*Phytotaxa*190 (1): 216–249
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.190.1.14

Taxonomic review based on new data of the reef-building alga *Porolithon onkodes* (Corallinaceae, Corallinales, Rhodophyta) along with other taxa found to be conspecific

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Abstract

Based on new studies of the type and of specimens from various localities in the Atlantic, Indian and Pacific oceans, *Porolithon onkodes* was reaffirmed as a distinct species, but of variable morphological appearance. The following taxa were found to conform to the present-day diagnosis of *P. onkodes* and they are thus considered heterotypic synonyms thereof: *P. antillarum*, *P. cocosicum P. pachydermum* and *P. sandvicense*. Despite the suggested reproductive isolation of these taxa, there is no valid taxonomic reason for their separation as the characters considered diagnostic of *P. onkodes* were found to be present in all of them. Also, while molecular analysis using ITS sequence data has suggested that *P. onkodes* and *P. pachydermum* are distinct species, the complex and unpredictable evolutionary behaviour of ITS reduce its use for phylogenetic analysis. In many tropical Indo-Pacific and tropical eastern Atlantic regions, *P. onkodes* has been reported to be one of the single-most important ecological species because of its wide distribution. Similarly, *P. pachydermum* has been documented as one of the single-most important ecological species in many areas of the tropical and subtropical western Atlantic. As the two taxa are here shown to be conspecific, it is logical to suggest that *P. onkodes* is arguably one of the most widespread tropical to subtropical non-geniculate coralline algae. *Porolithon onkodes* not only occurs largely throughout the Indo-Pacific, but as a result of the present study, is now known to commonly occur throughout the tropical and subtropical regions of the eastern and notably western Atlantic Ocean.

Key words: *Hydrolithon*; Porolithoideae, reef frame-builder; taxonomy

Introduction

The ecological importance of non-geniculate coralline red algae as cementers and primary reef frame-builders of the coral reef margin has been well documented (Setchell 1926, Taylor 1950, Lee 1967, Littler & Doty 1975, Adey *et al*. 1982, Keats *et al*. 1997). Species ascribed to the genus *Porolithon* Foslie have been highlighted as being particularly important (Lee 1967, Adey 1978, Littler 1973, Littler & Doty 1975, Adey *et al*. 1982, Gherardi & Bosence 1999, 2001, Littler & Littler 2000, 2003, Villas Bôas *et al*. 2005, Figueiredo *et al*. 2008). Notably, *Porolithon onkodes* (Heydrich) Foslie *emend.* A.Kato & Baba (Kato *et al*. 2011: 669) has been reported to be one of the single-most important non-geniculate coralline algae in the tropical Indo-Pacific and tropical eastern Atlantic regions because of its wide distribution (Lee 1967, Littler 1973, Littler & Doty 1975, Gordon *et al*. 1976, Adey *et al*. 1982, Ballesteros & Afonso-Carrillo 1995, Payri *et al*. 2001, Littler & Littler 2003).

The genus *Porolithon* has undergone much taxonomic revision (see Penrose & Woelkerling 1988, 1992, Bittner *et al*. 2011, Kato *et al*. 2011). Within the recently erected subfamily Porolithoideae A.Kato & Baba (Kato *et al*. 2011: 669) (Corallinaceae), algae belonging to this genus are characterised by: 1) having thalli that are unsegmented (i.e. non-geniculate); 2) lacking secondary pit connections, but bearing lateral cell fusions between contiguous filaments; 3) lacking a basal layer of palisade cells; 4) possessing trichocytes in large, tightly packed horizontal fields (that lack vegetative filaments between them); 5) having their tetrasporangial conceptacles formed by filaments peripheral to the fertile area and interspersed among the tetrasporangial initials; and 6) possessing spermatangia that develop on the floor of the male conceptacle chamber. Within tetrasporangial conceptacles the pore canals are lined by a ring of conspicuous, enlarged cells that arise from filaments interspersed among the

 Accepted by Rafael Riosmena-Rodriguez: 29 Mar 2014; published: 24 Dec. 2014

sporangial initials. These pore canal cells do not protrude into the pore canal but are orientated more-or-less perpendicularly to the roof surface. *Porolithon onkodes* is a well-known and readily recognised tropical species (Gordon *et al*. 1976, Adey *et al*. 1982, Keats & Chamberlain 1994, Littler & Doty 1975, Payri *et al*. 2001, Littler & Littler 2003) and its taxonomy has been well documented (Penrose & Woelkerling 1992, Keats & Chamberlain 1994). In our continued efforts to better understand the taxonomy of the non-geniculate coralline algae, we have found a number of taxa to conform to the current understanding of what characterises *P. onkodes*. Here we report on these findings and make suggestions to the biogeographical and ecological implications thereof.

Material and Methods

Type specimens were obtained from BM, PC, NY and TRH. Fragments of type material were first fixed in 1 part liquid detergent: 4 parts commercial formalin in distilled water (4 % formaldehyde) for at least 48 hours prior to examination. This method was found useful for rehydrating the material. For representative material, 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. For scanning electron microscopy (SEM), air-dried material was fractured using forceps, diagonal cutters, or a small hammer and chisel. Fractures perpendicular to a leading edge were 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 24 hrs prior to examination, coated with gold for 4–6 min in an Edwards S150B sputter coater, and examined with a Hitachi X650 scanning electron microscope at an accelerating voltage of 25 kV.

Specimens for histological examination were prepared following Maneveldt & van der Merwe (2012). 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 mins 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 Historesin 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 mins; for more rapid hardening, specimens were placed immediately in an oven at 60 °C for approximately 10–20 mins.

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 hrs. 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 & 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).

Results

Porolithon Foslie

Foslie (1909: 57) originally established the genus *Porolithon* to encompass those taxa that lack secondary pit connections, possess a monomerous thallus, have uniporate sporangial conceptacles with a central columella, and most importantly, the thallus bearing trichocytes in horizontally arranged fields. Adey *et al*. (1982) added to the diagnosis by commenting on the 'pustulous' (pustulate) nature of the tightly packed trichocyte fields, making

reference to the blister-like appearance of the slightly raised trichocyte fields. Later it was concluded that the characters said to be diagnostic of the type of *Porolithon* were not reliable, as the types of both the genera *Spongites* and *Hydrolithon* were shown to possess the same characters (Woelkerling 1985, Penrose & Woelkerling 1988). Both *Porolithon* and *Hydrolithon* were subsequently subsumed in *Spongites*, the oldest available name for the complex (Penrose & Woelkerling 1988). During their course of study on the southern Australian taxa of *Spongites* (*sensu lato*), Penrose & Woelkerling (1992) demonstrated that two distinct patterns of tetrasporangial conceptacle development occurred and they concluded that *Spongites* and *Hydrolithon* were distinct genera.

In *Hydrolithon*, the tetrasporangial conceptacle roof developed both from filaments peripheral to the fertile area and from filaments interspersed among the developing tetrasporangia. Here the pore canals of the tetrasporangial conceptacles were lined by a ring of conspicuous, enlarged cells that arose from filaments interspersed among the sporangial initials. These pore canal cells did not protrude into the pore canal and were orientated more-or-less perpendicularly to the roof surface. Based on this new evidence, however, Penrose & Woelkerling (1992) still considered *Porolithon* and *Hydrolithon* to be congeneric, with *Hydrolithon* having nomeclatural priority.

Recently, two independent studies (Bittner *et al*. 2011, Kato *et al*. 2011) demonstrated, using molecular analyses, that *Porolithon* and *Hydrolithon* are indeed separate taxa. Kato *et al*. (2011: 669) showed convincingly that the former subfamily Mastophoroideae needed to be split and they proposed, among others, the erection of the subfamily Porolithoideae A.Kato & Baba having *Porolithon* Foslie *emend.* A.Kato & Baba as the type genus and *Porolithon onkodes* (Heydrich) Foslie as the type species to the genus.

Porolithon onkodes (Heydrich) Foslie, 1909: 57
(Figs 1–24)

Basionym:—*Lithothamnion onkodes* Heydrich, 1897: 6–7 (Figs 1–11).

Homotypic synonyms:—*Goniolithon onkodes* (Heydrich) Foslie, 1898: 8; *Lithophyllum onkodes* (Heydrich) Heydrich, 1901: 533; *Spongites onkodes* (Heydrich) Penrose & Woelkerling, 1988: 173; *Hydrolithon onkodes* (Heydrich) Penrose & Woelkerling, 1992: 83.

Lectotype:—TRH!, A26-1494. Tami Island, northwest edge of Huon Gulf, Papua New Guinea; Heydrich no. 97 (designated by Adey *et al*. 1982: 9). Previous references to typification were by Penrose & Woelkerling 1988: 162 (as *Porolithon*), Penrose & Woelkerling 1992: 83, Verheij 1993: 47, Woelkerling 1993: 164, Keats & Chamberlain 1994: 8, Barry & Woelkerling 1995: 140 and Penrose 1996: 263 (as *Hydrolithon*).

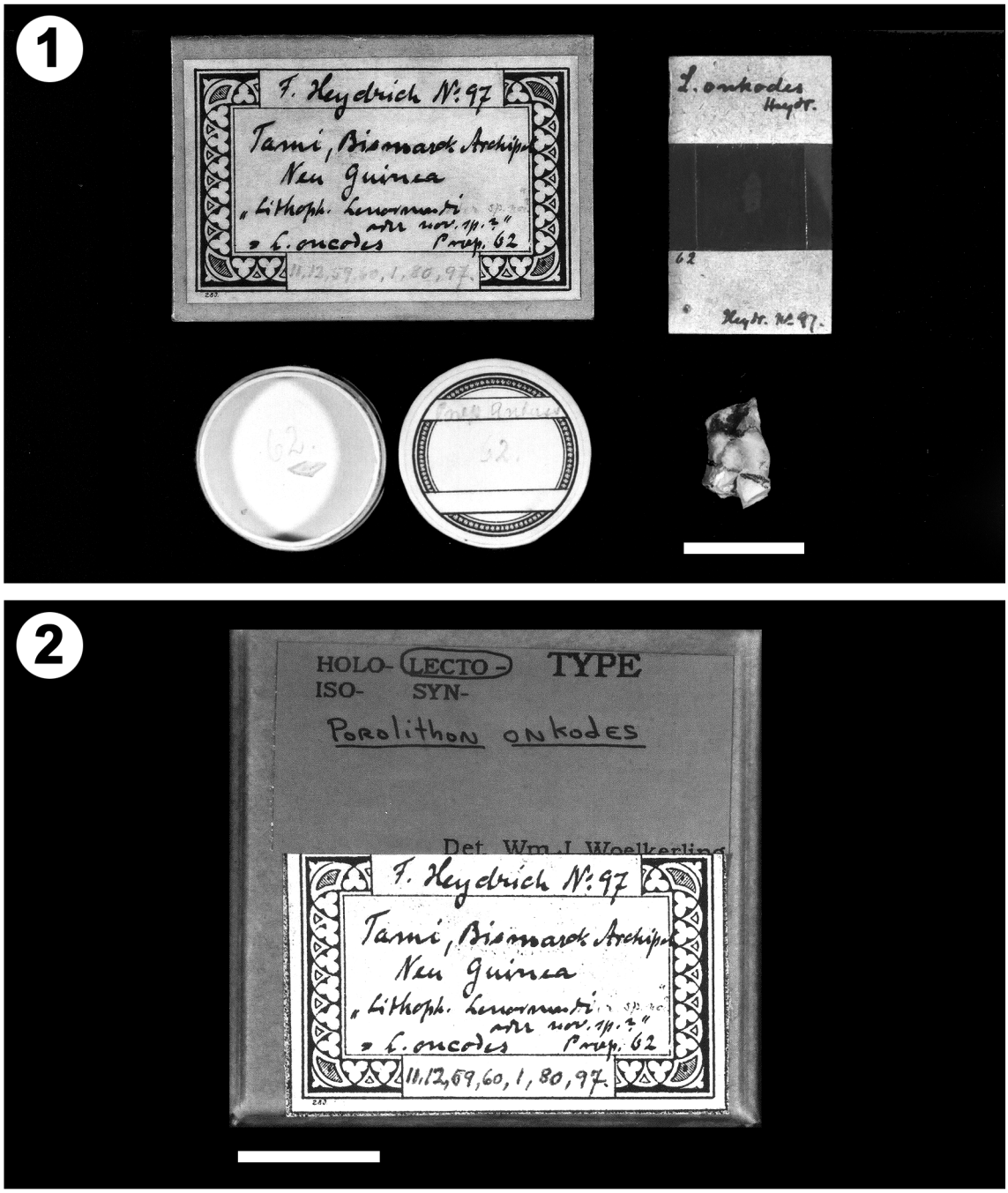
Isolectotype:—Material exists in PC! (unnumbered, General Herbarium box collection [filed in non-geniculate coralline type collections cabinet under basionym, see Woelkerling & Lamy 1998]). The PC material sent on loan was found to belong to a species of *Neogoniolithon* (the fragment possessed very large [~ 1000 μm] uniporate sporangial conceptacles that displayed peripheral roof development, numerous long vertical chains of trichocytes and coaxial medullary filaments). The PC isolectotype likely contains a mixture of species. No attempt was made at requesting additional material to determine whether any authentic *onkodes* was present.

Etymology:—'*onkodes*', *onco* = swollen, puffed out, bulky (Stearn 1973). Heydrich (1897) did not explain the origin of the epithet. It possibly makes reference to the granular texture of the thallus surface owing to the presence of abundant pustulate, horizontally arranged trichocyte fields. This may have given the surface a swollen, puffed out appearance. Alternatively, Heydrich (1897) may simply have referred to the growth form of the coralline growing over lumpy coral.

Specimens examined:—In addition to the lectotype, 30 representative specimens were examined during this study.

COMOROS. Chimoni (27.xi.1992, *D.W. Keats*, UWC 92/542); Treasure Cove, Le Galawa (3.xii.1992, *D.W. Keats*, UWC 92/581).

FIJI. Makaluva Island, Suva Lagoon, Suva (24.iv.1994, *D.W. Keats & G. Yeo*, UWC 94/1002); Usborne Passage, Great Astrolabe Reef (2.vi.1994, *D.W. Keats*, UWC 94/1030); Herald Passage, Great Astrolabe Reef (10.vi.1994, *D.W. Keats*, UWC 94/1074); Beqa Lagoon (16.vii.1994, *D.W. Keats*, UWC 94/1128); Suva Barrier Reef (11.viii.1994, *D.W. Keats*, UWC 94/1157; 21.ix.1994, *D.W. Keats*, UWC 94/1207); East of Dravuni, Great Astrolabe Reef (23.viii.1994, *D.W. Keats*, UWC 94/1175, UWC 94/1179); Fish Patch, Suva Barrier Reef (13.x.1994, *D.W. Keats*, UWC 94/1253; 9.xi.1994, *D.W. Keats*, UWC 94/1269; 22.xi.1995, *D Keats*, UWC 95/1509; 13.xi.1999, *D.W. Keats*, UWC 99/FJ-04).

