conceptacle pore plate	3–5	3–4	4–6	2–4	4–5	4–5	3–5
No. of pore rosette cells	5–8	5–8	5–7	6–7	6–8	7–8	6–9
Tetrasporangium length	65–113 µm	65–97 µm	65–135 µm	65–78 µm	50–98 µm	50–65 µm	81–147 µm
Tetrasporangium diameter	12–69 µm	30–48 µm	15–86 µm	21–65 µm	20–66 µm	22–33 µm	22–78 µm
Bisporangium length	69–103 µm	ND	50–147 µm	52–109 µm	74–100 µm	ND	ND
Bisporangium diameter	27–64 µm	ND	15–76 µm	18–49 µm	27–66 µm	ND	ND

(27.x.1991, D.W. Keats, UWC 91/95; 27.x.1991, D.W. Keats, UWC 91/96); False Bay, Partridge Point, epilithic on bed rock at a depth of 10–14 m (06.viii.1993, D.W. Keats & G.W. Maneveldt, UWC 93/95; 25.viii.1993, D.W. Keats, UWC 93/216); Fish Hoek Nature Reserve, epilithic on subtidal pebbles (13.vi.1990, D.W. Keats, UWC Cor-32; 13.vi.1990, D.W. Keats, UWC Cor-33; 13.vi.1990, D.W. Keats, UWC Cor-34; 13.vi.1990, D.W. Keats, UWC Cor-35); Kalk Bay, epilithic on small boulders in mid shore tide pools (16.i.2002, G.W. Maneveldt, UWC 2002/01; 24.viii.2002, G.W. Maneveldt, UWC 2002/08; 17.vii.2003, G.W. Maneveldt & S.T. Dlaza, UWC 2003/10; 13.viii.2003, G.W. Maneveldt & S.T. Dlaza, UWC 2003/11A; 13.viii.2003, G.W. Maneveldt & S.T. Dlaza, UWC 2003/13; 13.viii.2003, G.W. Maneveldt & S.T. Dlaza, UWC 2003/14; 13.viii.2003, G.W. Maneveldt & S.T. Dlaza, UWC 2003/16; 13.viii.2003, G.W. Maneveldt & S.T. Dlaza, UWC 2003/17; 13.viii.2003, G.W. Maneveldt & S.T. Dlaza, UWC 2003/19; 10.x.2003, S.T. Dlaza, UWC 2003/26); Holbaaipunt, epizoic on limpet (*S. cochlear*) and whelk (*Crepidula porcellana*) shells, and epilithic on pebbles and small boulders in low to midshore tide pools (23.vi.1990, D.W. Keats & I. Matthews, UWC Cor-25; 25.x.1991, D.W. Keats, UWC 91/75; 25.x.1991, D.W. Keats, UWC 91/76; 27.x.1991, D.W. Keats, UWC 91/95; 26.xi.1991, D.W. Keats, UWC 91/251; 26.xi.1991, D.W. Keats, UWC 91/252; 21.vi.1993, D.W. Keats & G.W. Maneveldt, UWC 93/72; 26.v.1994, D.W. Keats, UWC 94/129; 16.vi.1995, D.W. Keats, UWC 95/28); Betty's Bay, epilithic on pebbles and small boulders in low to midshore tide pools (03.i.1994, D.W. Keats, UWC 94/36); Cape Agulhas, L'Agulhas, epilithic on pebbles in low to midshore tide pools and sandy gullies (08.vii.2009, G.W. Maneveldt & E. Van der Merwe, UWC 09/135; 15.vi.2010, G.W. Maneveldt & E. Van der Merwe, UWC 10/129); Struisbaai, epilithic on pebbles and small boulders in low shore tide pools and sandy gullies (07.vii.2009, G.W. Maneveldt & E. Van der Merwe, UWC 09/116); De Hoop Nature Reserve, epilithic on pebbles in midshore tide pools (10.xii.1991, D.W. Keats, UWC 91/313); Stilbaai, Skulpiesbaai, epilithic on pebbles and small boulders in low shore tide pool (12.vi.2010, G.W. Maneveldt & E. Van der Merwe, UWC 10/103); Knysna Heads, epilithic on pebbles and small boulders in high to midshore tide pools (08.xii.1991, Y.M. Chamberlain, UWC 91/271; 07.iv.2008, G.W. Maneveldt & U. Van Bloemestein, UWC 08/26); Nature's Valley, epilithic on pebbles and small boulders in high to midshore tide pools (05.iv.2008, G.W. Maneveldt & U. Van Bloemestein, UWC 08/14).

South Africa. Eastern Cape Province: Tsitsikamma, Grootbank, dominant coralline epilithic on the bedrock in the low shore *cochlear* zone (10.iv.2008, G.W. Maneveldt & U. Van Bloemestein, UWC 08/37); Port Elizabeth, near Noordhoek, epilithic on pebbles and small to large boulders in intertidal surge pools (20.v.1992, D.W. Keats, UWC 92/122); Kei Mouth, epilithic on small boulder in high shore tide pools (11.vii.2010, G.W. Maneveldt & E. Van der Merwe, UWC 10/217).

3.4.2. Distribution

Known only from South Africa. Distributed from the Northern Cape Province (Groenriviermond), to at least the Kei Mouth in the Eastern Cape Province.

3.4.3. Habit

Thalli are non-geniculate, epilithic on the primary bedrock on the low shore intertidal zone, but more so on pebbles and small boulders (Fig. 75) in high to low shore intertidal rock pools and gullies, and occasionally epizoic on mollusc (limpets and whelks) shells. Thalli are firmly adherent, conforming to the substrate and are difficult to remove. Freshly collected living specimens are bright pink in colour, are encrusting (smooth) with a matt-like appearance, and have a visibly pitted appearance due to the sunken nature of the conceptacles (Figs. 1 and 2). Thalli are thin, measure up to 500 μm thick and lack protuberances.

3.4.4. Vegetative anatomy

The thallus is dorsiventrally organised and monomerous, and haustoria are absent. The medulla is plumose (non-coaxial) (Fig. 4),

comprising 5–10 cell layers, and measures 20–74 μm in thickness. Cells of the medullary filaments are elongate with rounded corners and are 2–4 times as long as wide. The cortex comprises the bulk of the thallus and comprise cells that are small, rounded to square and are uniformly bead-like in appearance. Fusions between cells of contiguous medullary and cortical filaments are abundant and frequently occupy most of the wall of adjoining cells; secondary pit connections have not been observed. Subepithallial initials are rounded to square to slightly flattened and in length are as short as or shorter than the cells immediately subtending them (Fig. 3). Epithallial cells occur in a single layer (up to 2 when shedding) and are rounded to oval to elliptical to flattened. Data on measured vegetative characters are summarised in Table 1.

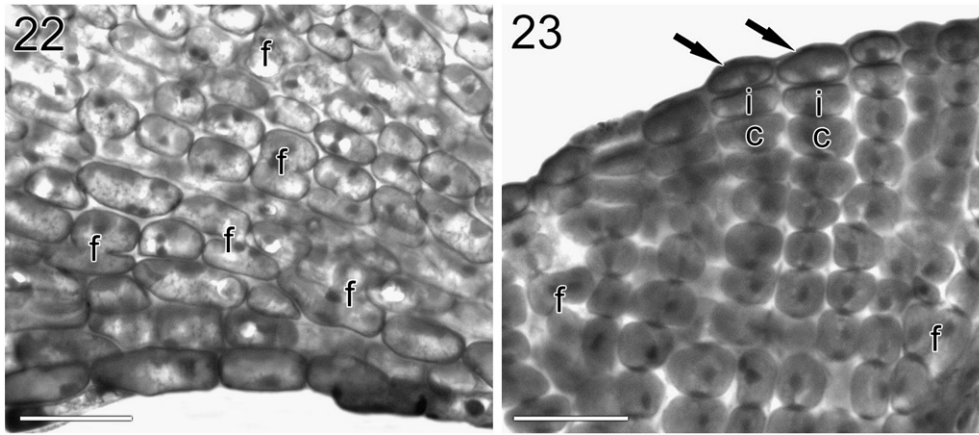
3.4.5. Reproductive anatomy

Gametangial thalli are dioecious. Spermatangial (male) conceptacles occur sunken in depressions that measure 370–450 μm in diameter (Fig. 5). Within depressions, conceptacles have raised (domed) roofs that extend above the immediately surrounding thallus surface (Figs. 5–6). Mature male conceptacle chambers are elliptical. Conceptacle initiation occurs deep (adventitious, 10 cell layers or more) in the dorsal region of the thallus (Fig. 7). The roof is formed from filaments that arise peripheral to the fertile area, the terminal initials of which are more elongate than their inward derivatives. As they divide, the newly forming filaments curve inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate. These cells project into the pore canal and are orientated more or less parallel to the conceptacle roof surface in fully developed conceptacles. Throughout the early development a protective layer of epithallial and cortical cells surrounds the conceptacle primordium (Fig. 8); this protective layer is shed once the pore canal is fully developed. The pore opening in fully developed conceptacles is often occluded by a mucilage plug (Fig. 6). Branched (dendroid) and unbranched (simple) spermatangial systems develop across the floor, walls and roof of mature male conceptacles (Figs. 6, 8–10). Senescent male conceptacles appear to be shed as no buried conceptacles were observed.

A single mature carpogonial (female) conceptacle was observed to occur in a depression 441 μm in diameter (Fig. 11). Within the depression, the conceptacle has a raised (domed) roof that extends above the immediately surrounding thallus surface. The carpogonial conceptacle chamber is elliptical. The conceptacle floor is located several (more than 20) cells below the thallus surface. The conceptacle pore canal cells project into the pore as papillae and are orientated more or less parallel to the conceptacle roof surface. The conceptacle pore is also occluded by a mucilage plug. Carpogonial branches develop across the floor of the conceptacle chamber, and comprised a single support cell and a hypogynous cell bearing a carpogonium extended into a trichogyne. Sterile cells are also present on the hypogynous cell.

After presumed karyogamy, carposporophytes develop within female conceptacles and form carposporangial conceptacles (Fig. 12). Carposporangial conceptacles are comparatively large and occur in depressions that measure 368–515 μm in diameter. Carposporangial conceptacle chambers are elliptical, but with flattened bottoms presumably caused by the growth of the expanding carpospores. The pore is unoccluded and the canal is similarly structured to carpogonial conceptacles (Figs. 12 and 13), but noticeably wider. A large central fusion cell is absent; instead a discontinuous fusion cell is present and several-celled gonimoblast filaments (incl. a terminal carposporangium) develop along the periphery of the conceptacle chamber (Fig. 14). The remains of unfertilized carpogonia persist across the dorsal surface of the fusion cell. Senescent carposporangial conceptacles appear to be shed as no buried conceptacles were observed.