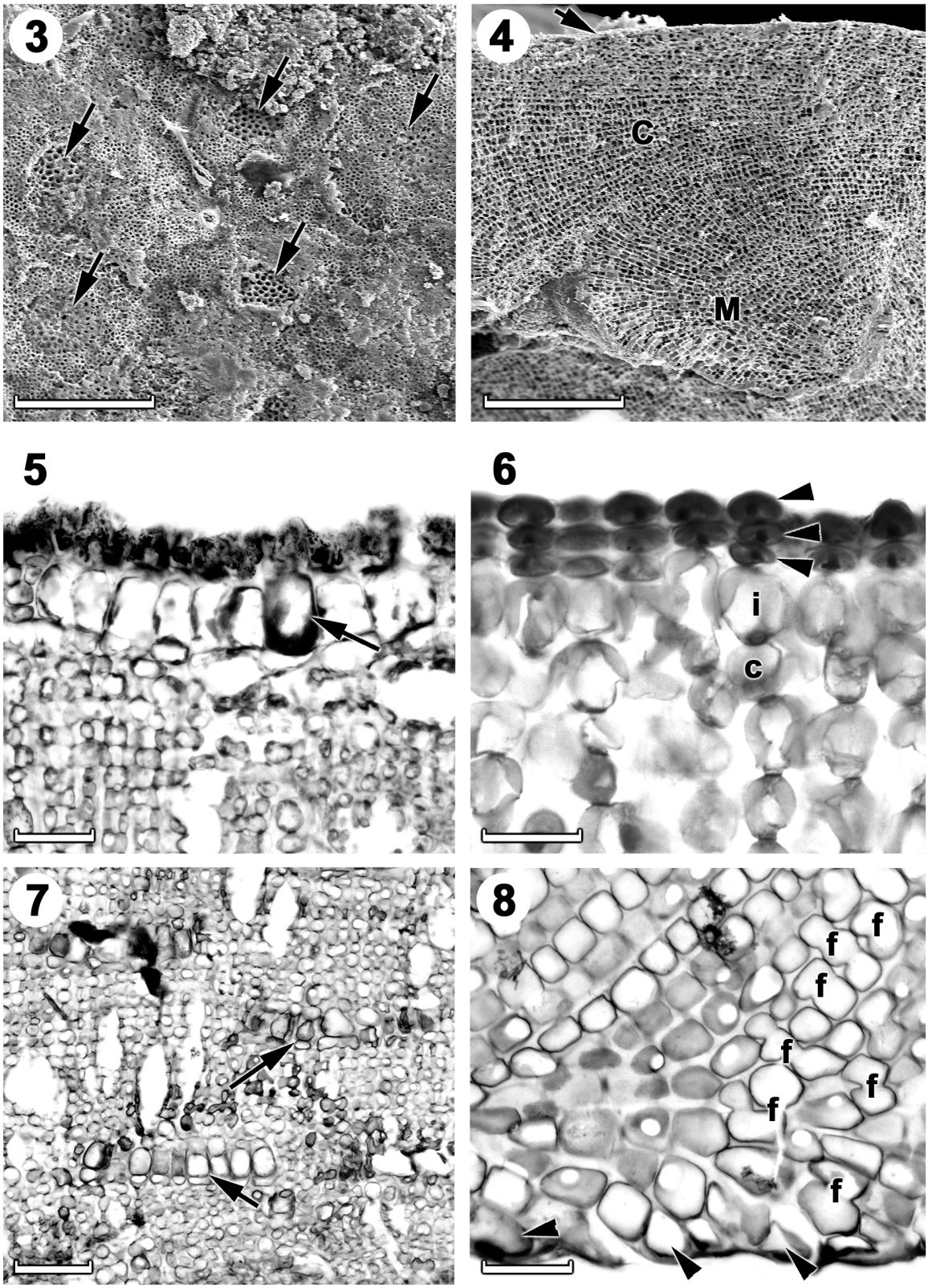


FIGURES 1–2. Lectotype of *Porolithon onkodes* (TRH A26-1494). **FIG. 1.** Slides and specimen fragments (scale bar = 20 mm). **FIG. 2.** Type specimen packaging (scale bar = 20 mm).

SOUTH AFRICA. KwaZulu-Natal: Sodwana Bay, Two mile Reef (21.i.1991, *D.W. Keats*, UWC COR/122; 24.i.1991, *D.W. Keats*, UWC COR/159; 3.vii.1991, *D.W. Keats*, UWC COR/324; 3.vii.1991, *D Keats*, UWC COR/326; 5.xi.1991, *D.W. Keats & Y.M. Chamberlain*, UWC 91/134; 7.xi.1991, *D.W. Keats & Y.M. Chamberlain*, UWC 91/169; 01.iii.2010, *L. Gersun & R.J. Anderson*, UCT M3A; 02.iii.2010, *L. Gersun & R.J. Anderson*, UCT M14A, UCT M18C); Five Mile Reef (24.i.1991, *D.W. Keats*, UWC COR/158; 2.vii.1991, *D.W. Keats*, UWC COR/314; 2.vii.1991, *D.W. Keats*, UWC COR/320).

TAIWAN. Hou Wan Bay, southern Taiwan (18.ix. 1998, *D.W. Keats, G.W. Maneveldt, J. Lewis & Jacson*, UWC 98/335; UWC 98/340); Long Dong (25.ix.1998, *D.W. Keats, G.W. Maneveldt, J. Lewis, Jacson & W. Wei Lung*, UWC 98/413).

TANZANIA. Bawi Island, Zanzibar (2.vii.1999, *D.W. Keats, G.W. Maneveldt & J. Kangwe*, UWC 99/114).



FIGURES 3–8. Vegetative anatomy of the lectotype of *Porolithon onkodes* (TRH A26-1494). **FIG. 3.** SEM of the thallus surface showing a number of pustulate, horozontal trichocyte fields (arrows) (scale bar = 200 μm). **FIG. 4.** Vertical fracture under SEM of a monomerous thallus showing the location of the epithallial cell layers (arrow) and cortical (C) and medullary filaments (M) (scale bar = 200 μm). **FIG. 5.** Vertical section of the dorsal region of the thallus through a single large trichocyte field (arrow) (scale bar = 30 μm). **FIG. 6.** Vertical section of the dorsal region of the thallus showing multiple layers of epithallial cells (arrowheads), a subepithallial initial (i) and a first cortical cell (c) (scale bar = 15 μm). **FIG. 7.** Vertical section of the thallus showing buried trichocyte fields (arrows) (scale bar = 60 μm). **FIG. 8.** Vertical section of the ventral region of the thallus showing a plumose medullary region terminating in elongate to domed-shaped inner epithallial cells (arrowheads) and bearing extensive cell fusions (f) between adjacent filaments (scale bar = 30 μm).

Distribution:—*Porolithon onkodes* is a subtropical to largely tropical species widely reported in the Indian, Pacific and eastern Atlantic Oceans, and occasionally also reported in the western Atlantic Ocean. See Guiry & Guiry (2013) for a detailed distribution list.

Appearance and vegetative structure:—The lectotype collection (Fig. 1) contains fragments that are adherent, measuring up to at least 2450 μm thick. Thalli are encrusting, smooth, lack protuberances and have adherent margins that are entire to lobed, but lack orbital ridges. Surface cells are thin to thick walled with centrally depressed centres, many bearing intact primary pit connections. The surface texture is matt and granular due to the presence of abundant tightly packed, pustulate, horizontally arranged trichocyte fields (Fig. 3).

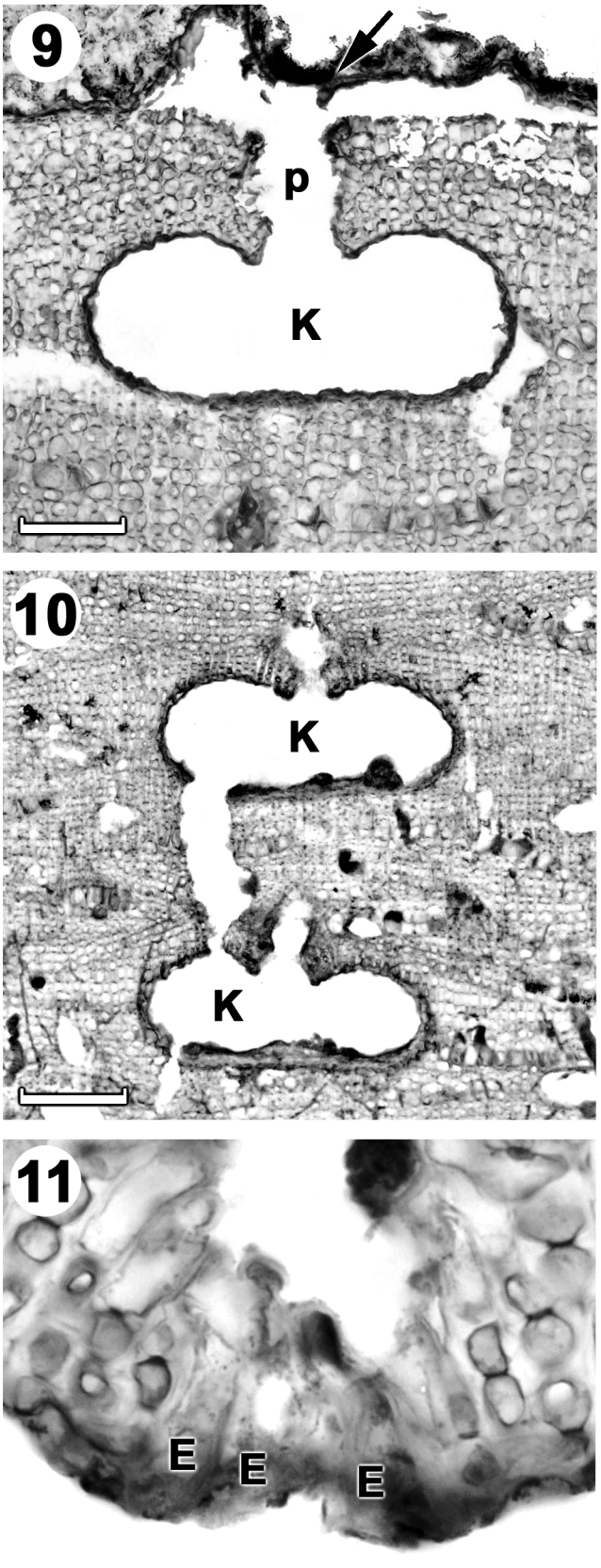
Lectotype thallus fragments are monomerous and dorsiventrally organised (Fig. 4). The medullary filaments comprise no more than 30 % of the thallus and consist of a central plumose (non-coaxial) core (Fig. 8), with cells that are squat to rectangular, 6–32 μm in length and 6–19 μm in diameter. Cortical filaments comprise the bulk of the thallus. Cells of cortical filaments are squat to rectangular, 5–15 μm in length and 5–16 μm in diameter. Subepithallial initials are squat to square, 6–12 μm in length and 6–12 μm in diameter. Epithallial cells are elliptical, 3–6 μm in length and 6–12 μm in diameter, and occur in 1–3 cell layers (mostly 2–3 but up to 5 when shedding) (Fig. 6). Fields of squarish to rectangular trichocytes commonly occur at the thallus surface in tightly packed pustulate horizontally arranged fields (Fig. 5). These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes are 15–43 μm in length and 11–21 μm in diameter. They are often overgrown and buried in the thallus in horizontal fields (Fig. 7). Cell fusions are abundant throughout the thallus; secondary pit connections were not seen. Data on measured characters in the lectotype are summarized in Table 1.

Features evident in the lectotype are also present in various other specimens examined (Figs 12–24). Thus thalli are monomerous, dorsiventrally organised, and have similar features and proportions (but greater ranges) of medullary and cortical filaments, subepithallial and epithallial cells, and trichocytes. Data on measured characters are summarized in Table 1. Greater variation, however, occurs in growth form across the species as a whole (Figs 12–14). Thalli are adherent, measuring up to at least 100 mm in diameter and 1–10 mm thick. Thalli are generally encrusting and smooth (Fig. 12) to warty (Fig. 13) to low lumpy when conforming to an irregular substratum. A hugely foliose, "honeycombed" form occurs in some shallow South Pacific coral reef areas in which upright lobes are produced (Fig. 14). At the bases of these upright lobes are found the tubular burrows of the chiton *Cryptoplax larvaeformis*. This growth form is evidently caused by growth in response to the grazing activities of the chiton (Littler & Littler 1999, 2003). Thallus colour is variable and generally pale greyish-pink in well-lit environments to deep pink or violet in low-light environments.

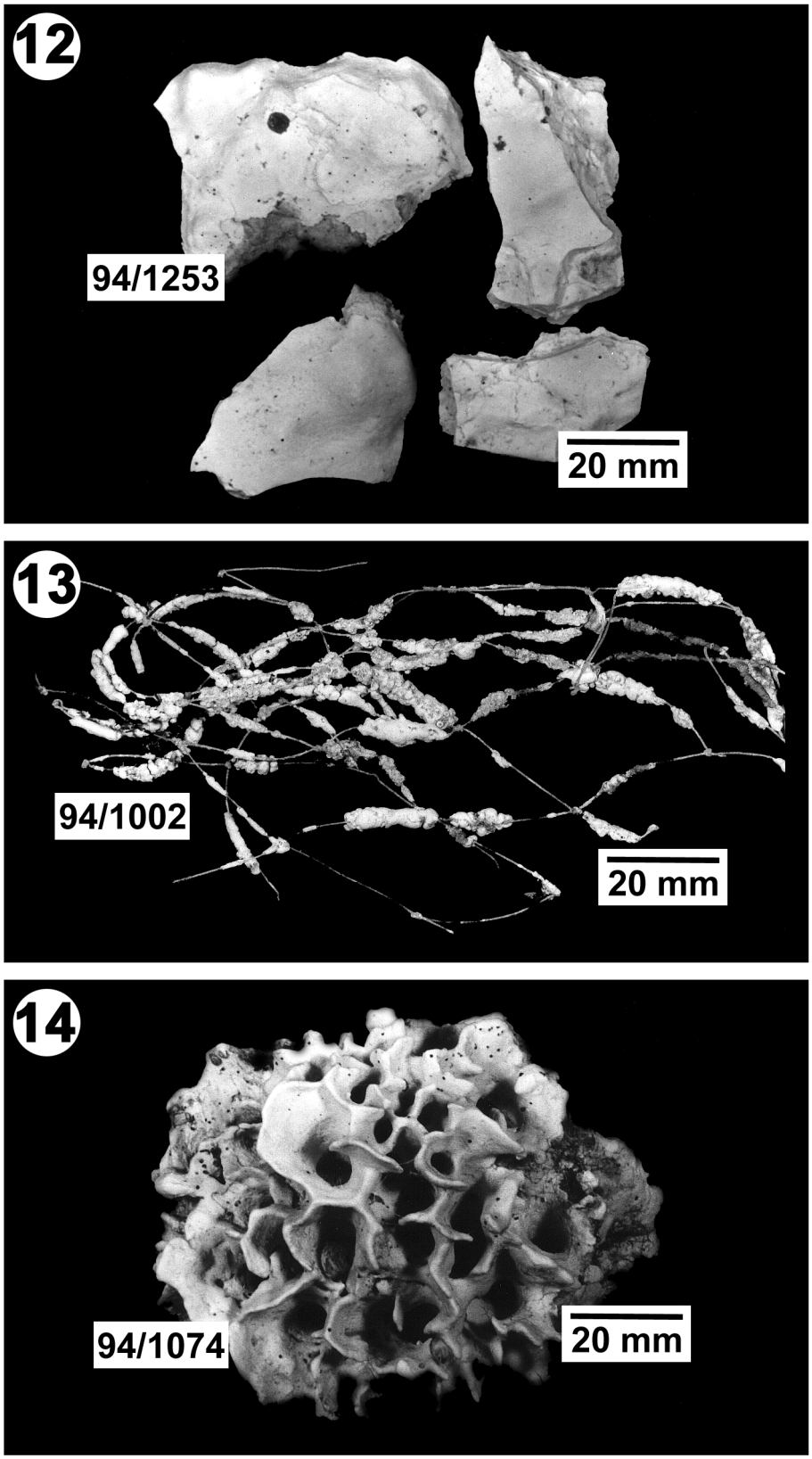
Reproduction:—The lectotype collection lacked gametangia, but did possess tetrasporangial material.