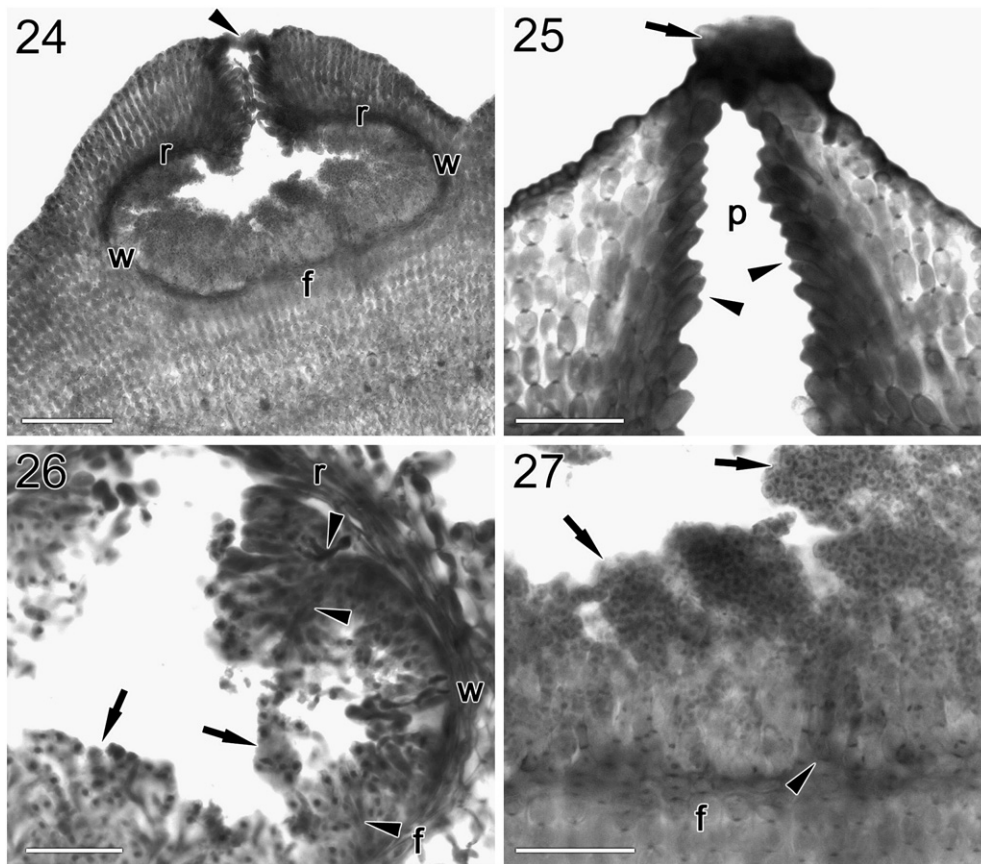
Tetrasporangial conceptacles are slightly to deeply sunken below the thallus surface in depressions measuring 274–490 μm in diameter (Figs. 15, 16 and 19). Conceptacle initiation occurs deep (adventitious, 10 cell layers or more) in the dorsal region of the thallus (Fig. 17).



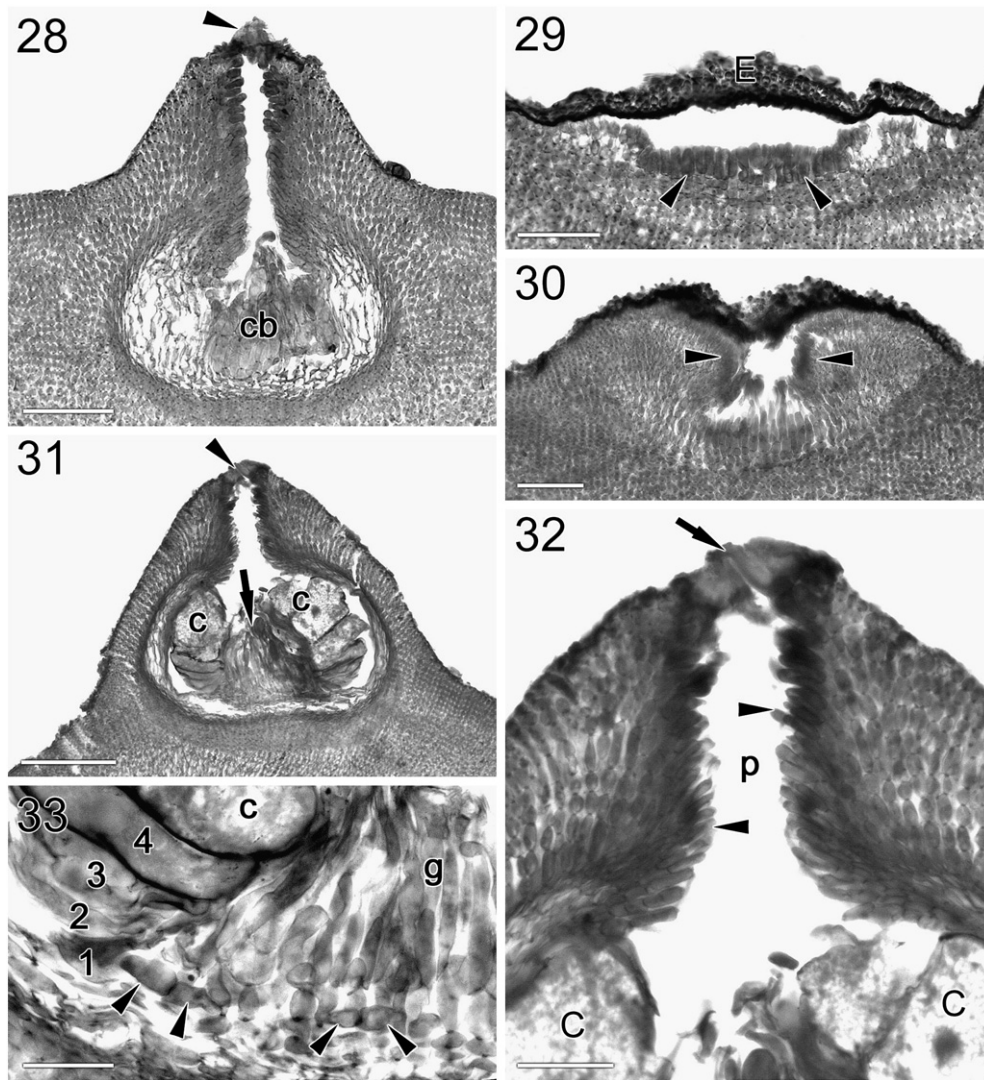
Figs. 22–23. Vegetative anatomy of *P. ferox* (UWC 10/125). 22.) Vertical section of the ventral region of the thallus showing medullary filaments running more or less parallel to the substrate. Note the cell fusions (f) between cells of adjoining filaments. Scale bar = 20 μ m. 23.) Vertical section of the dorsal region of the thallus showing subepithallial initials (i), the first cortical cell (c) and a single layer of epithallial cells (arrows). Scale bar = 15 μ m.

Tetrasporangial conceptacles are multiporate (Fig. 18) with roofs that are formed from filaments peripheral to and interspersed among the developing tetrasporangia. The lower segments of these interspersed filaments degenerate, creating the conceptacle chamber and leaving a roof 15–25 μ m thick composed of 3–5 cells (including an epithallial cell) (Figs. 19 and 21). Conceptacle chambers are rounded to elliptical. Zonately divided tetrasporangia are scattered across the chamber floor

(Fig. 20). Tetrasporangial conceptacle roofs bear apical pore plugs (Fig. 21). Pores are surrounded by 5–8 rosette cells with the pore opening slightly raised above the surrounding rosette cells (Fig. 18). Cells of the filaments lining the pore canal are squarish to slightly elongate and increase in size towards the conceptacle chamber (Figs. 19 and 21). Pore canal cells are, however, not markedly different (in shape, size or staining intensity) from the cells that make up the rest of the roof. Senescent



Figs. 24–27. Spermatangial (male) anatomy of *P. ferox* (UWC 09/111). 24.) Vertical section through a conceptacle showing spermatangial systems distributed across the floor (f), walls (w) and roof (r) of the conceptacle chamber. The pore opening is occluded by a mucilage plug (arrowhead). Scale bar = 50 μ m. 25.) Vertical section through the pore of a conceptacle showing pore canal cells (arrowheads) projecting into the pore canal (p) as papillae. The pore opening is occluded by a mucilage plug (arrow). Scale bar = 20 μ m. 26.) Magnified view of the roof (r), wall (w) and floor (f) of a conceptacle chamber showing branched spermatangial systems (arrowheads) interspersed amongst unbranched spermatangial systems. Spermatia (arrows) are clustered at the distal ends of the spermatangial branches. Scale bar = 20 μ m. 27.) Magnified view of the floor (f) of a conceptacle chamber showing weakly branched (arrowheads) spermatangial systems interspersed amongst unbranched spermatangial systems. Spermatia (arrows) are clustered at the distal ends of the spermatangial systems. Scale bar = 20 μ m.



Figs. 28–33. Female anatomy of *P. ferox* (UWC 09/111). 28.) Vertical section through a carposporangial conceptacle showing a mass of carposporangial branches (cb). The pore opening is occluded by a mucilage plug (arrowhead). Scale bar = 60 μ m. 29.) Vertical section through a very young carposporangial conceptacle showing development from a group of carposporangial initials (arrowheads). Note the protective layer of epithallial and cortical cells (E). Scale bar = 50 μ m. 30.) Vertical section through an immature carposporangial conceptacle showing roof development from the periphery (arrowheads). Scale bar = 50 μ m. 31.) Vertical section through a carposporangial conceptacle showing peripherally arranged gonimoblast filaments terminating in carpospores (C). The central region of the conceptacle chamber floor bears unfertilised carposporangial branches (arrow). The pore opening is occluded by a mucilage plug (arrowhead). Scale bar = 100 μ m. 32.) Vertical section through the pore of a carposporangial conceptacle showing pore canal cells (arrowheads) projecting into the pore canal (p) as papillae. The pore opening is occluded by a mucilage plug (arrow). Scale bar = 30 μ m. 33.) Magnified view of the floor of a carposporangial conceptacle showing a discontinuous fusion cell (arrowheads) bearing a peripherally arranged gonimoblast filament (1–4) terminating in a carpospore (C). The central region of the conceptacle chamber floor bears unfertilised carposporangial branches (g). Scale bar = 20 μ m.

tetrasporangial conceptacles appear to be shed as no buried conceptacles were observed. Data on measured reproductive characters are summarised in Table 2.

3.5. *Phymatolithon ferox* (Foslie) Maneveldt & E. Van der Merwe, comb. nov.

(Figs. 22–38 and 76)

Basionym: *Lithothamnion ferox* Foslie, 1907: 7.

Synonyms: *Leptophyllum ferox* (Foslie) Y.M. Chamberlain and Keats, 1994: 119; *Lithothamnion falsellum* f. *genuina* Foslie, 1900: 10; *Lithothamnion falsellum* f. *plicata* Foslie, 1900: 10; *Lithothamnion ferox* Foslie, 1907: 7; *Lithothamnion prolixum* Foslie, 1908: 9; *Mesophyllum ferox* (Foslie) W.H. Adey, 1970: 24; *Mesophyllum prolixum* (Foslie) Adey, 1970: 24.

Holotype: TRH, B15-2357. Natal, South Africa, A. Weber Van Bosse, undated. Foslie slide 706. Printz 1929: pl. 4, Fig. 9 (as *Lithothamnion*).