Tetrasporangial conceptacles are uniporate, more-or-less flush to only slightly raised above the surrounding thallus surface, measuring 205–400 μm in external diameter (Figs 9–10). Their chambers are elliptical to bean-shaped, 190–270 μm in diameter and 60–125 μm high, with the roof 43–74 μm (7–12 cells; incl. epithallial cell) thick. The conceptacle floor is located c. 18–19 cells below the surrounding thallus surface. No conceptacle primordia were found, but from the orientation of the conceptacle roof cells, it is presumed that the roof is formed from filaments peripheral to and interspersed among the tetrasporangial initials. A ring of enlarged, domed cells lines the base of the pore canal (Fig. 11). The pore-canal filaments are orientated more-or-less vertically, and do not project into the pore. There is a small central columella present (giving the conceptacle chamber its bean-shape), and zonately divided tetrasporangia are located peripheral to it. Tetrasporangia are 69–77 μm in length and 31–38 μm in diameter. Bisporangia were not seen. Tetrasporangial conceptacles often become buried in the thallus (Fig. 10) and often contain tetrasporangia; infilled conceptacles have not been observed. Data on measured reproductive characters in the lectotype are summarized in Table 2.

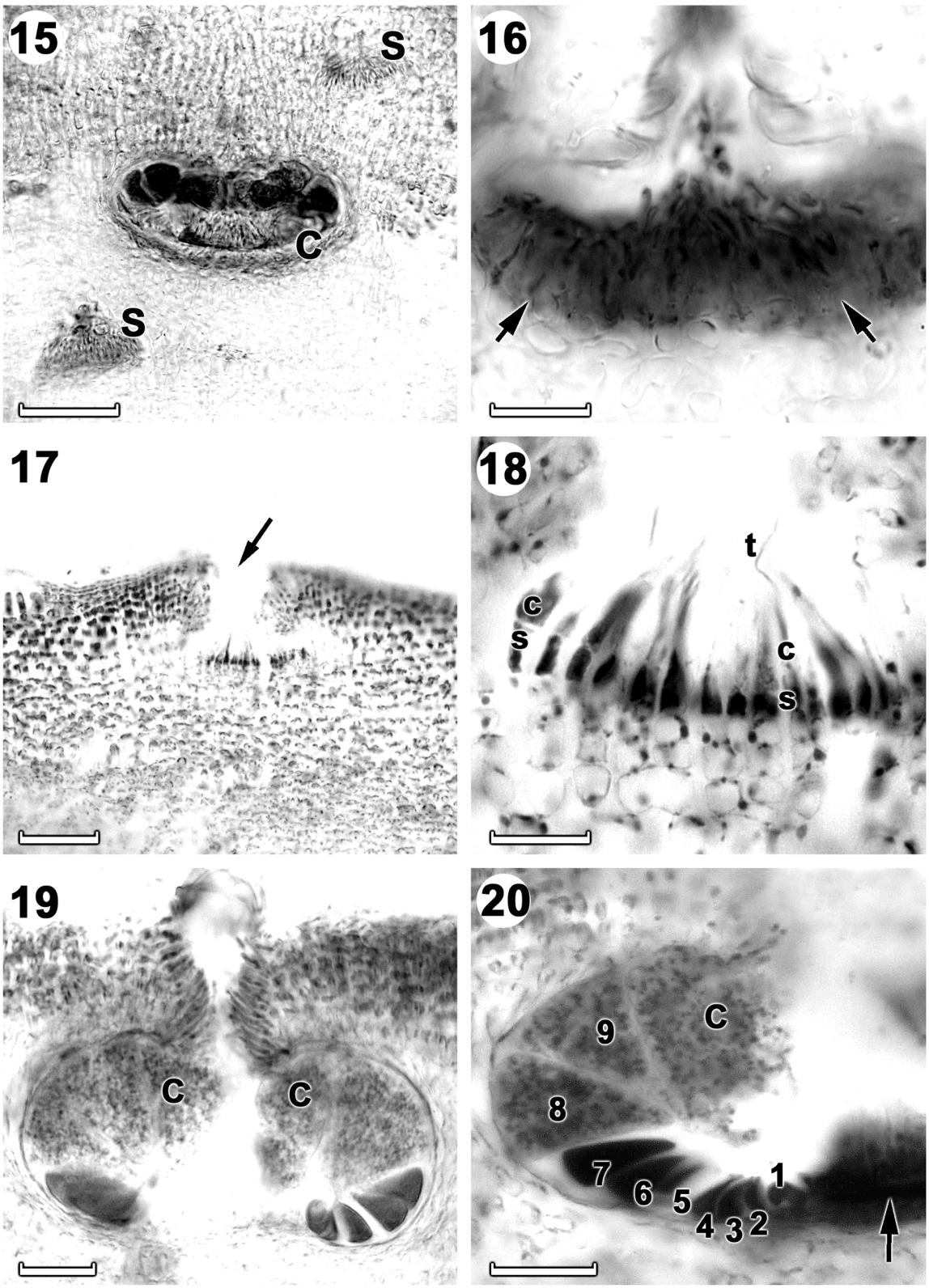
Representative specimens examined show that thalli may be monoecious (Fig. 15) or dioecious (Table 2). Spermatangial (male) conceptacles are generally small (Figs 15, 16) measuring about 120–275 μm in external diameter. Their roofs are usually more-or-less flush with the surrounding thallus surface, but are sometimes slightly raised, and they usually possess a small spout. The conceptacle chamber is wide and shallow to elliptical, 80–150 μm in diameter and 25–60 μm high, with the roof 19–37 μm thick; some buried conceptacles were found to have chambers measuring up to 315 μm in diameter. Spermatangial conceptacles are often seen buried in the thallus (Fig. 15). Simple spermatangial systems are borne only on the floor of the conceptacle chamber (Fig. 16).



FIGURES 9–11. Sporangial anatomy of the lectotype of *Porolithon onkodes* (TRH A26-1494). **FIG. 9.** Vertical section of the dorsal region of the thallus showing a single flush tetrasporangial conceptacle (K) with shedding layer of epithallial cells (arrow) and exposed pore canal (P) (scale bar = 60 µm). **FIG. 10.** Vertical section of the thallus showing buried, un-infilled tetrasporangial conceptacles (K) (scale bar = 150 µm). **FIG. 11.** Vertical section through the pore canal of a sunken tetrasporangial conceptacle showing the presence of a ring of enlarged cells (E) located at the base of the pore canal (scale bar = 15 µm).



FIGURES 12–14. Variable morphology of *Porolithon onkodes*. **FIG. 12.** Fragments of an epilithic and encrusting growth form (UWC 94/1253). **FIG. 13.** An encrusting to warty growth form on a fishing line (UWC 94/1002). **FIG. 14.** Dorsal view of a three-dimensional, hugely foliose, "honeycombed" growth form in which upright lobes are produced, at the bases of which are found the tubular burrows of the chiton *Cryptoplax larvaeformis* (UWC 94/1074).



FIGURES 15–20. Gametangial anatomy of *Porolithon onkodes*. **FIG. 15.** Vertical section of a monoecious thallus showing buried spermatangial (S) and carposporangial (C) conceptacles (UWC 94/1269) (scale bar = 60 μm). **FIG. 16.** Section through a spermatangial conceptacle showing simple spermatangial structures restricted to the conceptacle floor (arrows) (UWC COR/122) (scale bar = 15 μm). **FIG. 17.** Section through a slightly raised carpogonial conceptacle (arrow) (UWC COR/122) (scale bar = 60 μm). **FIG. 18.** Magnified view through a carpogonial conceptacle showing carpogonial branches distributed across the conceptacle floor bearing terminal trichogynes (t) subtended by a carpogonium (c) and a support cell (s) (UWC COR/122) (scale bar = 15 μm). **FIG. 19.** Section through a carposporangial conceptacle showing peripherally located gonimoblast filaments terminating in carpospores (C) (UWC COR/122) (scale bar = 30 μm). **FIG. 20.** Section through the periphery of a carposporangial conceptacle chamber showing a continuous solid discoid fusion cell (arrow), and a gonimoblast filament bearing 10 cells (numbered 1–9), including a terminal carpospore (C) (UWC COR/122) (scale bar = 30 μm).

TABLE 1. A comparison of the appearance and vegetative structure of the taxa under study compared against those of previously published, detailed records. Data from previously published records have been taken from both the descriptions and the figures. Unless otherwise stated, all measurements are in micrometres. ND = no data provided.

Character	*H. onkodes* (Penrose and Woelkerling 1988, 1992)	*H. onkodes* (Keats and Chamberlain 1994)	*P. onkodes* (lectotype)	*P. onkodes* (representative specimens)	*P. antillarum* (isotypes)
Growth form	encrusting	encrusting to slightly lumpy	encrusting	encrusting to warty to slightly lumpy to hugely foliose ("honeycombed")	hugely foliose ("honeycombed")
Primary thallus construction	monomerous and plumose	monomerous and plumose	monomerous and plumose	monomerous and plumose	monomerous and plumose
Contiguous filaments joined by …	cell fusions	cell fusions	cell fusions	cell fusions	cell fusions
Trichocyte arrangement	horizontal fields, singly	horizontal fields	horizontal fields	horizontal fields	horizontal fields
Individual trichocytes separated by normal vegetative filaments	Those in fields, NO	NO	NO	NO	NO
Trichocyte shape	ND	square to elongate	square to rectangular	square to elongate	square to rectangular
Trichocyte dimensions (L = length; D = diameter)	ND	L: 21–43; D: 9–21	L: 15–43; D: 11–21	L: 15–45; D: 6–25	L: 14–41; D: 6–21
Trichocytes buried	YES	YES	YES	YES	YES
No. of layers of epithallial cells	1–3	1–3	1–3(5)	1–3(5)	1–3(5)
Epithallial cell shape	ND	squat to elliptical	elliptical	squat to elliptical	squat to elliptical
Epithallial cell dimensions (L = length; D = diameter)	L: 3; D: 8–12	L: 2–5; D: 3–7	L: 3–6; D: 6–12	L: 2–7; D: 3–12	L: 3–7; D: 6–12
Subepithallial cell shape	ND	square to elongate	squat to square	square to rectangular	squat to square
Subepithallial cell dimensions (L = length; D = diameter)	ND	L: 4–11; D: 4–7	L: 6–12; D 6–12	L: 4–18; D 4–12	L: 4–19; D 6–12
Cortical cell shape	ND	ND	squat to rectangular	squat to rectangular	square to rectangular
Cortical cell dimensions (L = length; D = diameter)	L: 7–18; D: 6–15	L: 5–15; D: 4–10	L: 5–15; D: 5–16	L: 5–20; D: 4–16	L: 5–17; D: 5–12
Medullary cell shape	ND	ND	squat to rectangular	squat to elongate	square to elongate
% medulla is of thallus	ND	ND	≤ 30	≤ 33	≤ 44
Medullary cell dimensions (L = length; D = diameter)	L: 14–22; D: 8–13	L: 13–45; D: 6–12	L: 6–32; D: 6–19	L: 5–45; D: 5–25	L: 5–45; D: 5–15

..... continued on the next page

TABLE 1 (continued)

Character	*P. cocosicum* (holotype)	*P. sandvicense* (holotype)	*P. pachydermum* (isolectotype)	*P. pachydermum* (representative specimen)
Growth form	encrusting to slightly lumpy	hugely foliose ("honeycombed")	encrusting	encrusting to slightly lumpy
Primary thallus construction	monomerous and plumose	monomerous and plumose	monomerous and plumose	monomerous and plumose
Contiguous filaments joined by …	cell fusions	cell fusions	cell fusions	cell fusions
Trichocyte arrangement	horizontal fields	horizontal fields	horizontal fields	horizontal fields
Individual trichocytes separated by normal vegetative filaments	NO	NO	NO	NO
Trichocyte shape	square to elongate	square to rectangular	square to rectangular	square to elongate
Trichocyte dimensions (L = length; D = diameter)	L: 15–37; D: 9–20	L: 14–31; D: 9–25	L: 15–38; D: 7–22	L: 15–46; D: 7–27
Trichocytes buried	YES	YES	YES	YES
No. of layers of epithallial cells	1–3(5)	1–3(5)	1–3	1–3(5)
Epithallial cell shape	squat to elliptical	squat to elliptical	squat to elliptical	squat to elliptical
Epithallial cell dimensions (L = length; D = diameter)	L: 4–7; D: 5–12	L: 3–6; D: 5–11	L: 3–6; D: 5–12	L: 3–7; D: 5–12
Subepithallial cell shape	square to rectangular	square	square	square to rectangular
Subepithallial cell dimensions (L = length; D = diameter)	L: 6–19; D 5–12	L: 6–11; D 5–10	L: 5–12; D 5–12	L: 5–19; D 5–12
Cortical cell shape	square to rectangular	square to rectangular	square to rectangular	square to rectangular
Cortical cell dimensions (L = length; D = diameter)	L: 5–21; D: 5–12	L: 4–19; D: 6–12	L: 6–17; D: 4–12	L: 5–17; D: 4–12
Medullary cell shape	square to rectangular	square to rectangular	square to rectangular	square to rectangular
% medulla is of thallus	≤ 52	≤ 31	≤ 30(86)	≤ 33(86)
Medullary cell dimensions (L = length; D = diameter)	L: 6–25; D: 6–15	L: 6–26; D: 4–15	L: 6–31; D: 4–15	L: 6–31; D: 4–25

Carpogonial conceptacles are small and inconspicuous (Fig. 17) measuring only 110–175 μm in external diameter. Their roofs are more-or-less flush with the surrounding thallus surface. Conceptacle chambers are flask-shaped, 35–99 μm in diameter and 18–45 μm high. Chambers are usually found near the thallus surface but sometimes sunken to 62 μm deep, with a long pore canal leading to the surface. Three-celled carpogonial branches occur centrally on the chamber floor (Fig. 18). Completely immersed conceptacles containing carpogonia are commonly observed in thallus sections. Carposporangia develop in carpogonial conceptacles after presumed karyogamy.

Carposporangial conceptacles are relatively large, measuring 250–580 μm in external diameter (Fig. 19). Their roofs are flush with the surrounding thallus surface to slightly raised above it. Conceptacle chambers are elliptical to bean-shaped, 130–345 μm in diameter and 50–110 μm high with the roof 18–50 μm thick. The pore canal is lined with small filaments. The continuous central fusion cell is narrow and thick (discoid), with gonimoblast filaments borne peripherally (Fig. 20). Gonimoblast filaments are 5–11 (mostly 9–11) cells long including a terminal carpospore, 30–62 μm in length and 30–65 μm in diameter. Mature carpospores almost fill the conceptacle chamber.

TABLE 2. A comparison of the reproductive structure of the taxa under study compared against those of previously published, detailed records. Data from previously published records have been taken from both the descriptions and the figures. All measurements are in micrometres. ND = no data provided.

Character	*H. onkodes* (Penrose and Woelkerling 1992)	*H. onkodes* (Keats and Chamberlain 1994)	*P. onkodes* (lectotype)	*P. onkodes* (representative specimens)
Position of sporangial conceptacle relative to surrounding vegetative surface	slightly raised to flush	slightly raised to flush	slightly raised to flush	slightly raised to flush
Mature sporangial conceptacle external diameter	ND	ND	205–400	190–625
Mature sporangial conceptacle chamber diameter	245	115–250	190–270	115–380
Mature sporangial conceptacle chamber height	c. 60	60–130	60–125	55–170
Thickness of mature sporangial conceptacle roof	ND	40–55	43–74	25–75
No. of cells (incl. epithallial cells) in mature sporangial conceptacle roof filaments	3–9[1]	ND	7–12	5–12
Depth (no. of cells) of mature sporangial conceptacle floor	ND	ND	18–19	12–19
Sporangial conceptacle roof formation	from filaments surrounding and interspersed among the sporangial initials	from filaments surrounding and interspersed among the sporangial initials	from filaments surrounding and interspersed among the sporangial initials	from filaments surrounding and interspersed among the sporangial initials
Shape of sporangial conceptacle pore canal cells	enlarged	enlarged	enlarged	enlarged
Orientation of sporangial conceptacle pore canal cells	perpendicular to roof	perpendicular to roof	perpendicular to roof	perpendicular to roof
Sporangial conceptacle pore canal cells project into pore?	NO	NO	NO	NO
Sporangia dimensions	L: 56–80;	L: 25–120;	L: 69–77;	L: 25–120;
(L = length; D = diameter)	D: 22–32	D: 12–53	D: 31–38	D: 10–75
Sporangia arrangement	peripheral	peripheral	peripheral	peripheral
Central columella	present	present	present	present
Gametangial thalli	none seen	monoecious or dioecious	none seen	monoecious or dioecious
Spermatangial conceptacle external diameter	-	ND	-	120–275
Spermatangial conceptacle chamber diameter	-	185–314	-	80–150(315)
Spermatangial conceptacle chamber height	-	24–60	-	25–60
Spermatangia type	-	simple	-	simple
Arrangement of spermatangia	-	restricted to floor	-	restricted to floor
Carpogonial conceptacle external diameter	-	ND	-	110–175
Carpogonial conceptacle chamber diameter	-	37–95	-	35–99
Carpogonial conceptacle chamber height	-	18–40	-	18–45
No. of cells in carpogonial branches	-	3	-	3
Carposporangial conceptacle external diameter	-	ND	-	250–580
Carposporangial conceptacle chamber diameter	-	135–225	-	130–345
Carposporangial conceptacle chamber height	-	66–82	-	50–110
Shape of fusion cell	-	discoid and continuous	-	discoid and continuous
Arrangement of gonimoblast filaments	-	peripheral	-	peripheral
No. of cells in gonimoblast filament (incl. carpospore)	-	5–9	-	5–11
Carpospore dimentions	-	L: 30–62;	-	L: 30–62;
(L = length; D = diameter)		D: 60–63		D: 30–65

..... continued on the next page

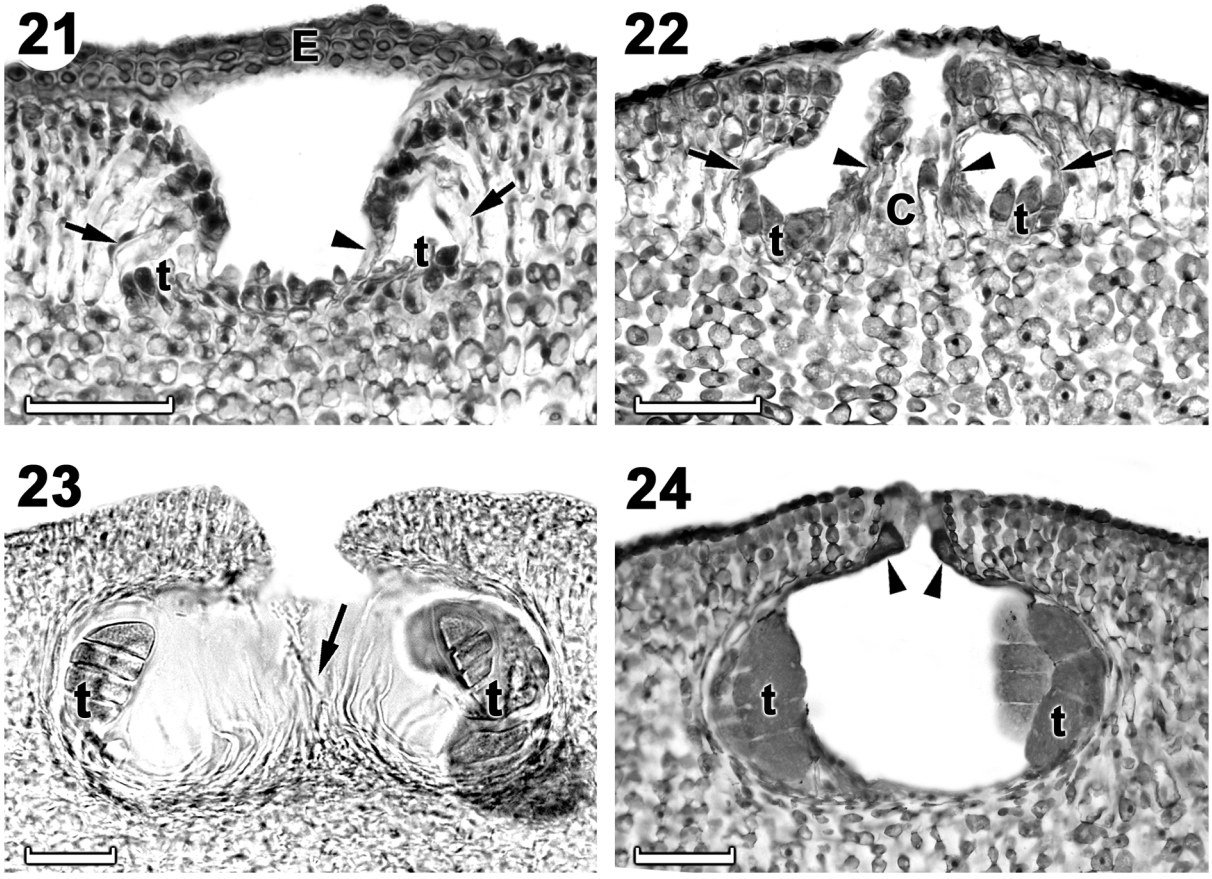
TABLE 2 (continued).

Character	*P. antillarum* (isotypes)	*P. cocosicum* (holotype)	*P. sandvicense* (holotype)	*P. pachydermum* (isolectotype)	*P. pachydermum* (representative specimen)
Position of sporangial conceptacle relative to surrounding vegetative surface	slightly raised to flush	slightly raised to flush to slightly sunken	slightly raised to flush	slightly raised to flush	slightly raised to flush
Mature sporangial conceptacle external diameter	300–500	275–450	250–400	450–675	250–675
Mature sporangial conceptacle chamber diameter	187–375	175–300	135–225	145–290	125–290
Mature sporangial conceptacle chamber height	50–180	60–150	70–100	50–170	50–170
Thickness of mature sporangial conceptacle roof	43–74	43–56	22–37	31–51	31–68
No. of cells (incl. epithallial cells) in mature sporangial conceptacle roof filaments	5–11	7–11	5–12	6–11	6–11
Depth (no. of cells) of mature sporangial conceptacle floor	13–19	12–20	12–18	13–19	9–19
Sporangial conceptacle roof formation	from filaments surrounding and interspersed among the sporangial initials	from filaments surrounding and interspersed among the sporangial initials	from filaments surrounding and interspersed among the sporangial initials	from filaments surrounding and interspersed among the sporangial initials	from filaments surrounding and interspersed among the sporangial initials
Shape of sporangial conceptacle pore canal cells	enlarged	enlarged	enlarged	enlarged	enlarged
Orientation of sporangial conceptacle pore canal cells	perpendicular to roof	perpendicular to roof	perpendicular to roof	perpendicular to roof	perpendicular to roof
Sporangial conceptacle pore canal cells project into pore?	NO	NO	NO	NO	NO
Sporangia dimensions	L: 37–155;	L: 35–99;	L: 37–78;	L: 31–87;	L: 31–87;
(L = length; D = diameter)	D: 15–93	D: 15–53	D: 12–31	D: 9–47	D: 9–47
Sporangia arrangement	peripheral	peripheral	peripheral	peripheral	mostly peripheral
Central columella	present	none seen	present	present	present
Gametangial thalli	dioecious ?	monoecious	none seen	none seen	none seen
Spermatangial conceptacle external diameter	none seen	125–200	-	-	-
Spermatangial conceptacle chamber diameter	-	93–155	-	-	-
Spermatangial conceptacle chamber height	-	22–37	-	-	-
Spermatangia type	-	simple	-	-	-
Arrangement of spermatangia	-	restricted to floor	-	-	-
Carpogonial conceptacle external diameter	none seen	none seen	-	-	-
Carpogonial conceptacle chamber diameter	-	-	-	-	-
Carpogonial conceptacle chamber height	-	-	-	-	-
No. of cells in carpogonial branches	-	-	-	-	-
Carposporangial conceptacle external diameter	335–600	300–450	-	-	-
Carposporangial conceptacle chamber diameter	160–240	175–374	-	-	-
Carposporangial conceptacle chamber height	40–100	56–109	-	-	-
Shape of fusion cell	discoid and continuous	discoid and continuous	-	-	-
Arrangement of gonimoblast filaments	peripheral	peripheral	-	-	-
No. of cells in gonimoblast filament (incl. carpospore)	?	9–11	-	-	-
Carpospore dimentions	L: 35–50;	L: 31–62;	-	-	-
(L = length; D = diameter)	D: 35–55	D: 31–43			

[1] It is unclear whether the epithallial cells have been included here.

Tetrasporangial features evident in the lectotype are also present in the various specimens examined and are summarized in Table 2. Greater variation, however, exists in the ranges of the measurements for this species as a whole. Unlike the lectotype for which conceptacle primordia was lacking, representative specimens clearly show conceptacle roof formation from filaments peripheral to the fertile area and from filaments interspersed among the tetrasporangial initials (Figs 21, 22). Similarly, a ring of enlarged, domed cells lines the base of the pore canal (Fig. 24) and the pore-canal filaments are orientated more-or-less vertically, and do not project into the pore. A central columella forms early in the development of the tetrasporangial conceptacle (Fig. 22), persists while the tetrasporangia mature (Fig. 23), but becomes much reduced or is entirely lost in mature conceptacles (Fig. 24). Conceptacles of all reproductive types were observed in the various representative specimens throughout the year.

Ecological observations:—The data presented here pertains mostly to representative specimens in UWC examined during the present study and thus refers to new observations.



FIGURES 21–24. Tetrasporangial anatomy of *Porolithon onkodes*. **FIG. 21.** Section through a young tetrasporangial conceptacle showing early roof development from filaments peripheral to the fertile arrow (arrows) and from filaments interspersed (arrowhead) among the sporangial initials (t). A multiple layer of epithallial cells (E) still persists as a protective covering over the developing conceptacle (UCT M18C) (scale bar = 50 μm). **FIG. 22.** Section through a young tetrasporangial conceptacle showing more advanced roof development from filaments peripheral to the fertile arrow (arrows) and from filaments interspersed (arrowheads) among the sporangial initials (t). Note the formation of a prominent central columella (C) (UCT M14A) (scale bar = 50 μm). **FIG. 23.** Section through a near mature tetrasporangial conceptacle showing zonately divided tetrasporangia (t) peripherally arranged around a prominent central columella (arrow) (UWC 94/1175) (scale bar = 30 μm). **FIG. 24.** Section through a more mature tetrasporangial conceptacle showing peripherally arranged, zonately divided tetrasporangia (t). The central columella is no longer visible in this older conceptacle. Note too the enlarged cells (arrowheads) lining the base of the pore canal (UCT M18C) (scale bar = 50 μm).

Porolithon onkodes is one of the most common corallines in the shallower areas of coral reefs (< 15 m), where it occurs on dead coral skeletons and other hard substrata (*pers. obs.*). It commonly occurs within a mixture of species belonging to the genera *Hydrolithon*, *Neogoniolithon*, *Pneophyllum, Porolithon*, *Lithophyllum* and *Titanoderma* within which *P. onkodes* is sometimes as abundant as all the other species taken together. It is frequently the dominant coralline on the intertidal areas of exposed reefs. The surface is usually grazed by sea urchins, chitons, limpets, and commonly shows deep bites from parrotfish feeding.

Remarks:—Data on the type material presented here are in greater detail, but those in common are more or less concordant with that presented in Penrose & Woelkerling (1988) with only minor differences (see Table 1). This is to be expected, as the study by Penrose & Woelkerling (1988) was aimed only at showing that differences in trichocyte occurrence and arrangement, basal region organisation and cell size, could not be used to delimit genera within the *Spongites* complex (which included the genera *Hydrolithon* and *Porolithon*); their aim was not to provide a complete description of the type material. As far as we can determine, the only major difference between the two studies is the reporting of trichocytes occurring singly in the observations by Penrose & Woelkerling (1988) (see also Penrose 1996) whereas in our study, trichocytes commonly occured in tightly packed pustulate horizontally arranged fields. We had also observed what appeared to be individually occurring trichocytes, but in serial sections, these proved to be trichocytes occurring at the periphery of the horizontal trichocyte fields. The individual trichocytes reported by Penrose & Woelkerling (1988), as well as Penrose (1996), possibly refer to similar such observed trichocytes.