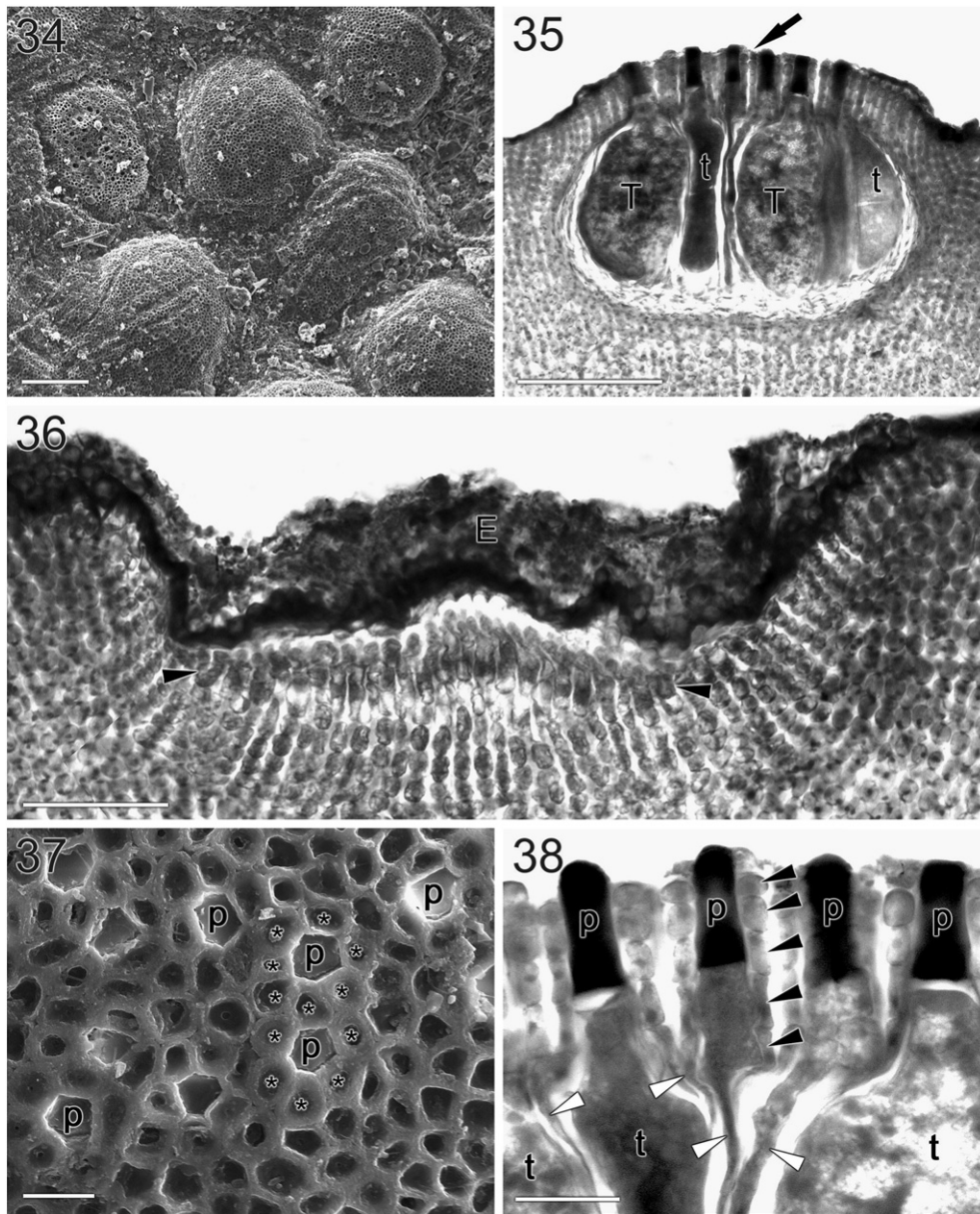
Etymology: *ferox*, fierce or spiny, possibly referring to the horn-like shape of a tubeworm encrusted with this species in the type specimen (see Printz, 1929: pl. 4, Fig. 9) (Chamberlain and Keats, 1994: 119).

3.5.1. Specimens examined

In total, thirty two (32) specimens were examined, these representing our entire collection for this taxon.

Namibia. Luderitz, Grossebuict, epilithic on bedrock on low shore and in mid to low shore tide pools (13.vii.1992, D.W. Keats, UWC 92/306).

South Africa. Northern Cape Province: Groenriviermond, epilithic on bedrock in the mid shore and epizoic on worm tubes (08.v.1993, D.W. Keats & G.W. Maneveldt, UWC 93/47; 27.ii.1994, D.W. Keats, UWC 94/34).

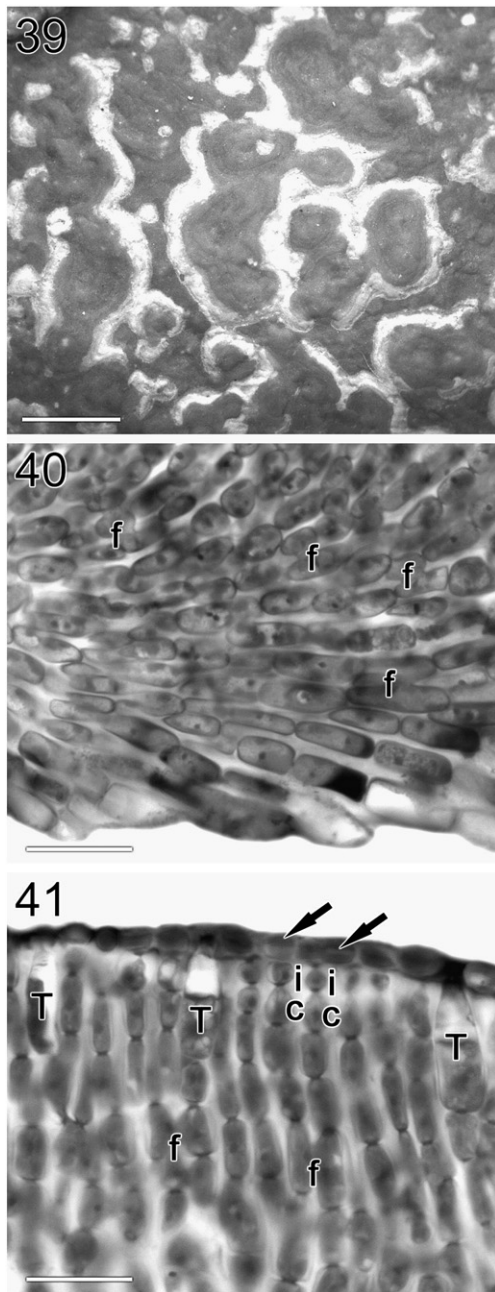


Figs. 34–38. Tetrasporangial anatomy of *P. ferox*. 34.) SEM of the thallus surface showing raised conceptacles (UWC 09/109). Scale bar = 100 μm . 35.) Vertical section through a conceptacle showing mature (T) and incompletely divided (t) tetrasporangia distributed across the chamber floor. Note the raised conceptacle roof (arrow) (UWC 10/125). Scale bar = 90 μm . 36.) Vertical section through a young conceptacle showing adventitious development from a group of tetrasporangial initials (between arrowheads) deep within the thallus. Note the protective layer of epithallial and cortical cells (E) (UWC 09/109). Scale bar = 50 μm . 37.) SEM of a conceptacle pore plate showing multiple pores (p) surrounded by rosette cells (*) (UWC 09/109). Scale bar = 10 μm . 38.) Magnified view of the outer surface of a conceptacle showing tetrasporangia (t) bearing apical pore plugs (p) in the pore plate. The cells lining the pore canal (black arrowheads) are not different to those from the rest of the pore plate. Note the remains of the interspersed filaments (white arrowheads) that gave rise to the conceptacle roof (UWC 10/125). Scale = 20 μm .

South Africa. Western Cape Province: Oudekraal, epilithic on bedrock on the mid shore (27.i.1994, *D.W. Keats*, UWC 94/20). Kommetjie, epiphytic on *Spongites yendoi* (23.xi.1991, *D.W. Keats*, UWC 91/235). Cape of Good Hope, epilithic on bedrock on the mid shore (27.x.1991, *D.W. Keats*, UWC 91/98). Kalk Bay, epizoic on barnacles on the mid shore (16.i.2002, *G.W. Maneveldt*, UWC 2002/02). Dalebrook, epiphytic on *Spongites yendoi* on the lower intertidal zone (21.xi.1991, *D.W. Keats*, UWC 91/203). Holbaaipunt, epilithic on bedrock and epizoic on worm tubes on the mid to lower intertidal zone (10.vi.1990, *D.W. Keats* & *I. Matthews*, UWC Cor-14; 10.vi.1990, *D.W. Keats*, UWC Cor-15; 23.vi.1990, *D.W. Keats* & *I. Matthews*, UWC Cor-18; 23.vi.1990, *D.W. Keats* & *I. Matthews*, UWC Cor-23; 17.xi.1990, *D.W. Keats*, UWC Cor-93; 20.xi.1990, *D.W. Keats*, UWC Cor-95); (20.xi.1990, *D.W. Keats*, UWC Cor-96; 16.ii.1991, *D.W. Keats*, UWC Cor-182; 29.v.1991, *D.W. Keats*,

UWC Cor-225; 26.xi.1991, *D.W. Keats*, UWC 91/253; 22.xii.1991, *D.W. Keats*, UWC 91/335; 05.v.1992, *D.W. Keats*, UWC 92/89; 16.vi.1992, *D.W. Keats*, UWC 92/154; 26.v.1994, *D.W. Keats*, UWC 94/126). Brandfontein, epilithic on bedrock in the high intertidal zone (09.vii.2009, *G.W. Maneveldt* & *E. Van der Merwe*, UWC 09/146). Struisbaai, epilithic on bedrock and epizoic on worm tubes in mid intertidal gullies (06.vii.2009, *G.W. Maneveldt* & *E. Van der Merwe*, UWC 09/109; 06.vii.2009, *G.W. Maneveldt* & *E. Van der Merwe*, UWC 09/111). Stilbaai, Jongensfontein, epizoic on worm tubes on exposed mid-shore flats (13.vi.2010, *G.W. Maneveldt* & *E. Van der Merwe*, UWC 10/125). Knysna Heads, epilithic on bedrock and epizoic on worm tubes on the high shore (07.iv.2008, *G.W. Maneveldt* & *E. Van der Merwe*, UWC 08/27).

South Africa. Eastern Cape Province: Tsitsikamma National Park, Storms River Mouth, epizoic on worm tubes on the lower intertidal



Figs. 39–41. Morphology and vegetative anatomy of *P. foveatum* (UWC 10/123). 39.) Magnified view of the thallus surface showing secondary margins (white scrolls) scattered across the thallus surface giving it an imbricate appearance. Scale bar = 1.5 mm. 40.) Vertical section of the ventral region of the thallus showing a plumose (non-coaxial) medulla with filaments running more or less parallel to the substrate and curving upwards to form cortical filaments. Note the cell fusions (f) between cells of adjoining filaments. Scale bar = 20 μ m. 41.) Vertical section of the dorsal region of the thallus showing subepithallial initials (i), the first cortical cell (c) and a single layer of slightly dark-staining epithallial cells (arrows). Note the cell fusions (f) between cells of adjoining filaments and the solitary trichocytes (T). Scale bar = 20 μ m.

zone (12.vii.1991, D.W. Keats, UWC 91/273). Port Elizabeth, near Noordhoek, epilithic on bedrock on the mid-shore (20.v.1992, D.W. Keats, UWC 92/120). Kei Mouth, epilithic on bedrock and epizoid on worm tubes on the high shore (11.vii.2010, G.W. Maneveldt & E. Van der Merwe, UWC 10/203; 11.vii.2010, G.W. Maneveldt & E. Van der Merwe, UWC 10/204).

Mozambique. Inhaca Island, habitat unknown (01.vii.1991, G. Branch, UWC 91/260).

3.5.2. Distribution

Known from Namibia, South Africa and Mozambique, but most common from the Northern Cape Province (Groenriviermond) to the Western Cape Province (Cape Agulhas).

3.5.3. Habit

Thalli are non-geniculate, epilithic on the primary bedrock and epizoid on worm tubes and barnacles. Thalli are loosely adherent, thin and fragile and are easily removed from the substratum. Freshly collected living specimens are mauvish grey in colour, varying from being encrusting (smooth) to warty to lumpy. Warty thalli bear abundant flat-topped protuberances that are unbranched and measure up to 10 mm in length and up to 3 mm in diameter. The thallus surface is often heavily grazed. Margins appear whitish. Secondary margins form characteristic mouth-like structures where they meet (Fig. 76). Thalli are thin and measure up to 500 μ m thick.