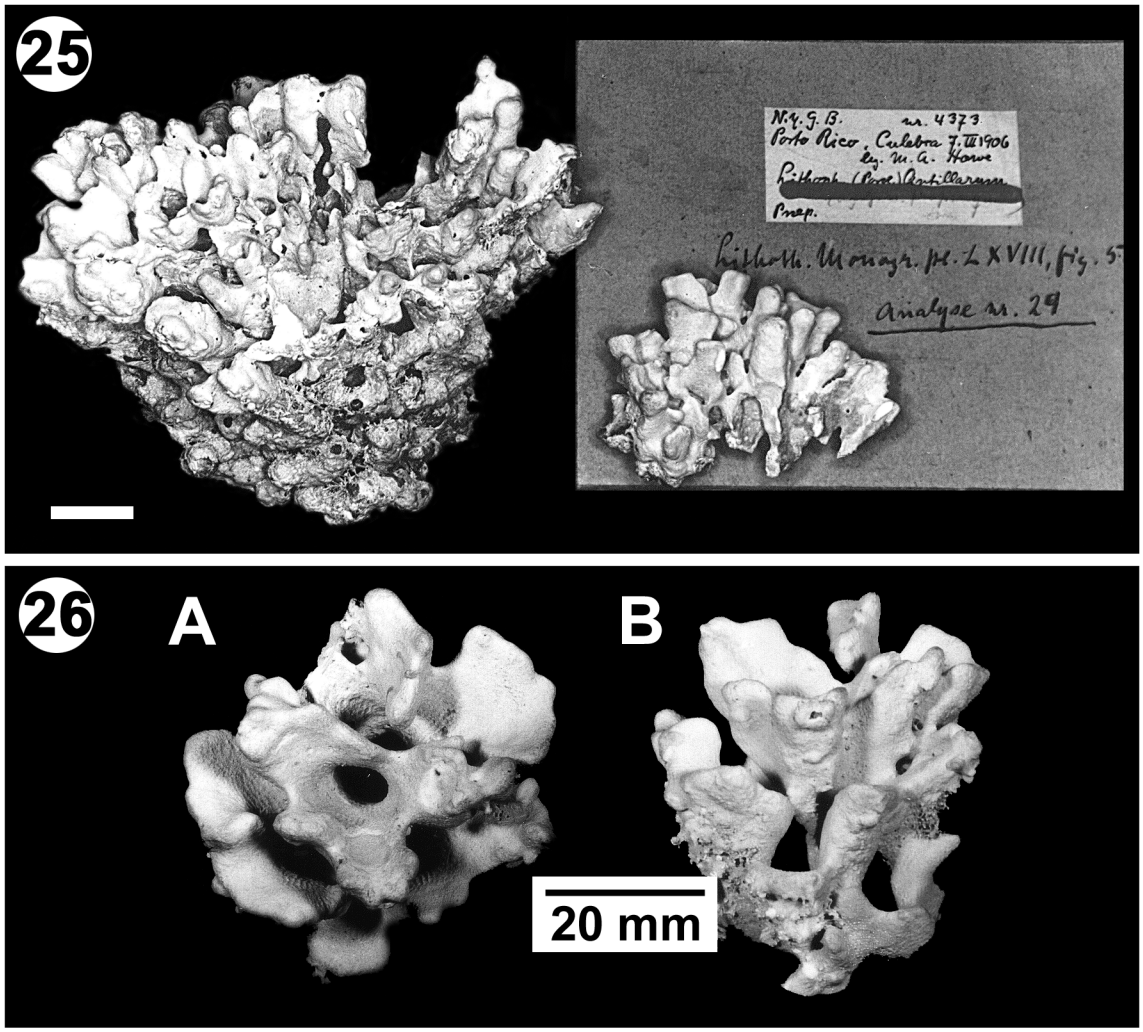
Porolithon antillarum (Foslie & M.A.Howe) Foslie, 1909: 57
(Figs 25–38)

Basionym:—*Lithophyllum antillarum* Foslie & Howe, 1906: 579.
Synonyms:—None.
Holotype:—NY. Culebra, Puerto Rico; Howe no. 4373. Previous references to typification were by Adey & Lebednik 1967: 47 (as *Lithophyllum*), Adey 1970: 10 (as *Porolithon*), Tittley *et al*. 1984: 8, Woelkerling 1993: 28 and Woelkerling & Lamy 1998: 300.
Isotype:—NY, PC & TRH! (A27-1565). Culebra, Puerto Rico; Howe no. 4373; BM!, algal collection box 899.

Etymology:—"*antillarum*", *antill* referring to the Antilles, the group of islands in the Caribbean Sea + *arum* = of (Stearn 1973). Foslie & Howe (1906) did not explain the origin of the epithet, but it presumably makes reference to the type locality within the Antilles.

Distribution:—*Porolithon antillarum* is reported from the tropical and subtropical western Atlantic Ocean (Foslie & Howe 1906, Taylor 1960, Wynne 2011).

Appearance and vegetative structure:—The following combined description is based on the isotype collections from TRH (Fig. 25) and BM (Fig. 26); no representative specimens for this taxon were available for verification. The isotype collections contain fragments that are hugely foliose, bearing lobes measuring up to 105 mm in height and 114 mm in diameter. Grazing scars are very obvious features of the surfaces of the fragments. Encrusting portions of the thalli are generally flat and measure up to 900 μm thick, lack protuberances and have adherent to free margins that are entire to lobed, but lack orbital ridges. Lobed portions of the thalli measure up to 7 mm thick, up to 26 mm in width and up to 38 mm in height. Surface cells are generally thick walled with shallow to deep concave centers, many bearing intact primary pit connections. The surface is course and granular due to the presence of abundant grazing scars and tightly packed, pustulate, horizontally arranged trichocyte fields (Fig. 27). The thallus is monomerous and dorsiventrally organised (Figs 28, 31). Medullary filaments comprise roughly 17–44 % of the thallus thickness and consist of a central plumose (non-coaxial) core (Figs 28, 31). Cells of medullary filaments are square to elongate, 5–45 μm in length and 5–15 μm in diameter. When a thallus bearing an extremely thin medullary region is sectioned parallel to the growing edge, a falsely dimerous thallus is often observed (Fig. 32). In the lobes, the medullary filaments are generally coaxial. The cortex is relatively thick (up to 83 % of the thallus). Cells of cortical filaments are square to rectangular, 5–17 μm in length and 5–12 μm in diameter. Subepithallial initials are square to rectangular, 4–19 μm in length and 6–12 μm in diameter. Epithallial cells are squat to elliptical, 3–7 μm in length and 6–12 μm in diameter, and occur in 1–3 cell layers (mostly 2–3 but up to 5 when shedding) (Fig. 29). Fields of squarish to rectangular trichocytes (Fig. 28) commonly occur at the thallus surface in tightly packed, pustulate horizontally arranged fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes are 14–41 μm in length and 6–21 μm in diameter. They are often overgrown and buried in the thallus in horizontally arranged fields (Fig. 30). Cell fusions are abundant throughout the thallus; secondary pit connections were not seen. Data on combined measured characters in the isotypes are summarized in Table 1.

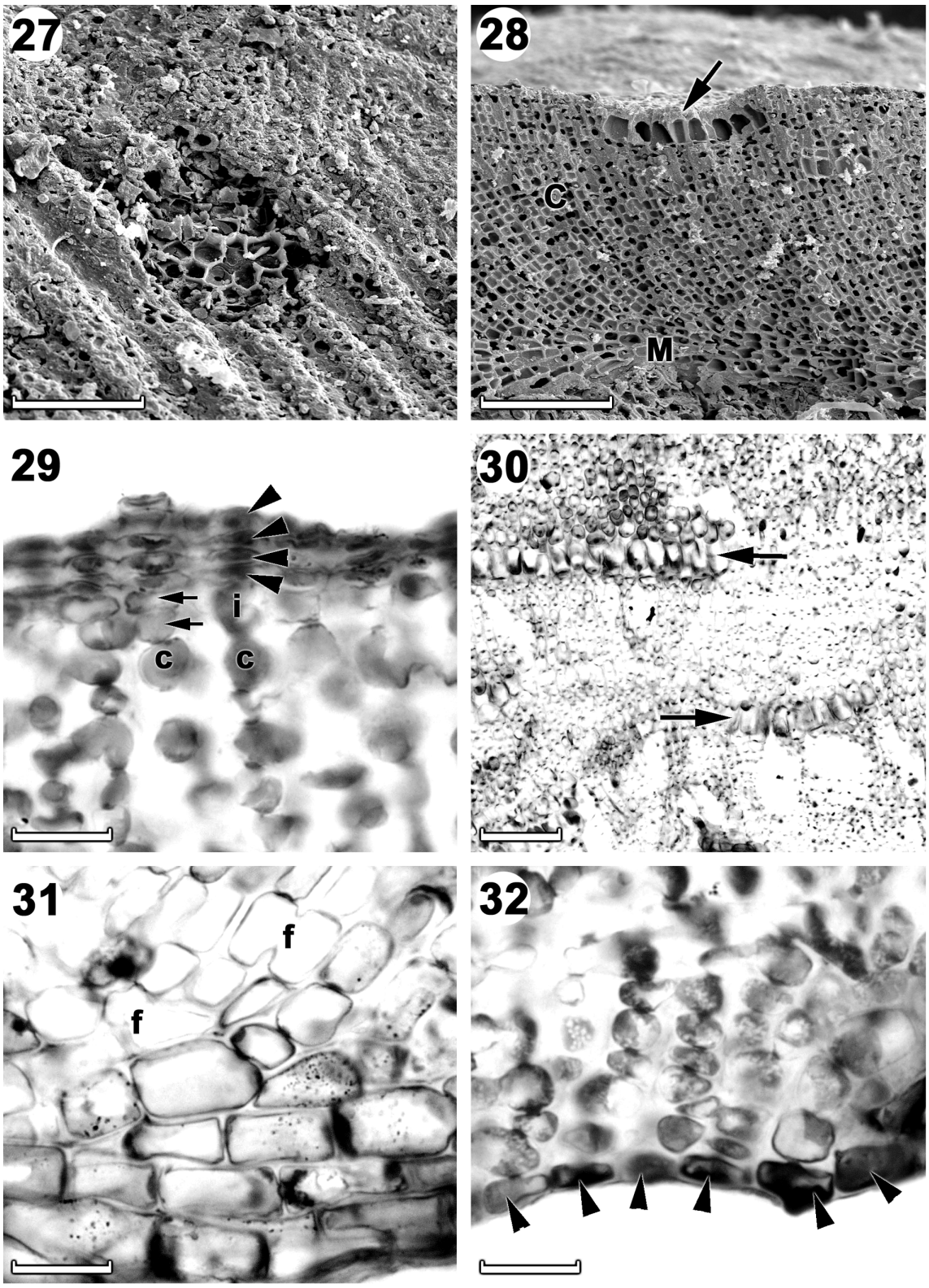


FIGURES 25–26. Morphology of the *Porolithon antillarum* isotypes. **FIG. 25.** Isotype from TRH (A27-1565) (scale bar = 20 mm). **FIG. 26.** Isotype from BM (899). A. Dorsal view. B. Lateral view of the same fragment in A.

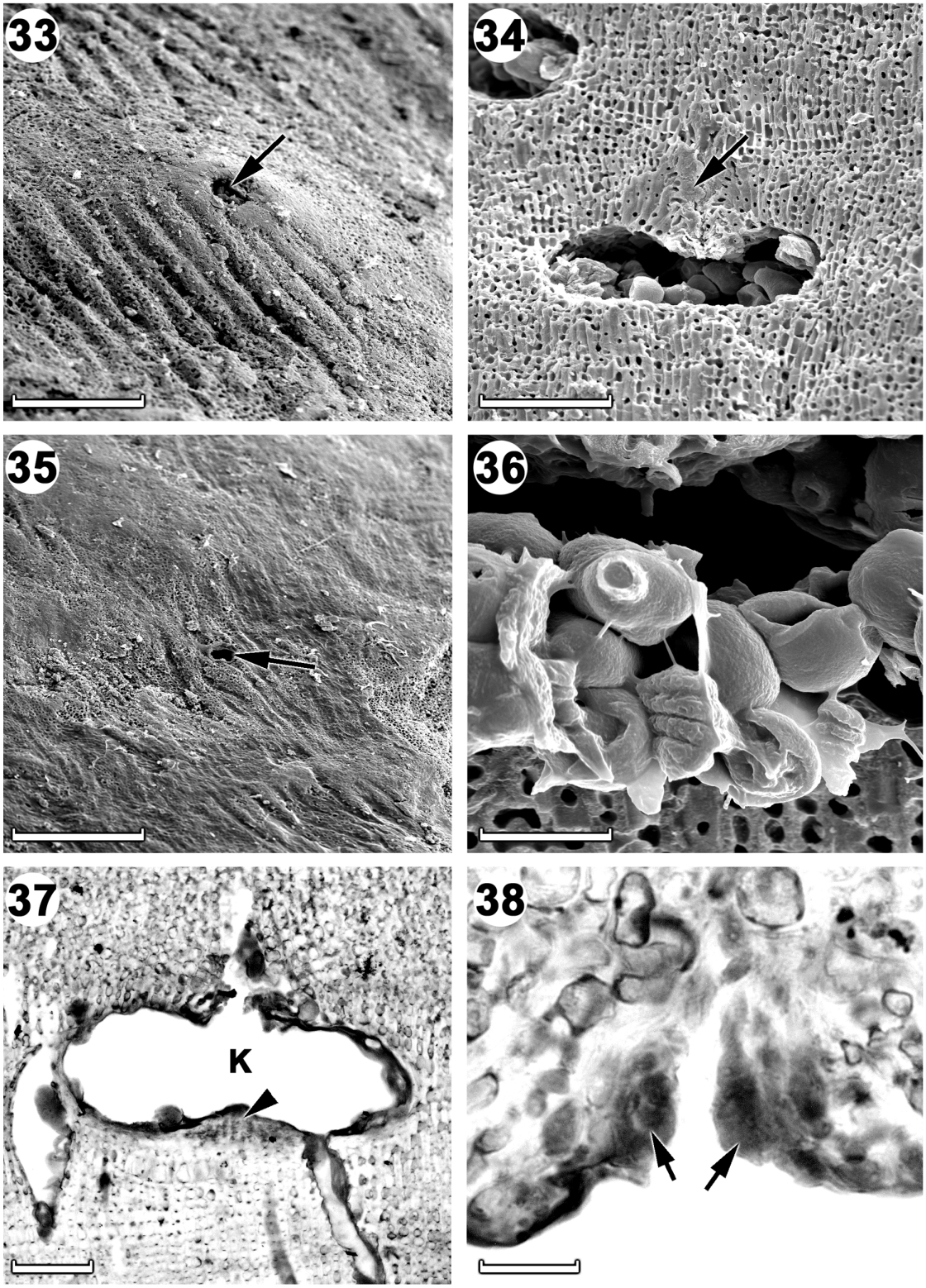
Reproduction:—Although spermatangial and carpogonial thalli were not seen, gametangial thalli appear to be dioecious.