3.5.4. Vegetative anatomy

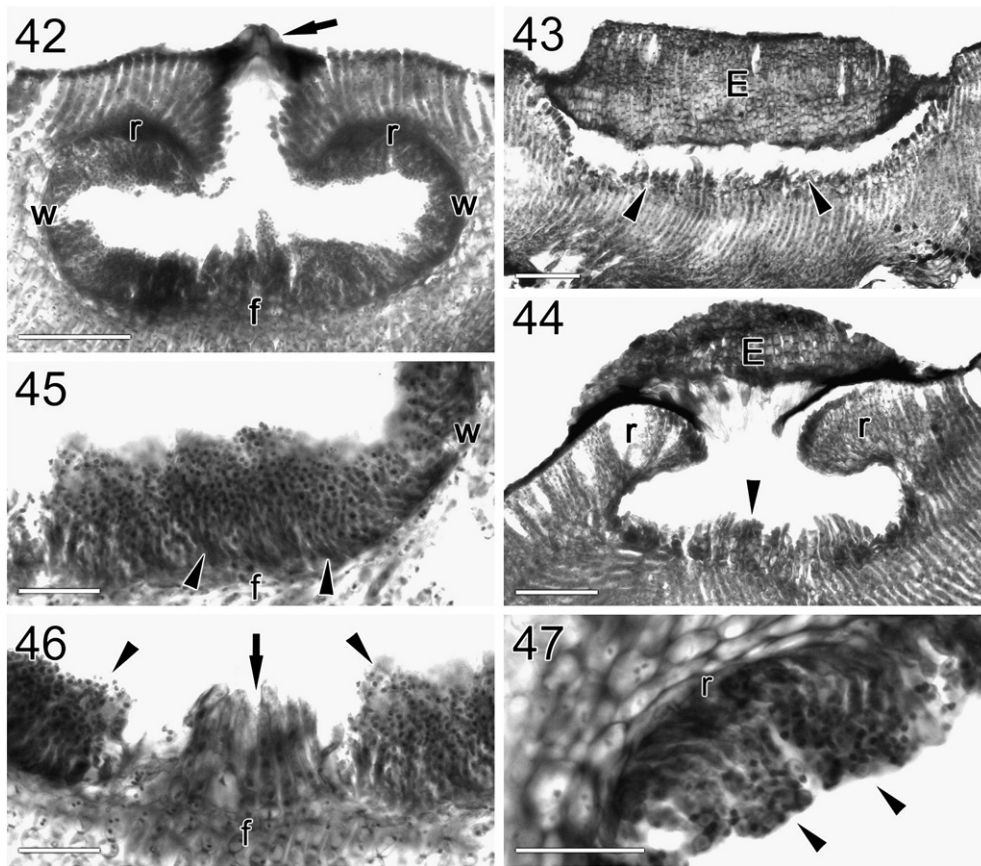
The thallus is dorsiventrally organized and monomerous, and haustoria are absent. The medulla is plumose (non-coaxial) (Fig. 22), comprising several cell layers that measure 74–172 μ m in thickness. Cells of the medullary filaments are square to elongate with rounded corners. The cortex comprises roughly half the thallus. Cells of cortical filaments are square to oval to rectangular (Fig. 23). Fusions between cells of contiguous medullary and cortical filaments are abundant and frequently occupy most of the wall of adjoining cells; secondary pit connections have not been observed. Subepithallial initials are square to flattened and in length are as short as or shorter than the cells immediately subtending them (Fig. 23). Epithallial cells occur in a single layer and are squarish to oval to flattened. Data on measured vegetative characters are summarised in Table 1.

3.5.5. Reproductive anatomy

Gametangial thalli are dioecious. Spermatangial (male) conceptacles are comparatively large and raised above the surrounding thallus surface (Fig. 24). Their chambers are elliptical. Male conceptacle primordia have not been observed. Conceptacle roof filaments project into the pore canal as papillae in fully developed conceptacles (Fig. 25). The pore opening is often occluded by a mucilage plug (Fig. 24). Both branched (dendroid) and unbranched (simple) spermatangial systems develop across the floor (weakly branched), walls and roof of the mature male conceptacle (Figs. 24, 26 and 27). Senescent male conceptacles appear to be shed from the thallus surface as no buried conceptacles were observed.

Of all carpogonial conceptacles observed, only one was fully developed and was raised above the thallus surface (Fig. 28). The conceptacle chamber is roundish. Carpogonial conceptacle primordia have not been observed. In young conceptacles, the roof is formed from filaments that arise peripheral to the fertile area, the terminal initials of which are more elongate than their inward derivatives (Fig. 29). As they divide, the newly forming filaments curve inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate (Fig. 30). These cells project into the pore canal and are orientated more or less parallel to the conceptacle roof surface in fully developed conceptacles. Throughout the early development a protective layer of epithallial and cortical cells surrounds the conceptacle primordium (Figs. 29 and 30); this protective layer is shed once the pore canal is fully developed. The pore canal in fully developed conceptacles is occluded by a mucilage plug (Fig. 28).

After presumed karyogamy, carposporophytes develop within female conceptacles and form carposporangial conceptacles. Carposporangial conceptacles are comparatively large and raised well above the surrounding thallus (Fig. 31). Chambers are roundish. The pore canal is lined by papillate cells that protrude into the pore canal (Fig. 32). The conceptacle pore is occluded by a mucilage plug (Figs. 31 and 32). A large central fusion cell is absent; instead a discontinuous fusion cell



Figs. 42–47. Spermatangial (male) anatomy of *P. foveatum* (UWC 10/123). 42.) Vertical section through a conceptacle showing spermatangial systems distributed across the floor (f), walls (w) and roof (r) of the conceptacle chamber. The pore opening is occluded by a mucilage plug (arrowhead). Scale bar = 50 μm . 43.) Vertical section through a young conceptacle showing adventitious development from a group of spermatangial initials (between arrowheads) deep within the thallus. Note the thick layer of protective epithallial and cortical cells (E). Scale bar = 50 μm . 44.) Vertical section through an immature conceptacle showing roof development (r) from the periphery and a protective layer of epithallial and cortical cells (E). Scale bar = 50 μm . 45.) Magnified view of the periphery of a conceptacle chamber showing branched spermatangial systems (arrowheads) interspersed amongst unbranched spermatangial systems on the conceptacle floor (f), and only unbranched spermatangial systems on the conceptacle wall (w). Scale bar = 20 μm . 46.) Magnified view of the centre of a conceptacle chamber floor (f) bearing different-looking spermatangial structures (arrow) that are surrounded by more conventional-looking unbranched spermatangial structures (arrowheads). Scale bar = 20 μm . 47.) Magnified view of the roof (r) of a conceptacle chamber showing unbranched spermatangial systems. Scale bar = 20 μm .

is present and several-celled gonimoblast filaments (incl. a terminal carposporangium) develop along the periphery of the conceptacle chamber (Figs. 31 and 33). Senescent carposporangial conceptacles appear to be shed from the thallus surface as no buried conceptacles were observed.

Tetrasporangial conceptacles are raised well above the surrounding thallus surface (Figs. 34 and 35), and vary greatly in external diameter. Conceptacle initiation occurs mostly deep (adventitious, 10 cell layers or more) in the dorsal region of the thallus (Figs. 36). Tetrasporangial conceptacles are multiporate (Figs. 35, 37 and 38) with roofs that are formed from filaments peripheral to and interspersed among the developing tetrasporangial (Fig. 38). The lower segments of these interspersed filaments degenerate, creating the conceptacle chamber and leaving a roof 22–42 μm thick composed of 4–6 cells (including an epithallial cell that is sometimes missing). Conceptacle chambers are elliptical. Zonately divided tetrasporangia are scattered across the chamber floor (Fig. 35). Tetrasporangial conceptacle roofs bear apical pore plugs (Figs. 35 and 38). Pores are surrounded by 5–7 (mostly 6) rosette cells that are flush toward the pore opening (Fig. 37). The cells of the filaments lining the pore canal are rectangular to elongate and not markedly different (in shape, size or staining intensity) from the cells that make up the rest of the roof. Senescent tetrasporangial conceptacles appear to be shed from the thallus surface as no buried conceptacles were observed. Data on measured reproductive characters are summarised in Table 2.

3.6. *Phymatolithon foveatum* (Y.M.Chamberlain & Keats) Maneveldt & E.Van der Merwe, comb. nov.

(Figs. 39–53 and 77)

Basionym: *Leptophytum foveatum* Y.M.Chamberlain and Keats, 1994: 115–119, Figs. 32–48.

Synonyms: None.

Holotype: L, 993.052 539. Yzerfontein, west coast of the Western Cape Province, South Africa. Y.M. Chamberlain & D.W. Keats.

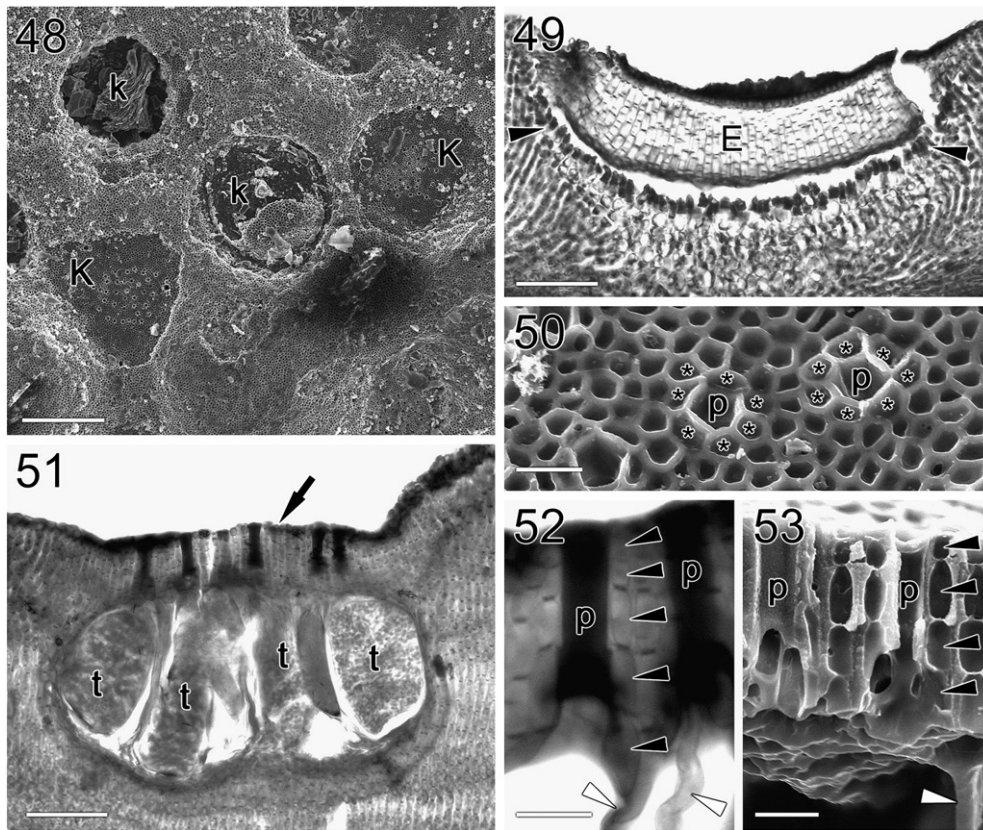
Etymology: *foveatum* after the Latin *foveatus* meaning pitted. The epithet makes reference to the pitted nature of the thallus surface (Chamberlain and Keats, 1994: 115).

3.6.1. *Specimens examined*

In total, twelve (12) specimens were examined, these representing our entire collection for this taxon.

Namibia. Swakopmund, epilithic on the primary bedrock in low shore tide pools and epizoic on mollusc shells in the low shore and upper sublittoral zone (05.vii.1993, D.W. Keats, G.W. Maneveldt & Y. Chamberlain, UWC 93/150; 05.vii.1993, D.W. Keats, G.W. Maneveldt & Y. Chamberlain, UWC 93/153B).

South Africa. Northern Cape Province: Port Nolloth, epilithic on the primary bedrock on the low shore, sublittoral fringe and subtidal zone to 2 m deep, and epizoic on the low shore on shells of the limpet *S. argenvillei* (07.v.1993, D.W. Keats, UWC 93/23; 07.v.1993, D.W. Keats,



Figs. 48–53. Tetrasporangial anatomy of *P. foveatum* (UWC 09/114). 48.) SEM of the thallus surface showing multiporate conceptacles (K) sunken in depressions. Some conceptacles (k) have been partly or entirely shed. Scale bar = 150 μm . 49.) Vertical section through a young developing conceptacle showing adventitious development from a group of tetrasporangial initials (between arrowheads) deep within the thallus. Note the protective layer of epithallial and cortical cells (E). Scale bar = 50 μm . 50.) SEM of a conceptacle pore plate showing multiple pores (p) surrounded by rosette cells (*). Scale bar = 10 μm . 51.) Vertical section through a conceptacle showing tetrasporangia (t) distributed across the chamber floor. Note the multiporate roof (arrow) bearing densely staining pore plugs. Scale bar = 50 μm . 52.) Magnified view of the conceptacle pore plate showing apical pore plugs (p). The cells lining the pore canal (black arrowheads) are not different to those from the rest of the pore plate. Note the remains of the interspersed filaments (white arrowheads) that gave rise to the conceptacle roof. Scale = 10 μm . 53.) Fracture through a conceptacle pore plate under SEM showing multiple pore canals (p). The cells lining the pore canal (black arrowheads) are not different to those from the rest of the pore plate. Note the remains of an interspersed filament (white arrowhead) that gave rise to that portion of the conceptacle roof. Scale = 10 μm .

UWC 93/30; 17.vii.1993, D.W. Keats & G.W. Maneveldt, UWC 93/164; 26.ii.1994, D.W. Keats, UWC 94/30). Groenriviermond, epilithic on the primary bedrock on the low shore and in tide pools, and epizoid on limpet (*S. argenvillei* and *S. cochlear*) shells in the low shore (08.v.1993, D.W. Keats & G.W. Maneveldt, UWC 93/46).

South Africa. Western Cape Province: Kalk Bay, epizoid on winkle (*Oxystele sinensis*) shells in the subtidal zone (19.viii.2008, G.W. Maneveldt & R. Eager, UWC 08/53). Holbaai, epilithic on the primary bedrock and epizoid on limpet (*S. cochlear*) shells on the low shore (03.iii.1995, D.W. Keats, UWC 95/05). Struisbaai, epilithic on bedrock in low shore tide pools (06.vii.2009, G.W. Maneveldt & E. Van der Merwe, UWC 09/114). Stilbaai, Jongensfontein, epilithic on the primary bedrock and epizoid on worm tubes in low shore tide pools (13.vi.2010, G.W. Maneveldt & E. Van der Merwe, UWC 10/123). Tsitsikamma, Nature's Valley, epilithic on the primary bedrock on the low shore (06.iv.2008, G.W. Maneveldt & U. Van Bloemestein, UWC 08/21).

3.6.2. Distribution

Distributed from Namibia (Swakopmund) to at least Tsitsikamma (Nature's Valley) in the Western Cape Province.

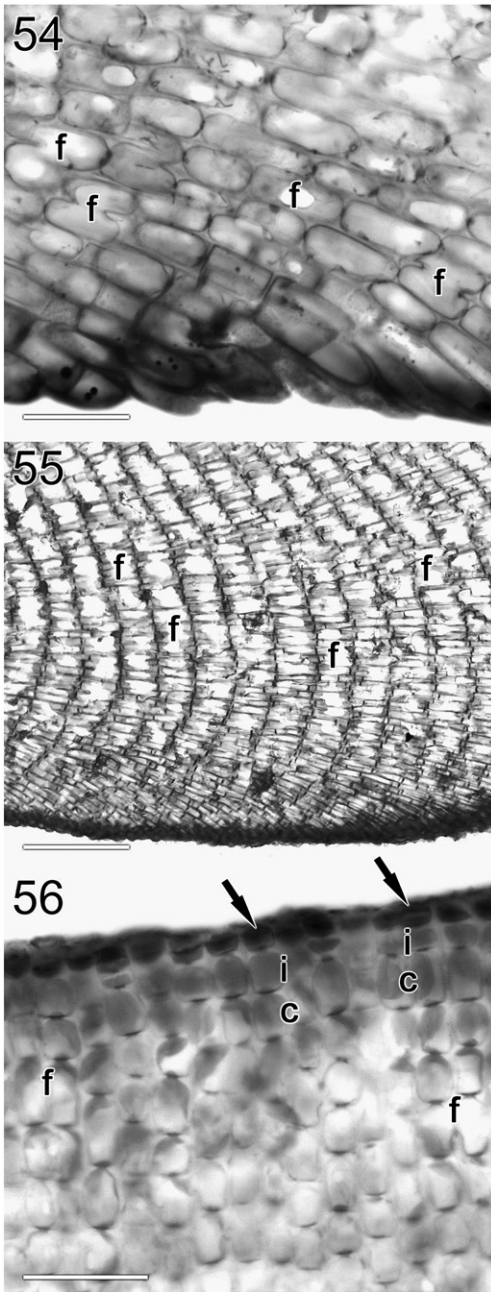
3.6.3. Habit

Thalli are non-geniculate, epilithic on the primary bedrock, and epizoid on worm tubes and mollusc (limpet and winkle) shells. Freshly

collected living specimens are brownish-pink in colour, are matt, encrusting (smooth) and firmly adherent (Fig. 77), and sometimes appear uneven and nodular as a result of conforming to the substrate. The surface has a pitted appearance due to the sunken nature of the conceptacles. Their primary margins are slightly raised and abundant secondary margins occur throughout the thallus surface, giving the thallus an imbricate appearance (Fig. 39). Thalli are thin, measure up to 500 μm thick and lack protuberances.

3.6.4. Vegetative anatomy

The thallus is dorsiventrally organised and monomerous, and haustoria are absent. The medulla is plumose (non-coaxial) (Fig. 40), comprising 2–7 cell layers, and measures 10–49 μm in thickness. Cells of the medullary filaments are rectangular to elongate with rounded corners and are 2–5 times as long as wide. The cortex comprises the bulk of the thallus thickness. Cells of cortical filaments vary from square to elongate (Fig. 41). Fusions between cells of contiguous medullary and cortical filaments are abundant and frequently occupy most of the wall of adjoining cells; secondary pit connections have not been observed. Solitary trichocytes occur throughout the cortex (Fig. 41). Subepithallial initials are square to oval to squat and in length are as short as or shorter than the cells immediately subtending them. An epithallial cell layer is often not intact, but when it is it occurs in a single layer (Fig. 41). Epithallial cells are rounded to elliptical. Data on measured vegetative characters are summarised in Table 1.



Figs. 54–56. Morphology and vegetative anatomy of *P. repandum*. 54.) Vertical section of the ventral region of the thallus showing a plumose (non-coaxial) medulla. Note the cell fusions (f) between cells of adjoining filaments (UWC 93/171). Scale bar = 20 μ m. 55.) Vertical section of the thallus showing a coaxial medulla. Note the cell fusions (f) between cells of adjoining filaments (UWC 93/201). Scale bar = 100 μ m. 56.) Vertical section of the dorsal region of the thallus showing subepithallial initials (i), the first cortical cell (c) and a single layer of slightly dark-staining epithallial cells (arrows). Note the cell fusions (f) between cells of adjoining filaments (UWC 93/171). Scale bar = 20 μ m.

3.6.5. Reproductive anatomy

Gametangial thalli are dioecious. Spermatangial (male) conceptacles are comparatively large and occur sunken in depressions that measure 220–550 μ m in diameter. In depressions, conceptacle roofs are slightly raised above the surrounding depressed thallus (Fig. 42). Mature male conceptacle chambers are elliptical. Conceptacle initiation occurs deep (adventitious, 10 cell layers or more) in the dorsal region of the thallus (Fig. 43). The roof is formed from filaments that arise peripheral to the fertile area (Fig. 44), the terminal initials of which are more elongate than their inward derivatives. As they divide, the newly forming filaments curve inwards to form the roof and pore, with the terminal

initials along the pore canal becoming papillate. These cells project into the pore canal in fully developed conceptacles. Throughout the early development a protective layer of epithallial and cortical cells surrounds the conceptacle primordium (Figs. 43 and 44); this protective layer is shed once the pore canal is fully developed. The pore opening in fully developed conceptacles is often occluded by a mucilage plug (Fig. 42). Branched (dendroid) and unbranched (simple) spermatangial systems develop across the floor (Figs. 45 and 46), while those on the walls and roof of the mature male conceptacles are unbranched only (Figs. 45 and 47). The central region of the conceptacle floor often contains different-looking spermatangial structures that we were unable to classify (Fig. 46). Senescent male conceptacles appear to be shed as no buried conceptacles were observed.

Neither carpogonial (female) nor carposporangial thalli were observed.

Tetrasporangial conceptacles are flush with the surrounding thallus surface, to deeply sunken in depressions that measure 290–500 μ m in diameter (Figs. 48 and 51). Conceptacle initiation occurs mostly deep (adventitious, 10 cell layers or more) in the dorsal region of the thallus (Fig. 49). Tetrasporangial conceptacles are multiporate (Figs. 8 and 50) with roofs that are formed from filaments peripheral to and interspersed among the developing tetrasporangia (Fig. 52). The lower segments of these interspersed filaments degenerate, creating the conceptacle chamber and leaving a roof 25–42 μ m thick composed of 4–5 cells (including an epithallial cell that is sometimes missing) (Figs. 52 and 53). Conceptacle chambers are elliptical. Zonately divided tetrasporangia are scattered across the chamber floor (Fig. 51). Tetrasporangial conceptacle roofs bear apical pore plugs (Figs. 51 and 52). Pores are surrounded by 6–8 rosette cells and the pore opening is slightly raised above the surrounding rosette cells (Fig. 50). Cells of the filaments lining the pore canal are rectangular to elongate with the basal cell the longest (Figs. 52 and 53); the cells are, however, not markedly different (in shape, size or staining intensity) from the cells that make up the rest of the roof. Senescent tetrasporangial conceptacles appear to be shed as no buried conceptacles were observed. Data on measured reproductive characters are summarised in Table 2.

3.7. *Phymatolithon repandum* (Foslie) Wilks and Woelkerling, 1994: 190–192

(Figs. 54–74 and 78)

Basionym: *Lithothamnion repandum* Foslie, 1904: 4.

Synonyms: *Leptophytum absonum* (Foslie) Adey, 1970: 29; *Leptophytum asperulum* (Foslie) Adey, 1970: 29; *Leptophytum repandum* (Foslie) Adey, 1970: 30; *Lithothamnion absonum* Foslie, 1907: 6–7; *Lithothamnion asperulum* (Foslie) Foslie, 1907: 6; *Lithothamnion lenormandii* f. *australe* Foslie, 1901: 8; *Lithothamnion repandum* f. *asperulum* Foslie, 1906: 5. Additional information on these binomials and information on synonymy are provided by Wilks and Woelkerling (1994).

Lectotype: TRH, unnumbered; Half Moon Bay, Port Phillip Bay, Victoria, Australia; J. Gabriel, 14 January 1899. Designated by Adey in Adey and Lebednik (1967: 83). Additional data are provided by Woelkerling (1993: 189).