Carposporangial conceptacles are flush to slightly raised above the thallus surface, are large and measure 335–600 μm in external diameter (Fig. 33). Their chambers are bean-shaped, 160–240 μm in diameter and 40–100 μm high with the roof 43–55 μm thick. The pore canal is lined with papillate filaments (Fig. 34). The continuous central fusion cell is narrow and thick (discoid), with gonimoblast filaments borne peripherally. Intact gonimoblast filaments were not found. Carpospores measures 35–50 μm in length and 35–55 μm in diameter. Mature carpospores almost fill the conceptacle chamber.

Tetrasporangial conceptacles are more-or-less flush, but also slightly sunken to slightly raised above the rest of the thallus and measure 300–500 μm in external diameter (Fig. 35). Their chambers are elliptical to bean-shaped, 187–375 μm in diameter and 50–180 μm high, with the roof 43–74 μm (5–11 cells; incl. epithallial cell) thick. The conceptacle floor is located 13–19 cells below the surrounding thallus surface. No conceptacle primordia were found, but from the orientation of the conceptacle roof cells, it is presumed that the roof is formed from filaments peripheral to and interspersed among the tetrasporangial initials. A ring of enlarged, domed cells lines the base of the pore canal (Fig. 38). The pore-canal filaments are orientated more-or-less vertically, and do not project into the pore. Through secondary overgrowth, however, buried conceptacles may bear papillate cells along their pore canals. There is a small central columella present (giving the conceptacle chamber its bean-shape) (Fig. 37), and zonately divided tetrasporangia (Fig. 36) are located peripheral to it. Tetrasporangia are 37–155 μm in length and 15–93 μm in diameter. Bisporangia were not seen. Tetrasporangial conceptacles often become buried in the thallus and often contain preserved tetrasporangia; infilled conceptacles have not been observed. Data on measured reproductive characters in the isotypes are summarized in Table 2.



FIGURES 27–32. Vegetative anatomy of the isotype material of *Porolithon antillarum*. **FIG. 27.** Thallus surface under SEM showing a large pustulate, horizontally arranged trichocyte field. Note the grazing scars (BM 899) (scale bar = 60 μm). **FIG. 28.** Vertical fracture of the thallus under SEM showing cortical filaments (C), medullary filaments (M) and a large trichocyte field (arrow) at the surface (BM 899) (scale bar = 120 μm). **FIG. 29.** Vertical section of the dorsal region showing multiple layers of epithallial cells (arrowheads), an undivided subepithallial initial (i), a recently divided subepithallial initial (arrows) and a first cortical cell (c) (TRH A27-1565) (scale bar = 15 μm). **FIG. 30.** Vertical section of the thallus showing buried trichocyte fields (arrows) (BM 899) (scale bar = 60 μm). **FIG. 31.** Vertical section of the ventral region showing a monomerous, plumose thallus with cell fusions (f) between adjacent filaments (TRH A27-1565) (scale bar = 15 μm). **FIG. 32.** Magnified view of the ventral region of the thallus sectioned parallel to the growing edge showing an extremely thin ventral region, giving a false impression of being dimerous (arrowheads) (TRH A27-1565) (scale bar = 15 μm).



FIGURES 33–38. Carposporangial and tetrasporangial anatomy of the isotype material of *Porolithon antillarum*. **FIG. 33.** A single slightly raised carposporangial conceptacle (arrow) under SEM. Note the large number of grazing scars at the surface (BM 899) (scale bar = 150 μm). **FIG. 34.** Vertical fracture of the thallus under SEM showing a buried carposporangial conceptacle with pore canal cells comprised of papillate cells that project into the pore canal (arrow) (BM 899) (scale bar = 100 μm). **FIG. 35.** A single flush to slightly sunken tetrasporangial conceptacle (arrow) under SEM (TRH A27-1565) (scale bar = 300 μm). **FIG. 36.** Close-up of a tetrasporangial conceptacle chamber under SEM showing zonately divided tetrasporangia (TRH A27-1565) (scale bar = 30 μm). **FIG. 37.** Vertical section through a buried tetrasporangial conceptacle showing un-infilled chamber (K) and a small central columella (arrowhead) (TRH A27-1565) (scale bar = 60 μm). **FIG. 38.** Close-up of the pore canal of a buried tetrasporangial conceptacle showing enlarged cells (arrows) located at the base of the pore canal (TRH A27-1565) (scale bar = 15 μm).

Remarks:—*Porolithon antillarum* is a poorly known species and despite the large collection made by Howe in 1906 (see Woelkerling 1993) it is based on a collection of specimens made from a single locality in Culebra, Puerto Rico. We have been unable to find any new records of this species in the literature. Nonetheless, this review of the isotype collections has led us to conclude that *P. antillarum* is the hugely foliose, "honeycombed" form of *P. onkodes* (see Fig. 14), which is commonly found throughout the South Pacific (see also Littler & Littler 1999, 2003). We therefore consider that *P. antillarum* is conspecific with *P. onkodes* and is thus a heterotypic synonym thereof.

Porolithon cocosicum Lemoine, 1930: 49
(Figs 39–46)

Basionym:—*Porolithon cocosicum* Lemoine, 1930: 49 (see also Chapman 1971: 169).
Synonyms:—None.
Holotype:—BM!. Cocos Island (Costa Rica), Pacific Ocean (St. George Expedition of 1923–1924); algal box collection no. 316. Previous references to typification were by Tittley *et al*. 1984: 13. Holotype fragment exists in PC! (unnumbered, General Herbarium box collection [filed in non-geniculate coralline type collections cabinet under basionym, see Woelkerling & Lamy 1998]).

Etymology:—'*cocosicum*' after the Cocos Island (Costa Rica) from where collected.

Distribution:—*Porolithon cocosicum* is reported only from the eastern Pacific Ocean (Lemoine 1930, Fernández-García *et al*. 2011).

Appearance and vegetative structure:—The following description is based on the holotype fragment from PC (tetrasporangial material) (Figs 39, 40, 44–46) and the holotype slide no. 5369 from BM (gametangial material) (Figs 41–43); no representative specimens for this taxon were available for verification.

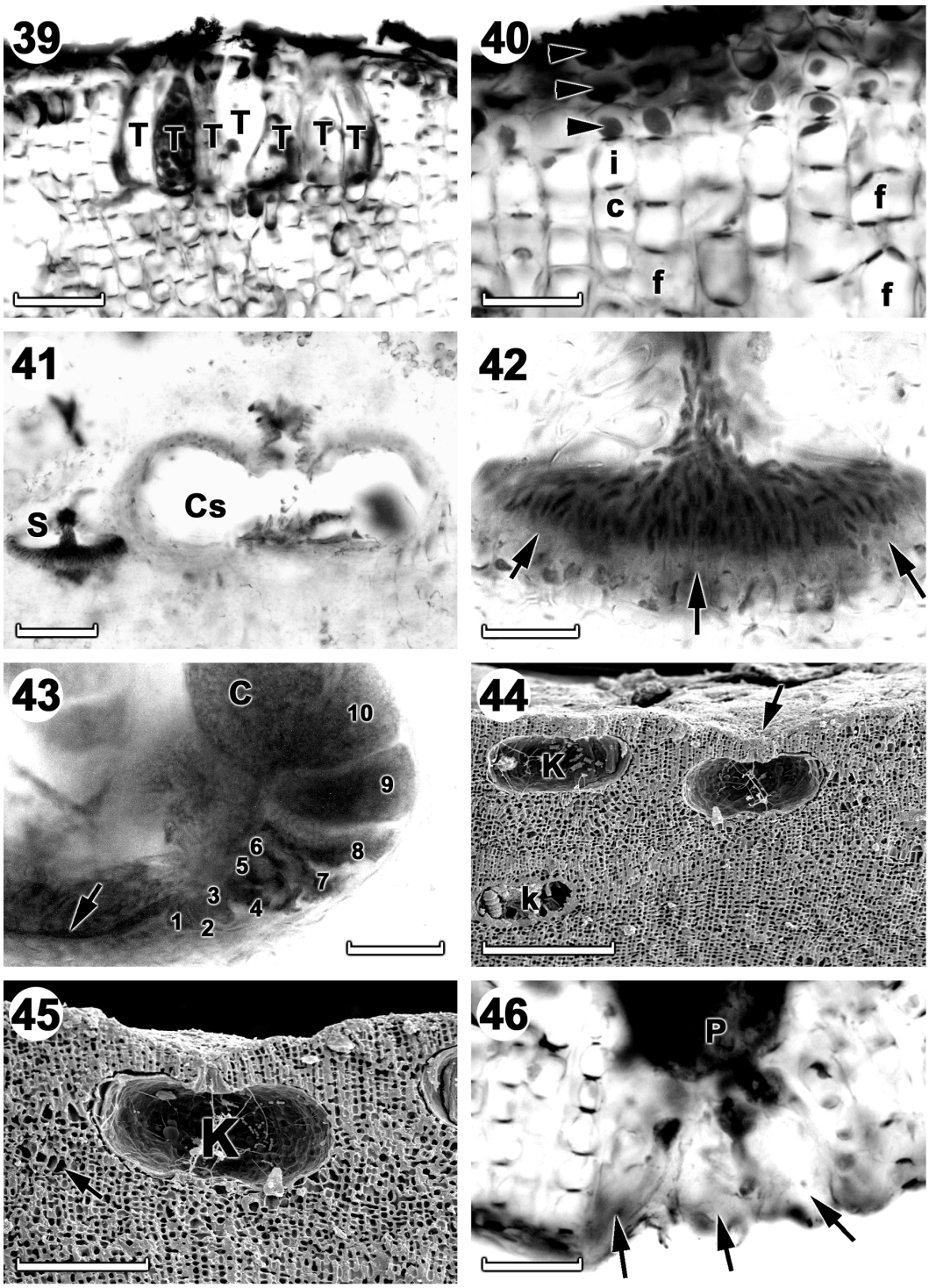
Holotype fragments are adherent and encrusting, measuring up to 330 μm thick. Thalli are encrusting, smooth and featureless, lacking protuberances but may also be slightly lumpy (Lemoine 1930: Pl. 4, Fig 4). Margins have not been observed. Surface cells are generally thick walled with shallow to deep centrally depressed centres, many bearing intact primary pit connections. The surface texture is matt and granular due to the presence of numerous tightly packed, pustulate, horizontally arranged trichocyte fields.

The thallus is monomerous and dorsiventrally organised. The medullary filaments comprise 8–52 % of the thallus and consist of a central plumose (non-coaxial) core, with cells that are square to rectangular, 6–25 μm in length and 6–15 μm in diameter. The cortical filaments comprise up to 92 % of the thallus with cells that are square to rectangular, 5–21 μm in length and 5–12 μm in diameter. Subepithallial initials are mostly square to rectangular, 6–19 μm in length and 5–12 μm in diameter. Epithallial cells are squat to elliptical, 4–7 μm in length and 5–12 μm in diameter, and occur in 1–3 cell layers (mostly 2–3 but up to 5 when shedding) (Fig. 40). Fields of squarish to elongate trichocytes (Fig. 39) commonly occur at the thallus surface in tightly packed, pustulate horizontally arranged fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal vegetative filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes are 15–37 μm in length and 9–20 μm in diameter. Trichocytes are often overgrown and buried in the thallus in horizontal fields. Cell fusions are abundant throughout the thallus; secondary pit connections were not seen. Data on measured characters in the holotype are summarized in Table 1.

Reproduction:—Gametangial thalli are monoecious (Fig. 41).

Spermatangial conceptacles are small, measuring about 125–200 μm in external diameter. Their roofs are usually more-or-less flush with the surrounding thallus surface, but are sometimes slightly raised. Conceptacle chambers are wide and shallow to elliptical, 93–155 μm in diameter and 22–37 μm high, with the roof 19–37 μm thick. Spermatangial conceptacles are often seen buried in the thallus (Fig. 41); infilling has not been observed. Simple spermatangial systems are borne only on the floor of the conceptacle chamber (Figs 41, 42).

Carpogonial conceptacles have not been observed.



FIGURES 39–46. Vegetative and reproductive anatomy of the holotype of *Porolithon cocosicum*. **FIG. 39.** Vertical section of the dorsal region of the thallus through a pustulate, horizontally arranged trichocyte field (T) (PC unnumbered) (scale bar = 30 μm). **FIG. 40.** Vertical section of the dorsal region of the thallus showing multiple layers of epithallial cells (arrowheads), subepithallial initials (i), a first cortical cell (c) and cell fusions (f) between adjacent cortical filaments (PC unnumbered) (scale bar = 15 μm). **FIG. 41.** Section through a monoecious thallus showing a buried spermatangial (S) and carposporangial (Cs) conceptacles (BM 316 slide no 5369) (scale bar = 60 μm). **FIG. 42.** Section through a buried spermatangial conceptacle showing simple spermatangial systems restricted to the conceptacle floor (arrows) (BM 316 slide no 5369) (scale bar = 15 μm). **FIG. 43.** Section through a carposporangial conceptacle showing a thin, discoid and continuous central fusion cell (arrow) bearing a peripheral gonimoblast filament. The gonimoblast filaments may comprise up to 11 cells (numbered 1–10) including a terminal carpospore (C) (BM 316 slide no 5369) (scale bar = 15 μm). **FIG. 44.** Vertical fracture of the thallus under SEM showing a raised (K), sunken (arrow) and un-infilled buried (k) tetrasporangial conceptacle (PC unnumbered) (scale bar = 200 μm). **FIG. 45.** Vertical fracture under SEM through a slightly sunken tetrasporangial conceptacle (K). Note the buried horizontally arranged trichocyte field (arrow) (PC unnumbered) (scale bar = 120 μm). **FIG. 46.** Section through the pore (P) and pore canal of a buried tetrasporangial conceptacle showing a ring of enlarged cells (arrows) located at the base of the pore canal (PC unnumbered) (scale bar = 15 μm).

Carposporangial conceptacles are relatively large, measuring 300–450 μm in external diameter. Their chambers are elliptical to bean-shaped, 175–374 μm in diameter and 56–109 μm high with the roof 56–62 μm thick (Fig. 41). The pore canal is lined with small filaments. The continuous central fusion cell is narrow and thick (discoid) with gonimoblast filaments borne peripherally (Fig. 43). Gonimoblast filaments are 9–11 cells long including a terminal carpospore that measures 31–62 μm in length and 31–43 μm in diameter. Mature carpospores almost fill the conceptacle chamber.

Tetrasporangial conceptacles are slightly sunken to flush to slightly raised above the rest of the thallus surface and measure 275–450 μm in external diameter (Figs 44, 45). Their chambers are elliptical to spherical, 175–300 μm in diameter and 60–150 μm high, with the roof 43–56 μm (7–11 cells) thick. The conceptacle floor is located 12–20 cells below the thallus surface. No conceptacle primordia were found, but from the orientation of the conceptacle roof cells, it is presumed that the roof is formed from filaments peripheral to and interspersed among the tetrasporangial initials. A ring of enlarged, domed cells lines the base of the pore canal (Fig. 46). The pore-canal filaments are usually orientated more-or-less vertically, and do not tilt markedly into the pore. A central columella has not been seen, but zonately divided tetrasporangia are found to occur peripherally in the conceptacle chamber. Sporangia measure 35–99 μm in length and 15–53 μm in diameter. Bisporangia were not seen. Tetrasporangial conceptacles often become buried in the thallus and often contain tetrasporangia (Fig. 44); infilled conceptacles have not been observed. Data on measured reproductive characters in the holotype are summarized in Table 2.