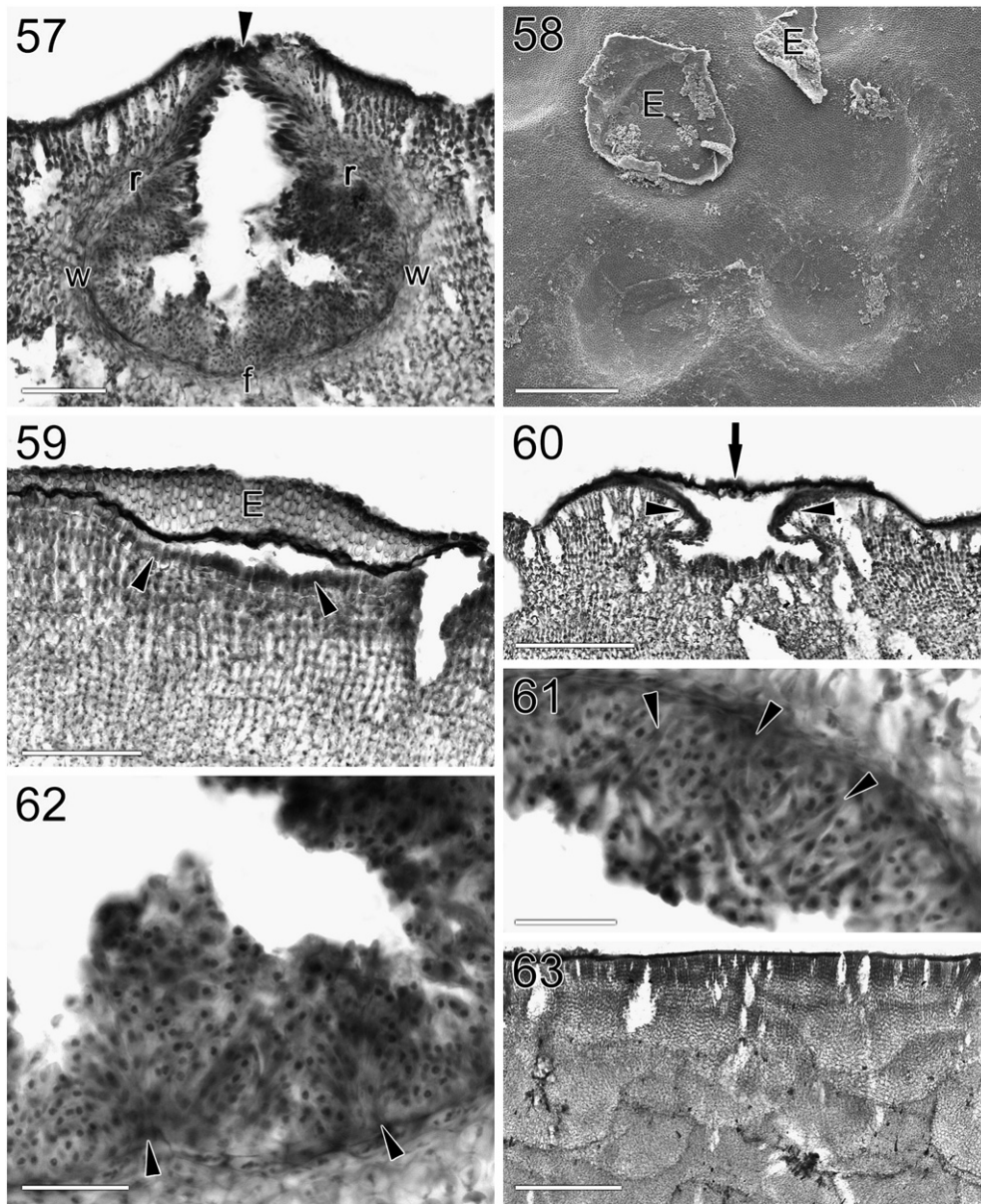
Etymology: Foslie (1904) did not explain the origin of the epithet. Presumably it is derived from the Latin *repandus*, which means having a slightly uneven and waved margin (Stearn, 1973).

3.7.1. Specimens examined

In total, nine (9) specimens were examined, these representing our entire collection for this taxon.

South Africa. Northern Cape Province: Groenriviermond, epilithic on boulders in low shore tide pools (17.vii.1993, D.W. Keats, UWC 93/171).

South Africa. Western Cape Province: Oudekraal, epilithic on the primary bedrock and on boulders in subtidal (to 10 m) sand inundated channels among kelp (19.i.1994, D.W. Keats & G.W. Maneveldt, UWC



Figs. 57–63. Spermatangial (male) anatomy of *P. repandum*. 57.) Vertical section through a conceptacle showing spermatangial systems distributed across the floor (f), walls (w) and roof (r) of the conceptacle chamber. The pore opening is occluded by a mucilage plug (arrowhead) (UWC 94/16). Scale bar = 50 μ m. 58.) SEM of the thallus surface showing young developing conceptacles (depressions), some of which still bear the protective layer of epithallial and cortical cells (E) (UWC 93/201). Scale bar = 200 μ m. 59.) Vertical section through a young developing conceptacle showing adventitious development from a group of spermatangial initials (between arrowheads) within the thallus. Note the layer of protective epithallial and cortical cells (E) (UWC 93/52). Scale bar = 75 μ m. 60.) Vertical section through an immature conceptacle showing the roof development from the periphery (arrowheads). Note the remains of the protective layer of epithallial and cortical cells (arrow) (UWC 94/16). Scale bar = 150 μ m. 61.) Magnified view of the conceptacle chamber roof (r) showing branched spermatangial systems (arrowheads) (UWC 94/16). Scale bar = 20 μ m. 62.) Magnified view of the conceptacle chamber floor showing branched spermatangial systems (arrowheads) interspersed amongst unbranched spermatangial systems (UWC 94/16). Scale bar = 20 μ m. 63.) Vertical section of the thallus showing infilled crescent-shaped scars (UWC 94/16). Scale bar = 200 μ m.

94/16; 27.i.1994, D.W. Keats & G.W. Maneveldt, UWC 94/18). Cape Hangklip, epilithic on the primary bedrock and on boulders in subtidal zone. Common at 8–10 m depth (19.viii.1993, D.W. Keats, UWC 93/200; UWC 93/201). Holbaaipunt, epilithic on the primary bedrock and on boulders in shallow subtidal sand inundated channels (21.v.1993, D.W. Keats, UWC 93/52; 21.vi.1993, D.W. Keats, UWC 93/63; UWC 93/68; 26.v.1994, D.W. Keats, UWC 94/128).

3.7.2. Distribution

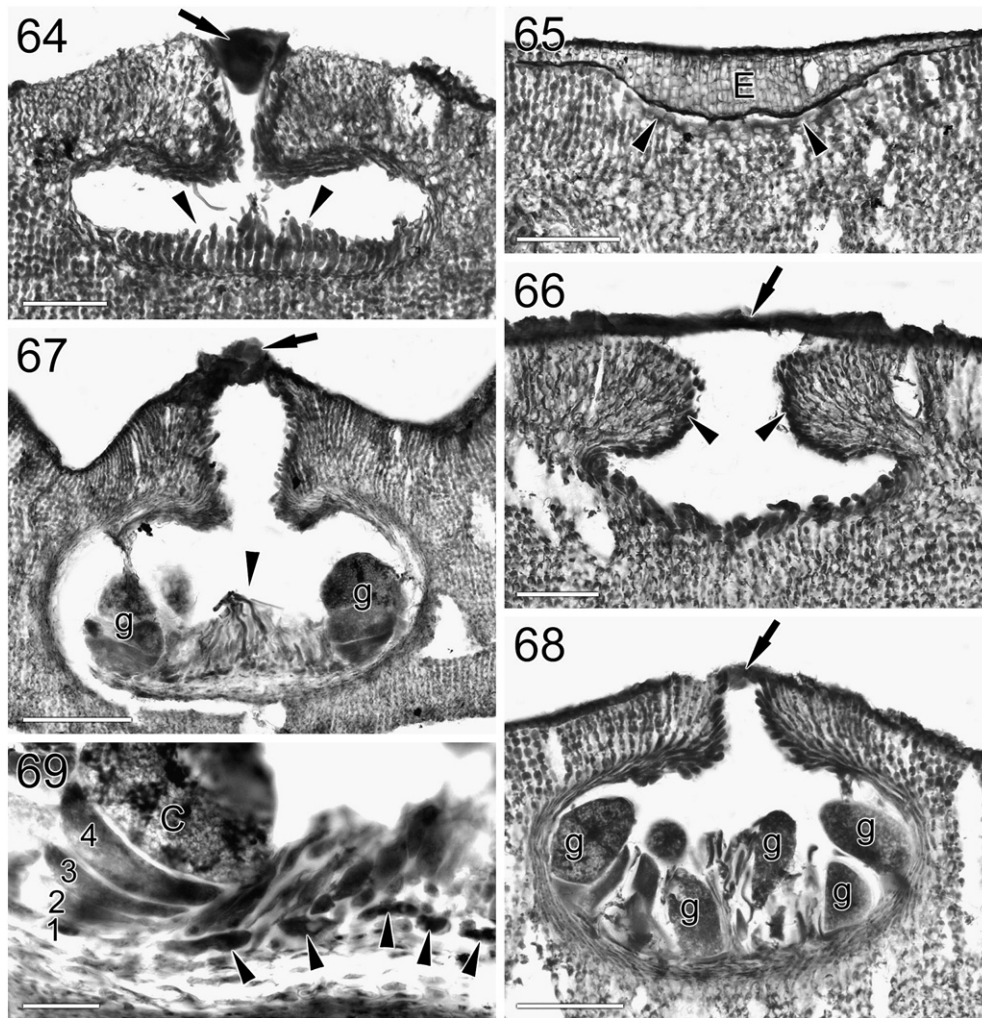
Distributed from Groenriviermond (Northern Cape) to Holbaaipunt in the Western Cape Province.

3.7.3. Habit

Thalli are non-geniculate, epilithic on the primary bedrock and on boulders, mostly in the subtidal where it has been collected to depths of 10 m. Freshly collected living specimens are variable in colour from dull pinkish to reddish to brownish to purplish brown, are matt, and thalli are encrusting to warty to lumpy to fruticose (Fig. 78). Thalli are thick and measure up to 1860 μ m with protuberances that measure up to 3 mm in length.

3.7.4. Vegetative anatomy

The thallus is dorsiventrally organised and monomerous, and haustoria are absent. The medulla is mostly plumose (non-coaxial)



Figs. 64–69. Female anatomy of *P. repandum*. 64.) Vertical section through a carposporangial conceptacle showing carposporangial branches (arrowheads) across the conceptacle chamber floor. The pore opening is occluded by a mucilage plug (arrow) (UWC 93/200). Scale bar = 50 μm . 65.) Vertical section through a conceptacle primordium showing adventitious development from a group of vegetative cells (arrowheads) within the thallus (UWC 93/171). Scale bar = 75 μm . 66.) Vertical section through an immature carposporangial conceptacle showing roof development from the periphery (arrowheads). Note the remains of the protective layer of epithallial and cortical cells (arrow) (UWC 94/16). Scale bar = 50 μm . 67.) Vertical section through a carposporangial conceptacle showing peripherally arranged gonimoblast filaments (g). The central region of the conceptacle chamber floor bears unfertilised carposporangial branches (arrowhead). The pore opening is occluded by a mucilage plug (arrow) (UWC 93/200). Scale bar = 100 μm . 68.) Vertical section through a carposporangial conceptacle showing short gonimoblast filaments (g) distributed across the chamber floor. The pore opening is occluded by a mucilage plug (arrow) (UWC 94/16). Scale bar = 50 μm . 69.) Magnified view of a carposporangial conceptacle floor showing a discontinuous fusion cell (arrowheads) bearing a peripherally arranged gonimoblast filament (1–4) terminating in a carpospore (C) (UWC 93/200). Scale bar = 20 μm .