Remarks:—In her description of this taxon, Lemoine (1930: 49) distinguished *P. cocosicum* from *P. onkodes* (from the Pacific) (see also Lemoine 1911) and *P. pachydermum* (as *P. onkodes* f. *pachyderma* Foslie – from the western Atlantic) by the presence of a monomerous thallus (with a thick medullary region) as opposed to the presence of both a monomerous (with a thin medullary region) and a dimerous thallus she considered diagnostic of the latter two taxa. This study has shown that when extremely thin monomerous thalli are sectioned parallel to the growing margin or at right angles to the growing thallus, it gives the false impression of being dimerous (see e.g. Fig. 32). This may be what led Lemoine (1911, 1930) to conclude that *P. onkodes* and *P. pachydermum* bore both monomerous and dimerous thalli. Like earlier researchers (e.g. Penrose & Woelkerling 1988; Keats & Chamberlain 1994) this study has not recorded any dimerous thalli in *P. onkodes*. Based on our findings, *P. cocosicum* matches the description of *P. onkodes*. We therefore consider *P. cocosicum* to also be conspecific with *P. onkodes* and thus a heterotypic synonym thereof.

Porolithon pachydermum (Foslie) Foslie, 1909: 57
(Figs 47–59)

Basionym:—*Lithophyllum onkodes* f. *pachydermum* Foslie, 1904: 5.
Homotypic synonyms:—*Lithophyllum pachydermum* (Foslie) Adey & Lebednik, 1967: 47; *Hydrolithon pachydermum* (Foslie) Bailey, Gabel & Freshwater, 2005: 3 (see also Bailey *et al*. 2004: 8).
Lectotype:—TRH, A26-1553. St. Croix (?), US Virgin Islands (West Indies); Ørsted no 548. Previous references to typification were by Adey & Lebednik 1967: 47 (as *L. pachydermum*) and Adey 1970: 11 (as *P. pachydermum*).
Isolectotype:—BM! (unnumbered as *L. pachydermum*).

Etymology:— "*pachydermum*", *pachy* = thick, stout + *derma* = skin (Stearn 1973). Foslie (1904) did not explain the origin of the epithet. It could be making reference to an elephant-skin-like surface (as in pachyderm) or simply just be referring to the multiple layers of epithallial cells.

Specimens examined:—In addition to the isolectotype material sent on loan from BM, only one representative specimen was examined during this study.
BERMUDA. Astwood Cove, Warwich; low-shore exposed rocky platform (13.ii.2000, *D.W. Keats*, UWC 2000/106B).

Distribution:—*Porolithon pachydermum* is a largely tropical species widely reported from the Caribbean Islands and the tropical western Atlantic Ocean. See Guiry & Guiry (2013) for a detailed distribution list.

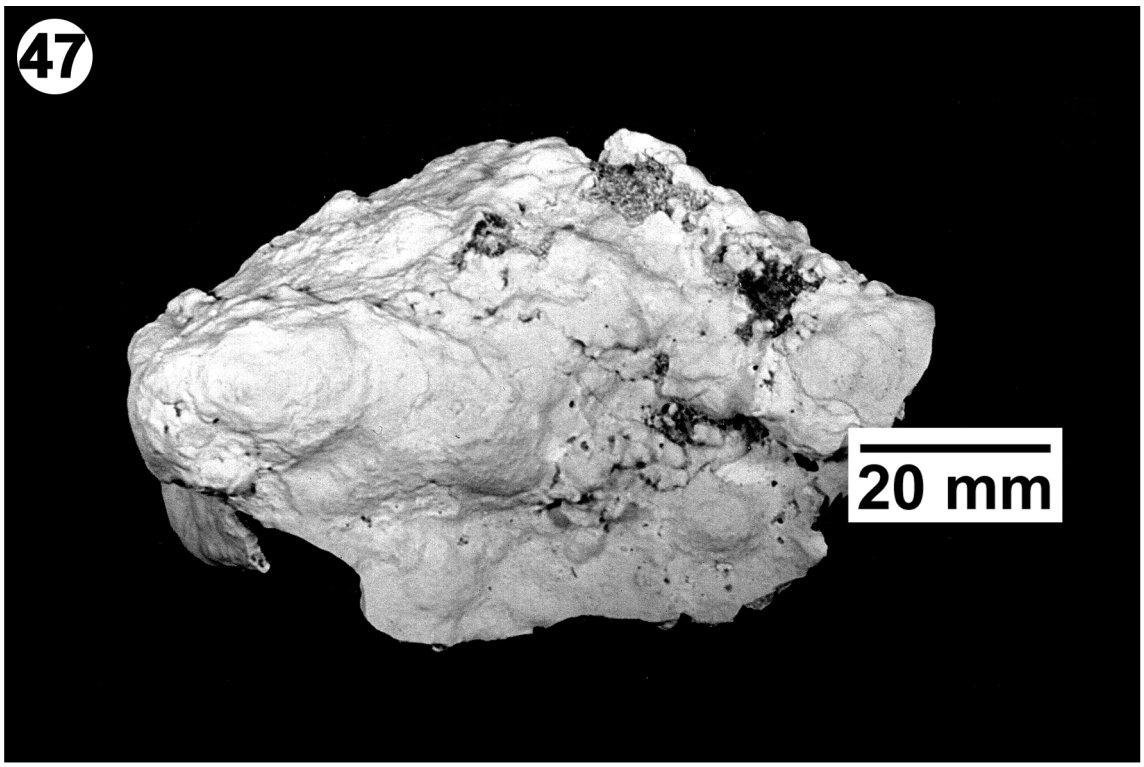
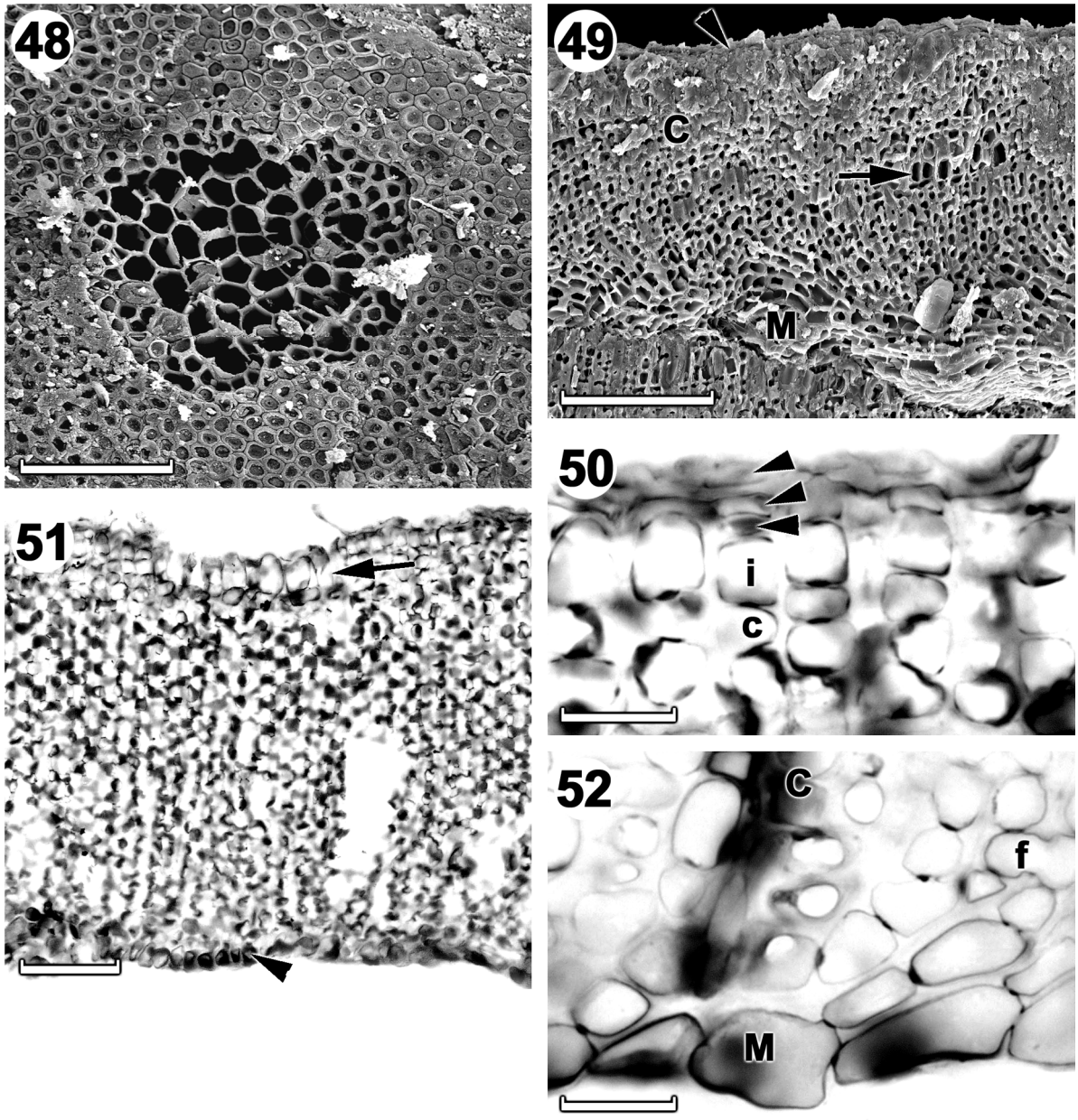


FIGURE 47. The isolectotype of *Porolithon pachydermum* (BM unnumbered).

Appearance and vegetative structure:—The following description is based on the isolectotype material housed at BM (Fig. 47). The isolectotype collection is adherent and encrusting, measuring up to at least 3025 μm thick. Thalli are flat and smooth, lacking protuberances and have free to adherent margins that are entire to lobed, but lack orbital ridges. Surface cells are thin to thick walled with centrally depressed centres, many bearing intact primary pit connections. The surface texture is matt and granular due to the presence of numerous tightly packed, pustulate, horizontally arranged trichocyte fields (Fig. 48).

Isolectotype thallus fragments are monomerous and dorsiventrally organised (Fig. 49). The medullary filaments generally comprise 9–30 % of the thallus (up to 86 % in very thin sections) and consist of a central plumose (non-coaxial) core (Fig. 52), with cells that are square to rectangular, 6–31 μm in length and 4–15 μm in diameter. Where the medullary filaments comprise a very small portion of the thallus thickness, it often gives the false impression of being dimerous when sectioned parallel to the growing margin (Fig. 51). Cortical filaments in the isolectotype comprise 14–91 % of the thallus with cells that are square to rectangular, 6–17 μm in length and 4–12 μm in diameter. Subepithallial initials are squarish, 5–12 μm in length and 5–12 μm in diameter. Epithallial cells are squat to elliptical, 3–6 μm in length and 5–12 μm in diameter, and occur in 1–3 cell layers (mostly 2–3) (Fig. 50). Fields of squarish to rectangular trichocytes commonly occur at the thallus surface in tightly packed, pustulate horizontally arranged fields (Fig. 51). These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes are 15–38 μm in length and 7–22 μm in diameter. They are often overgrown and buried in the thallus in horizontal fields (Fig. 49). Cell fusions are abundant throughout the thallus; secondary pit connections were not seen. Data on measured characters in the isolectotype are summarized in Table 1.

Features evident in the isolectotype are also present in the representative specimen examined. Thalli surfaces are also generally smooth, encrusting and featureless, but tend to become low lumpy when conforming to an irregular substratum and often forms thick crusts as it frequently overgrows itself. The thallus surface is heavily grazed and is pale greyish pink in colour. Like the isolectotype collection, thalli are monomerous, dorsiventrally organised, and have similar features and proportions (with slightly greater ranges) of medullary and cortical filaments, subepithallial and epithallial cells, and trichocytes. Epithallial cells, however, occur in up to 5 layers when shedding (but mostly 2–3 layers). Data on measured characters in the representative specimen are summarized in Table 1.

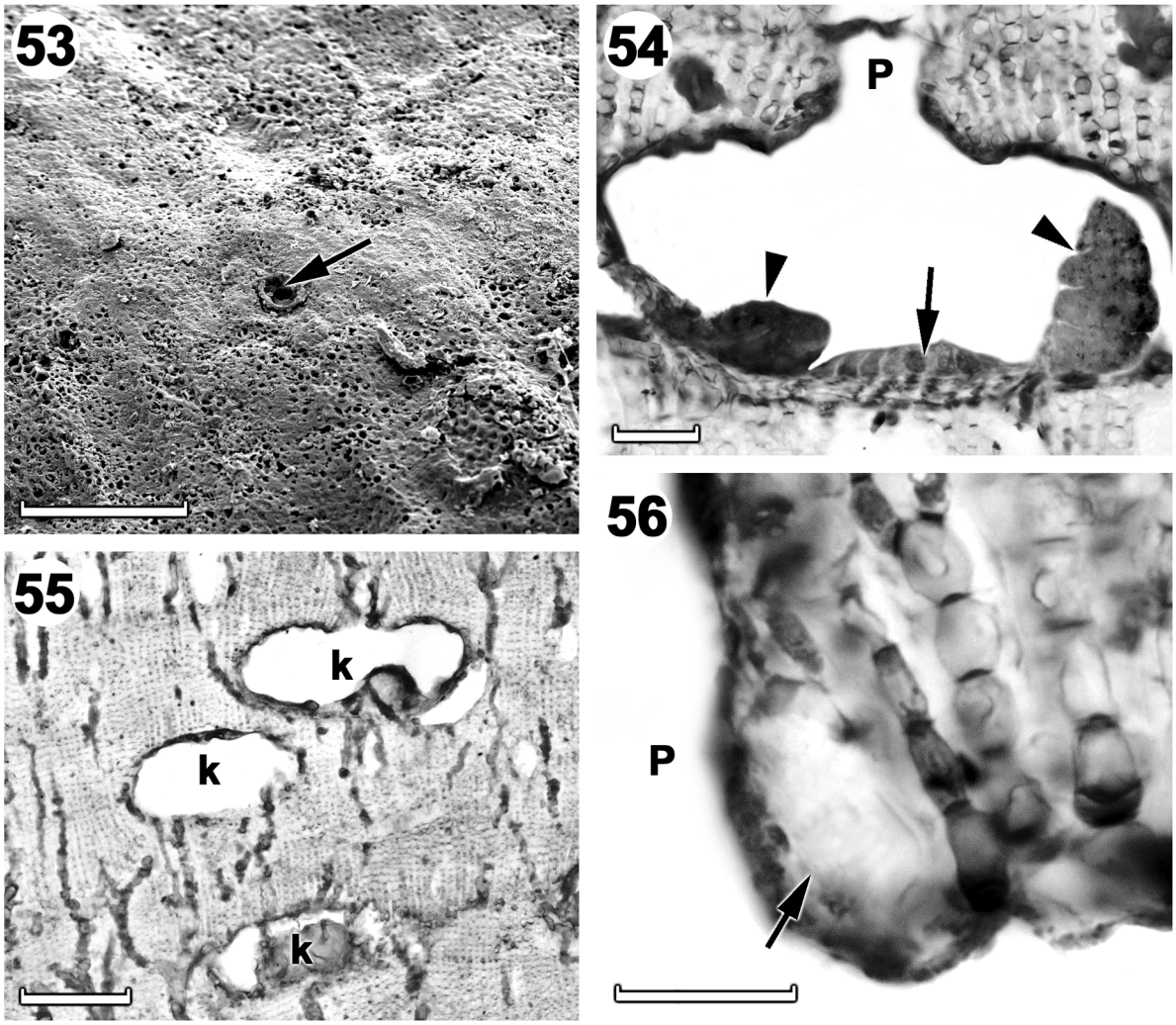


FIGURES 48–52. Vegetation anatomy of the isolectotype of *Porolithon pachydermum* (BM unnumbered). **FIG. 48.** Thallus surface under SEM showing a single large, horizontally arranged trichocyte field (scale bar = 60 μm). **FIG. 49.** Vertical fracture of a monomerous thallus under SEM showing the location of the epithallial cells (arrowhead) as well as cortical filaments (C), medulla filaments (M) and a buried trichocyte field (arrow) (scale bar = 120 μm). **FIG. 50.** Section of the dorsal region of the thallus showing multiple layers of epithallial cells (arrowheads), a subepithallial initial (i) and a first cortical cell (c) (scale bar = 15 μm). **FIG. 51.** Vertical section of the thallus sectioned more or less parallel to the growing edge thallus showing a single large, horizontal trichocyte field (arrow) at the surface and an extremely thin ventral region, giving a false impression of being dimerous (arrowhead) (scale bar = 60 μm). **FIG. 52.** Section of the ventral region of the thallus showing a thin, monomerous, plumose medullary region (M) giving rise to cortical filaments (C) bearing cell fusions (f) between adjacent filaments (scale bar = 15 μm).