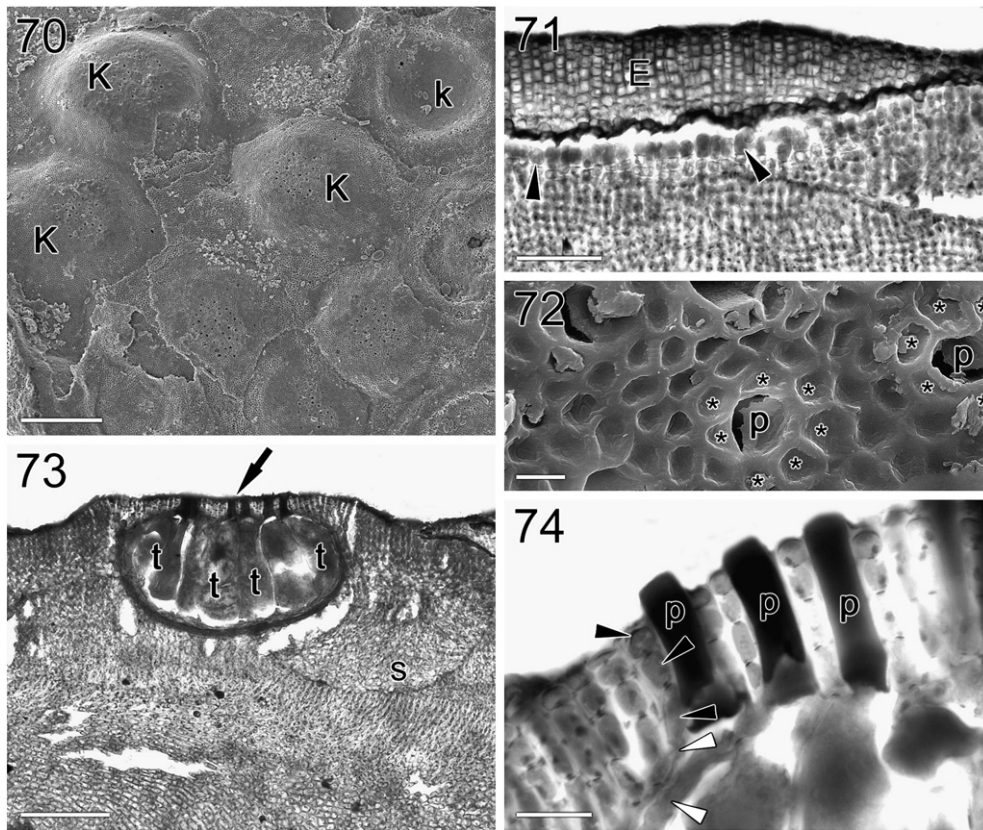
(Fig. 54), but sometimes also coaxial (Fig. 55) comprising several cell layers. In young coaxial thalli, the medulla comprises up to 70% of the thallus thickness. Cells of the medullary filaments are rectangular to elongate with rounded corners and are 2–4 times as long as wide. In plumose thalli, the cortex comprises the bulk of the thallus thickness. Cells of cortical filaments vary from being square to elongate (Fig. 56). Fusions between cells of contiguous medullary and cortical filaments are abundant and frequently occupy most of the wall of adjoining cells; secondary pit connections have not been observed in either the medullary or the cortical filaments. Trichocytes have not been observed. Subepithallial initials are square to oval to squat and in length are as short as or shorter than the cells immediately subtending them (Fig. 56). Epithallial cells are rounded to elliptical, are dark-staining, and occur in a single layer. Data on measured vegetative characters are summarised in Table 1.

3.7.5. Reproductive anatomy

Gametangial thalli are monoecious or dioecious. Spermatangial (male) conceptacles are variable in size and occur raised above the surrounding thallus surface (Fig. 57). Mature male conceptacles

chambers are rounded to elliptical. Conceptacle initiation occurs deep (adventitious, 7 cell layers or more) in the dorsal region of the thallus (Figs. 58 and 59). The roof is formed from filaments that arise peripheral to the fertile area (Fig. 60), the terminal initials of which are more elongate than their inward derivatives. As they divide, the newly forming filaments curve inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate. These cells project into the pore canal in fully developed conceptacles. Throughout the early development a protective layer of epithallial and cortical cells surrounds the conceptacle primordium (Figs. 59 and 60); this protective layer is shed once the pore canal is fully developed. The pore opening in fully developed conceptacles is often occluded by a mucilage plug (Fig. 57). Branched (dendroid) and unbranched (simple) spermatangial systems develop across the floor, walls and roof of the mature male conceptacles (Figs. 57, 61 and 62). Senescent male conceptacles appear to be shed as no buried conceptacles were observed, but infilling is evident as crescent-shaped scars (Fig. 63).

Carposporangial (female) conceptacles are raised above the thallus surface (Fig. 64). The conceptacle chamber is roundish to elliptical to flattened. Conceptacle initiation occurs deep (adventitious) in the



Figs. 70–74. Tetrasporangial anatomy of *P. repandum*. 70.) SEM of the thallus surface showing raised multiporate conceptacles (K) (UWC 93/201). Scale bar = 200 μm . 71.) Vertical section through a young developing conceptacle showing adventitious development from a group of tetrasporangial initials (between arrowheads) within the thallus. Note the protective layer of epithallial and cortical cells (E) (UWC 93/52). Scale bar = 50 μm . 72.) SEM of a conceptacle pore plate showing multiple pores (p) surrounded by rosette cells (*) (UWC 93/201). Scale bar = 5 μm . 73.) Vertical section through a conceptacle showing tetrasporangia (t) distributed across the chamber floor. Note the multiporate roof (arrow) bearing densely staining pore plugs and an infilled crescent-shaped scar (S) (UWC 93/171). Scale bar = 100 μm . 74.) Magnified view of the conceptacle pore plate showing apical pore plugs (p). The cells lining the pore canal (black arrowheads) are not different to those from the rest of the pore plate. Note the remains of the interspersed filaments (white arrowheads) that gave rise to the conceptacle roof (UWC 93/171). Scale = 10 μm .

dorsal region of the thallus (Fig. 65). The pore canal cells project into the pore as papillae, and are orientated more or less parallel to the conceptacle roof surface. Throughout the early development a protective layer of epithallial and cortical cells surrounds the conceptacle primordium (Fig. 65 and 66); this protective layer is shed once the pore canal is fully developed. The pore canal in fully developed conceptacles is occluded by a mucilage plug (Fig. 64). Carpogonial branches develop across the floor of the female conceptacle and comprise at least one support cell and a hypogynous cell bearing a carpogonium extended into a trichogyne. A sterile cell may also be present on the hypogynous cell.

After presumed karyogamy, carposporophytes develop within female conceptacles and form carposporangial conceptacles. Carposporangial conceptacles are comparatively large and raised well above the surrounding thallus (Fig. 67). Chambers are roundish to elliptical. The pore canal is lined by papillate cells that protrude into the pore canal. The conceptacle pore is occluded by a mucilage plug (Fig. 67). A large central fusion cell is absent; instead a discontinuous fusion cell is present and 3–5 celled gonimoblast filaments (incl. a terminal carposporangium) develop either along the periphery of the conceptacle chamber (Figs. 67 and 69) or are scattered across the floor (Fig. 68). Senescent carposporangial conceptacles appear to be shed as no buried conceptacles were observed, but infilling is evident as crescent-shaped scars (Fig. 63).

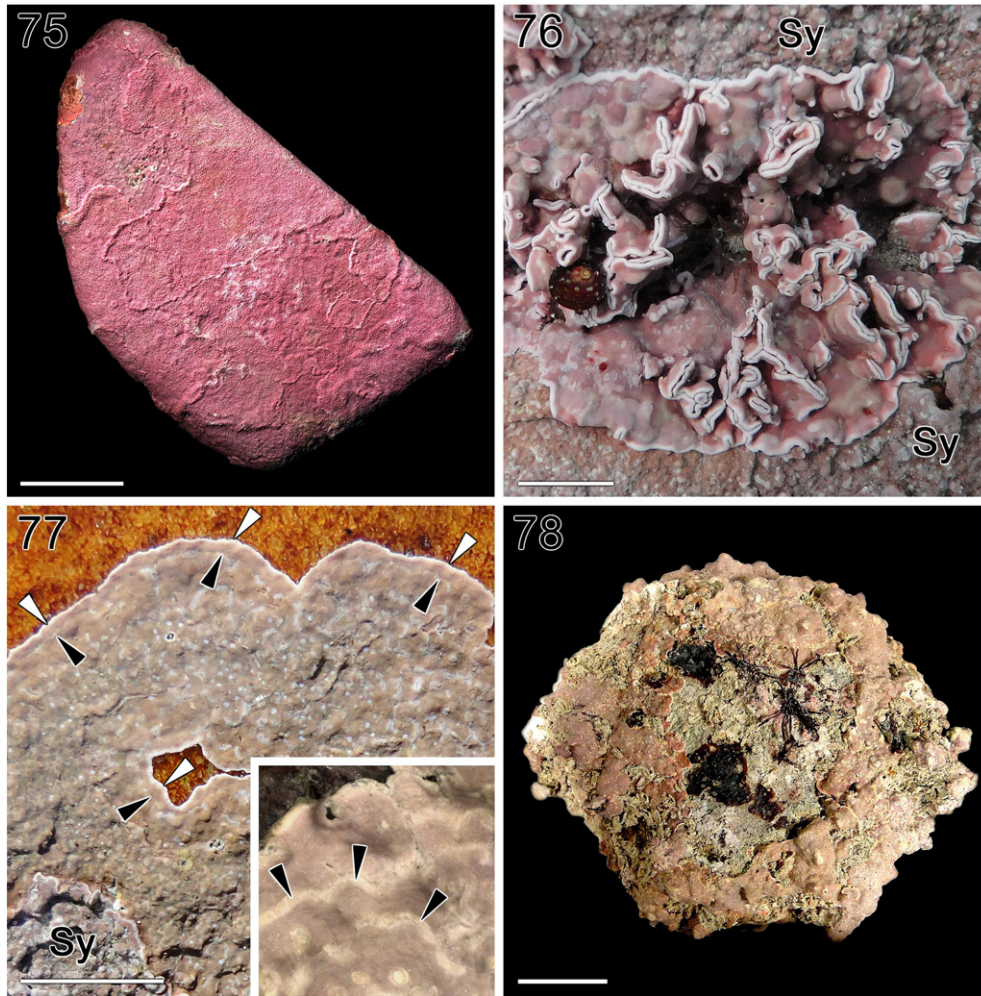
Tetrasporangial conceptacles are flush to mostly raised above the surrounding thallus surface and are variable in size (Fig. 70). Conceptacle initiation occurs deep (adventitious, 7 cell layers or more) in the dorsal region of the thallus and the young developing tetrasporangial initials are overlain by a layer of protective cortical and epithallial cells

(Fig. 71) that eventually become shed. Tetrasporangial conceptacles are multiporate (Figs. 70, 72 and 73) with roofs that are formed from filaments peripheral to and interspersed among the developing tetrasporangia (Fig. 74). The lower segments of these interspersed filaments degenerate, creating the conceptacle chamber and leaving a roof 20–27 μm thick composed of 3–5 (mostly 4) cells (including an epithallial cell). Conceptacle chambers are roundish to elliptical. Zonately divided tetrasporangia are scattered across the chamber floor (Fig. 73). Tetrasporangial conceptacle roofs bear apical pore plugs (Fig. 74). Pores are surrounded by 6–9 rosette cells and the pore opening is slightly raised above the surrounding rosette cells (Fig. 72). Cells of the filaments lining the pore canal are squarish to slightly elongate with the basal cell the longest (Fig. 74); the cells are, however, not markedly different (in shape, size or staining intensity) from the cells that make up the rest of the roof. Senescent tetrasporangial conceptacles appear to be shed as no buried conceptacles were observed, but infilling is evident (Fig. 73). Data on measured reproductive characters are summarised in Table 2.

Phymatolithon repandum from South Africa compares favourably to specimens reported from Australia, which is home to the type locality (Table 3). See Table 4 for a synopsis of the characters considered diagnostic of the four species of *Phymatolithon* now known to exist in South Africa.

4. Discussion

Phymatolithon, as delimited by Harvey et al. (2003), is the only known genus in the family Hapalidiaceae that: 1) possesses subepithallial initials



Figs. 75–78. Habit photographs of the four species of *Phymatolithon*. 75.) Several individuals of *P. acervatum* encrusting a tide pool boulder. 76.) *Phymatolithon ferox* produces numerous marginal upgrowths that form back to back, mouth-like structures where they meet. The species is often found co-existing with *Spongites yendoi* (Sy) in the mid-intertidal zone. 77.) *Phymatolithon foveatum* produces numerous secondary margins (black arrowheads) across its surface giving the coralline an imbricate appearance. These secondary margins run more or less parallel to the primary margin (white arrowheads). The species is often found co-existing with *Spongites yendoi* (Sy) in the lower intertidal zone. 78.) Several individuals of *P. repandum* encrusting a subtidal boulder (UWC 93/52).

that are as short as or shorter than the cells immediately subtending them; and 2) produces both branched (dendroid) and unbranched (simple) spermatangial filaments in male conceptacles. In addition to the other family characteristics, *P. acervatum*, *P. ferox* and *P. foveatum* reported here, possess these characters currently considered diagnostic of *Phymatolithon* and so rightly belong in the genus. Furthermore, *P. repandum* presented here is described in detail for the first time from South Africa and is found to compare favourably to specimens reported from Australia, home to the type locality.

Until this study, except for *P. foveatum*, no carpogonial (female) thalli had been reported for the taxa presented here. In their reporting of carposporangial thalli in *L. acervatum*, Chamberlain and Keats (1994) reported the absence of a central fusion cell although they did report discontinuous fusion cells for both *L. ferox* and *L. foveatum*. We confirm the absence of a (solid) central fusion cell, but have found a discontinuous fusion cell to exist that was often visible only in serial sections. The absence of a (solid) central fusion cell therefore does not necessarily mean the absence of a fusion cell altogether.

Most importantly, our research shows that features used to segregate the genus *Leptophytum* from *Phymatolithon* do not stand up to scrutiny. Among other features (see summaries by Düwel and Wegeberg, 1996; Woelkerling et al., 2002), the genus *Leptophytum* was previously separated from *Phymatolithon* by the presence of

branched spermatangial systems only on the centre of the floor of the male conceptacle in the former as opposed to branched systems across the entire male conceptacle floor in *Phymatolithon* (Adey, 1966; Lebednik, 1978; Chamberlain, 1990; Chamberlain and Irvine, 1994; Chamberlain and Keats, 1994; Adey et al., 2001). Both *L. acervatum* and *L. ferox* were reported by Chamberlain and Keats (1994) to possess this feature i.e. unbranched spermatangial systems on the floor, walls and roof of the male conceptacles, but branched spermatangial systems restricted to the centre of the floor of the male conceptacle. While no male thalli were previously observed and thus reported on for *L. foveatum*, Chamberlain and Keats (1994: 118) made the assumption that the latter species possessed the same spermatangial (male) characteristics said to be diagnostic of the genus *Leptophytum*. However, during our investigations on an extensive collection of material, we have found all three species to conform to the diagnostic characterisation of *Phymatolithon*. Düwel and Wegeberg (1996) suggested that the different elaborations of the spermatangial systems previously reported as diagnostic for both *Leptophytum* and *Phymatolithon* possibly represent various stages of development. We support this suggestion.

Another feature previously used to separate *Leptophytum* from *Phymatolithon*, was the depth of the tetrasporangial conceptacle initiation. In *Leptophytum*, tetrasporangial conceptacle initiation was reported to be shallow (no more than 3–5 cells below the thallus surface),

Table 3Comparison of *P. repandum* from South Africa (this study) and Australia based on selected characteristics. ND = no data.

Character	<i>P. repandum</i> (this study)	<i>P. repandum</i> (Wilks and Woelkerling, 1994)	<i>P. repandum</i> (Womersley, 1996)	<i>P. repandum</i> (Harvey et al., 2003)
Substrate	Epilithic on rock	Mostly epilithic on rock ¹	Epilithic on rock	Epilithic on rock
Growth form	Encrusting to warty to lumpy to fruticose	Encrusting to warty to fruticose	Encrusting to warty to fruticose	Encrusting to warty
Thallus thickness	To 1860 µm, protuberances to 3 mm	100 µm–1.5 mm	0.1–4.0 mm	Up to 1 mm, protuberances to 2 mm
Gametangial thalli	Monoecious or dioecious	ND	Monoecious or dioecious	Monoecious or dioecious
Spermatangial thalli				
Conceptacle placement	Raised above surrounding thallus surface	Raised above surrounding thallus surface	Raised above surrounding thallus surface	Slightly raised above or flush with surrounding thallus
External conceptacle diameter	320–580 µm	ND	ND	ND
Conceptacle chamber diameter	186–314 µm	100–250 µm	100–250 µm	120–215 µm
Conceptacle chamber height	71–137 µm	45–150 µm	45–150 µm	30–55 µm
Conceptacle roof thickness	27–70 µm	25–75 µm	25–75 µm	ND
Spermatangial systems	Branched and unbranched on floor, walls and roof	Branched and unbranched on floor, walls and roof	Branched and unbranched on floor, walls and roof	Branched only on floor to branched and unbranched on roof
Carpogonial thalli				
Conceptacle placement	Raised above surrounding thallus surface	Raised above to flush with surrounding thallus surface	Raised above to flush with surrounding thallus surface	Raised above surrounding thallus surface
External conceptacle diameter	400–500 µm	ND	ND	ND
Conceptacle chamber diameter	130–270 µm	112–300 µm	ND	95–135 µm
Conceptacle chamber height	54–113 µm	50–125 µm	ND	55–80 µm
Conceptacle roof thickness	83–127 µm	22–100 µm	ND	ND
Carposporangial thalli				
Conceptacle placement	Raised above surrounding thallus surface	Raised above to flush with surrounding thallus surface	Raised above to flush with surrounding thallus surface	Raised above surrounding thallus surface
External conceptacle diameter	430–640 µm	ND	ND	ND
Conceptacle chamber diameter	233–372 µm	112–300 µm	112–300 µm	95–135 µm
Conceptacle chamber height	75–159 µm	50–125 µm	50–125 µm	55–80 µm
Conceptacle roof thickness	96–115 µm	22–100 µm	ND	ND
Type of fusion cell	Large central fusion cell absent; fusion cell is instead discontinuous	Large central fusion cell absent; fusion cell is instead discontinuous ²	Large central fusion cell absent; fusion cell is instead discontinuous ³	Irregularly shaped and discontinuous
Distribution of gonimoblast filaments	Peripheral or scattered across the floor	Peripheral or scattered across the floor	ND	Scattered across the floor
No. of cells in gonimoblast filament	3–5	2–several-celled	Several-celled	Several-celled
Carpospore length	25–54 µm	17–63 µm	ND	ND
Carpospore diameter	34–74 µm	12–75 µm	12–75 µm	ND
Tetrasporangial thalli				
Conceptacle placement	Raised above to flush with surrounding thallus surface	Raised above to flush with surrounding thallus surface	Raised above surrounding thallus surface	Raised above to flush with surrounding thallus surface
External conceptacle diameter	270–600 µm	ND	ND	ND
Conceptacle chamber diameter	191–333 µm	96–300 µm	96–300 µm	120–205 µm
Conceptacle chamber height	88–147 µm	50–150 µm	50–150 µm	60–120 µm
Conceptacle roof thickness	20–27 µm	20–33 (42) µm	ND	ND
No. of cells in conceptacle pore plate	3–5	3–5	3–5	3–4
No. of pore rosette cells	6–9	ND	ND	ND
Tetra/bisporangium length	81–147 µm	32–125 µm	32–125 µm	45–95 µm
Tetra/bisporangium diameter	22–78 µm	15–80 µm	15–80 µm	16–70 µm

¹ Also epigenous on a glass bottle.² Fig. 10B shows a discontinuous fusion cell.³ Fig. 81B (same figure as in Wilks and Woelkerling, 1994), shows a discontinuous fusion cell.

Table 4Comparison of the characters collectively considered diagnostic of the four species of *Phymatolithon* now known to exist in South Africa.

Character	<i>P. acervatum</i>	<i>P. ferox</i>	<i>P. foveatum</i>	<i>P. repandum</i>
Substrate	Mostly epilithic on pebbles and small boulders	Epilithic on rock, epizoic on worm tubes	Epilithic on rock, epizoic on worm tubes and mollusk shells	Epilithic on rock
Growth form	Encrusting	Encrusting to warty to lumpy	Encrusting	Encrusting to warty to lumpy to fruticose
Thallus surface	Smooth, with a visibly pitted appearance	With secondary mouth-like margins and flat-topped protuberances	Smooth, with secondary, imbricate margins	Protuberant, without secondary margins
Thallus thickness	To 500 µm, not protuberant	To 500 µm, protuberances to 10 mm	To 500 µm, not protuberant	To 1860 µm, protuberances to 3 mm
Conceptacle placement	Sunken in depressions	Raised above surrounding thallus surface	Flush with the surrounding thallus surface to sunken in depressions	Raised above surrounding thallus surface
Gametangial thalli	Dioecious	Dioecious	Dioecious	Monoecious or dioecious
Distribution of gonimoblast filaments	Peripheral	Peripheral	Peripheral	Peripheral or scattered across the floor

while in *Phymatolithon* it was reported to be adventitious or ‘deep’ (several cells) within the dorsal region of the thallus (Adey, 1964, 1966, 1970; Chamberlain, 1990; Chamberlain and Irvine, 1994; Wilks and Woelkerling, 1994; Womersley, 1996; Adey et al., 2001; Athanasiadis and Adey, 2006). For the majority of material observed during this study, both gametangial and tetrasporangial conceptacle initiations were generally deep (more than 10 cells) within the dorsal region of the thallus.

As a consequence of the data presented here, we question the continued use and availability of the name *Leptophytum*. Firstly, it is important to note why, in much of the recent literature, the name has been placed in quotation marks. Maneveldt et al. (2008) used the name “*Leptophytum*” in quotation marks because South African taxa ascribed to this genus had not been formally transferred to *Phymatolithon* or reduced to synonymy. This usage was first proposed by Bailey and Chapman (1998: 694 [footnote to Table 1]; 700) as a result of the unresolved taxonomy of those taxa ascribed to ‘*Leptophytum*’ and for similar reasons mentioned by Maneveldt et al. (2008). This practice (of placing the name in quotation marks) has been adopted by other authors, notably in molecular studies (e.g. Broom et al., 2008; Bittner et al., 2011).

On the basis of anatomical studies of the relevant types and other specimens, Düwel and Wegeberg (1996) determined that *Leptophytum* Adey is a heterotypic synonym of *Phymatolithon* Foslie. Düwel and Wegeberg (1996: 482), however, did not preclude the possibility of a genus separate from *Phymatolithon* and as noted by Bailey and Chapman (1998: 700), “it is conceivable, but by no means certain, that a new genus may have to be erected to include some species once classified in ‘*Leptophytum*’”. Presently there appears to be no reliable morphological/anatomical features that can be used to establish such a new genus (Woelkerling et al., 2002). If future research does show that a genus separate from *Phymatolithon* is warranted, it should, however, be based on well-defined morphological/anatomical characters and not solely on molecular evidence (Bailey and Chapman, 1998; Woelkerling et al., 2002), a sentiment strongly iterated by Guiry (2012: 1059). Our data and interpretation support this view. Ironically, recent molecular data (e.g. Broom et al., 2008: 970; Bittner et al., 2011: 705 [Fig. 1]) has shown a closer affinity between *P. repandum* from New Zealand and South African ‘*Leptophytum*’ *acervatum* and ‘*Leptophytum*’ *ferox* than with congeners from *Phymatolithon*, providing molecular support for our findings.

In conclusion, not only are we the first to present a description of *P. repandum* for South Africa, previously only reported for the country (see Maneveldt et al., 2008: 560), we are the first to demonstrate that all taxa from South Africa previously classified under the name *Leptophytum*, indeed belong within the genus *Phymatolithon*. Our data supports previous conclusions that the characters upon which *Leptophytum* is based are unreliable for generic delimitation from *Phymatolithon*. We reiterate that the name *Leptophytum* is not available for use as a result of the study of Düwel and Wegeberg (1996). The only

exception would be if *P. lenormandii*, with which the type of *Leptophytum* Adey is conspecific (see Düwel and Wegeberg, 1996: 481), were determined not to belong to *Phymatolithon* and were also chosen as the type species of a separate genus.

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