Reproduction:—The isolectotype collection lacked gametangial material, but did possess tetrasporangial material.

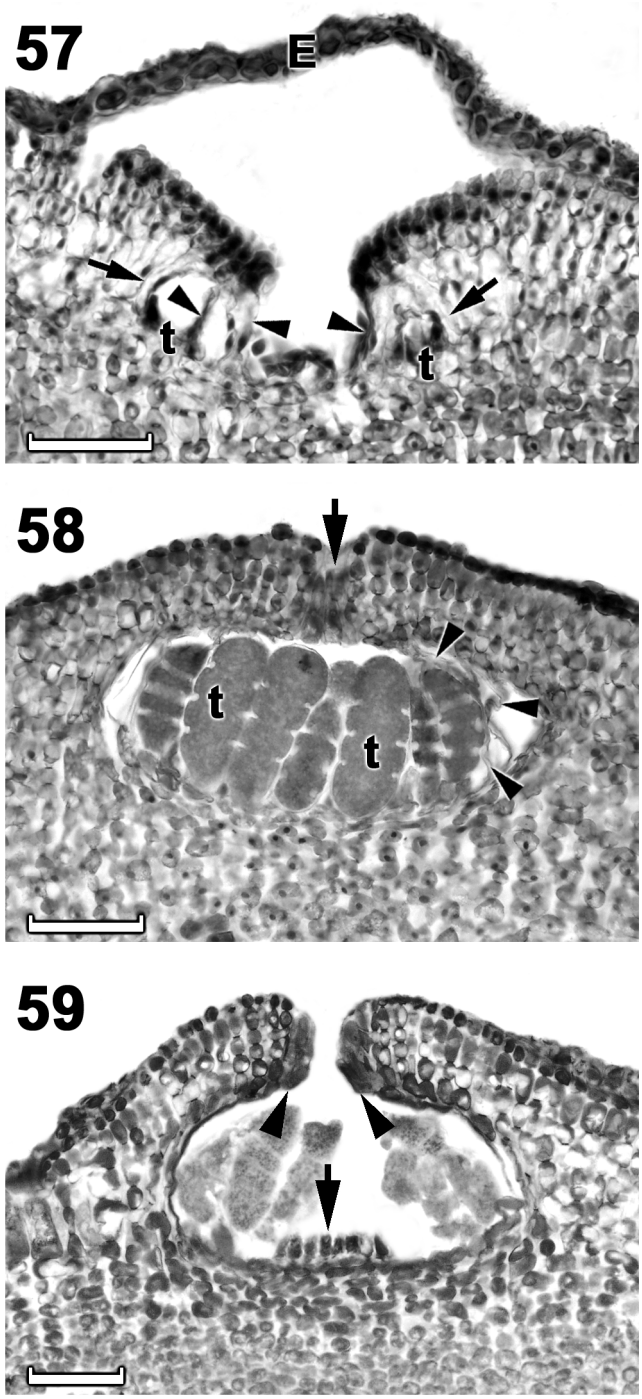
Tetrasporangial conceptacles are more-or-less flush to only slightly raised above the rest of the thallus, measuring 450–675 μm in external diameter (Fig. 53). Their chambers are elliptical to bean-shaped (Figs 54, 55), 145–290 μm in diameter and 50–170 μm high, with the roof 31–51 μm (6–11 cells; incl. epithallial cell) thick. The conceptacle floor is located 13–19 cells below the surrounding thallus surface. No conceptacle primordia were found, but from the orientation of the conceptacle roof cells, it is presumed that the roof is formed from filaments peripheral to and interspersed among the tetrasporangial initials. A ring of enlarged, domed cells lines the base of the pore canal (Fig. 56). The pore-canal filaments are orientated more-or-less vertically, and do not project into the

pore. There is a small central columella present (giving the conceptacle chamber its bean-shape) and zonately divided tetrasporangia are located peripheral to it (Fig. 54). Tetrasporangia are 31–87 μm in length and 9–47 μm in diameter. Bisporangia were not seen. Tetrasporangial conceptacles often become buried in the thallus (Fig. 55) and often contain tetrasporangia; infilled conceptacles have not been observed. Data on measured reproductive characters in the isolectotype are summarized in Table 2.



FIGURES 53–56. Sporangial anatomy of the isolectotype of *Porolithon pachydermum* (BM unnumbered). **FIG. 53.** Magnified view under SEM of a slightly raised uniporate (arrow) tetrasporangial conceptacle (scale bar = 150 μm). **FIG. 54.** Section through a tetrasporangial conceptacle showing the pore canal (P), the remains of a central columella (arrow) and peripherally arranged tetrasporangia (arrowheads) (scale bar = 30 μm). **FIG. 55.** Vertical section of the thallus showing buried, un-infilled tetrasporangial conceptacles (k) (scale bar = 120 μm). **FIG. 56.** Section through the pore canal (P) of a tetrasporangial conceptacle showing an enlarged cell (arrow) located at the base of the pore canal (scale bar = 15 μm).

The representative specimen examined possessed only tetrasporangial material. Unlike the isolectotype for which conceptacle primordia was lacking, the representative specimen clearly showed conceptacle roof formation from filaments peripheral to the fertile area and from filaments interspersed among the tetrasporangial initials (Fig 57). Similarly, a ring of enlarged, domed cells lines the base of the pore canal and the pore-canal filaments are orientated more-or-less vertically, and do not project into the pore (Figs 58, 59). A much reduced central columella is evident in mature conceptacles (Fig 59). Features evident in the isolectotype are also present in the representative specimen examined and are summarized in Table 2. Somewhat greater variation exists in the ranges of the measurements for the representative material.



FIGURES 57–59. Tetrasporangial anatomy of *Porolithon pachydermum* (UWC 2000/106B). **FIG. 57.** Section through a young tetrasporangial conceptacle showing early roof development from filaments peripheral to the fertile arrow (arrows) and from filaments interspersed (arrowhead) among the sporangial initials (t). A multiple layer of epithallial cells (E) still persists as a protective covering over the developing conceptacle (scale bar = 50 µm). **FIG. 58.** Section through a mature tetrasporangial conceptacle near the edge of the pore canal showing enlarged cells (arrow) lining the pore canal, zonately divided tetrasporangia (t) and the remains of filaments (arrowheads) still interspersed among the tetrasporangia that gave rise to the conceptacle roof. The central columella would not necessarily be visible in a section that was not completely through the conceptacle pore (scale bar = 50 µm). **FIG. 59.** Section through a mature tetrasporangial conceptacle showing enlarged cells at the base of the pore canal (arrowheads) and the remains of a central columella (arrow) (scale bar = 50 µm).

Ecological observations:—*Porolithon pachydermum* is reported to be one of the most common coral reef corallines in the intertidal and shallower areas (< 10 m) of the Caribbean West Indian coastline, including the US Virgin Islands (Foslie 1909, Printz 1929, Adey & Lebednik 1967, Adey 1978, Littler & Littler 2000) and the tropical continental shelf of Brazil (Gherardi & Bosence 1999, 2001, Villas Bôas *et al*. 2005, Figueiredo *et al*.

2008). Here it is often the dominant frame builder on algal ridges experiencing very high wave energy and characteristically occurs on the most exposed platforms (Adey 1978, Gherardi & Bosence 1999, 2001, Villas Bôas *et al*. 2005; Figueiredo *et al*. 2008; *pers*. *obs*.). The species commonly occurs with a mixture of other species belonging to the genera *Hydrolithon*, *Neogoniolithon*, *Porolithon*, and *Lithophyllum* with *L. congestum* being another prominent feature of mostly medium energy reefs (see also Steneck & Adey 1976, Figueiredo *et al*. 2008). On some Caribbean reefs, this species has been reported to have a "castle-like", three-dimensional, "honeycombed" appearance (Littler *et al*. 1995, Littler & Littler 2000). At the base of the coralline are found the tubular burrows of the chiton, *Choneplax lata* and the growth form is evidently caused by growth in response to the grazing activities of the chiton (Littler *et al*. 1995; Littler & Littler 2000).

Remarks:—Based on our findings, *Porolithon pachydermum* can be characterised by the following combination of features: 1) thallus thick, adherent, encrusting, generally lacking protuberances, but may be slightly lumpy; 2) thallus monomerous; 3) medullary filaments plumose, but often gives the false impression of being dimerous; 4) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally orientated, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 5) within fields, trichocytes are not separated by the cells of normal vegetative filaments; 6) epithallial cells occurring in 1–3 layers (up to 5 when shedding); 7) tetrasporangial conceptacles that are more-or-less flush to only slightly raised above the rest of the thallus surface; 8) the base of tetrasporangial conceptacle pore canals lined by a ring of vertically orientated, conspicuously enlarged cells that do not project into the pore canal; 9) the tetrasporangial conceptacle roof is formed from filaments peripheral to the fertile area and from filaments interspersed among the tetrasporangial initials; 10) the tetrasporangial conceptacle roof commonly 6–11 cells thick; 11) the tetrasporangial conceptacle floor commonly 9–19 cells below the surrounding thallus surface. All of these features evidently also occur in *P. onkodes* (Tables 1 & 2).

Despite the ubiquitous nature of *P. pachydermum* throughout the Caribbean Sea (Foslie 1909, Printz 1929, Lemoine 1964, 1966, Adey & Lebednik 1967, Adey 1978, Littler *et al*. 1995, Littler & Littler 2000) and along the continental shelf of tropical Brazil (Gherardi & Bosence 1999, 2001, Villas Bôas *et al*. 2005, Figueiredo *et al*. 2008), the species' taxonomy has never been well documented. Based on nuclear 18S rRNA gene sequences (Bailey *et al*. 2004 [invalid], 2005), the species was considered different to *P. onkodes* and transferred to the genus *Hydrolithon* under which *P. onkodes* was classified at that time. In the proceedings of the fourth International Seaweed Symposium, Lemoine (1964) commented on the species representative of the eight Melobesioid (as then defined) groups as defined by M.J. Feldmann (1946) in his description of the marine flora of the Atlantic Islands. Lemoine (1964) named a Pan tropical group of four species comprising: *P. onkodes* from the Atlantic and Indo-Pacific regions; *P. onkodes* from the Pacific; *P. oligocarpum* (Foslie) Foslie from the East Atlantic; and *P. pachydermum* from the western Atlantic (see also Lemoine 1966), and highlighted the close affinity of these four entities. It was then already suggested that these four entities might be synonymous.

The present study shows that *P. pachydermum* conforms to *P. onkodes*. Although Krishnamurthy & Jayagopal (1987) made a similar suggestion, their findings were inconclusive. Adey *et al*. (1982) even considered *P. onkodes* and *P. pachydermum* to be "pair species". Later Bailey *et al*. (2004 [invalid], 2005), after transferring *P. pachydermum* to *Hydrolithon*, considered *P. onkodes* (as *H. onkodes*) and *P. pachydermum* (as *H. pachydermum*) to be closely related, but not synonymous. This conclusion was reached because of a 0.34 % (i.e. 6 nucleotide differences out of 1770) difference in the genetic code of the two samples analysed. We disagree with the findings by Bailey *et al*. (2004 [invalid], 2005) for two reasons. Firstly, Bailey *et al*. (2004) did not analyse the type or 'topotype' material from these species (but rather material from Australia for *H. onkodes* and from Puerto Rico for *H. pachydermum*). Also problematic is that Bailey *et al*. (2004) failed to lodge voucher specimens for either of the two taxa they sequenced. This means that the identification of the material from which the molecular data was obtained, cannot be easily verified. Secondly, Bailey *et al*. (2004) based their findings exclusively on the internal transcription spacer (ITS) region of the nuclear ribosomal cistron. Notwithstanding the many important contributions of ITS sequence data to phylogenetic understanding, its complex and unpredictable behaviour has long been known to reduce its sole use for phylogenetic analysis (Álvarez & Wendel 2003). To overcome this shortcoming, virtually all recent molecular analyses now use multiple nuclear genes to improve phylogenetic understanding. Based on these findings and our extensive research, which considers many representative samples, we consider *P. pachydermum* to be conspecific with and a heterotypic synonym for *P. onkodes*, the latter having nomenclatural priority.

Porolithon sandvicense (Foslie) Foslie, 1909: 57
(Figs 60–67)

Basionym:—*Lithophyllum dentatum* f. *sandvicensis* Foslie, 1901: 11.
Homotypic synonyms:—*Lithophyllum sandvicense* Foslie, 1909: 45.
Holotype:—TRH!, A28-1605. Hawaiian Islands; Farlow no. XXX. Previous references to typification were by Adey & Lebednik 1967: 48 (as *L. sandvicense*) and Adey 1970: 11 (as *P. sandvicense*). Foslie (1909: 45) raised *L. dentatum* f. *sandvicensis* to the rank of species as *L. sandvicense*.

Etymology:—"*sandvicensis*", derived from the Sandwich Islands, the original name for the Hawaiian Islands; "*dentatum*", *dentatus* = toothed (Stearn 1973).

Distribution:—*Porolithon sandvicense* is reported only from the type locality.

Appearance and vegetative structure:—The following description is based on the holotype collection from TRH; no representative specimens for this taxon were available for verification.

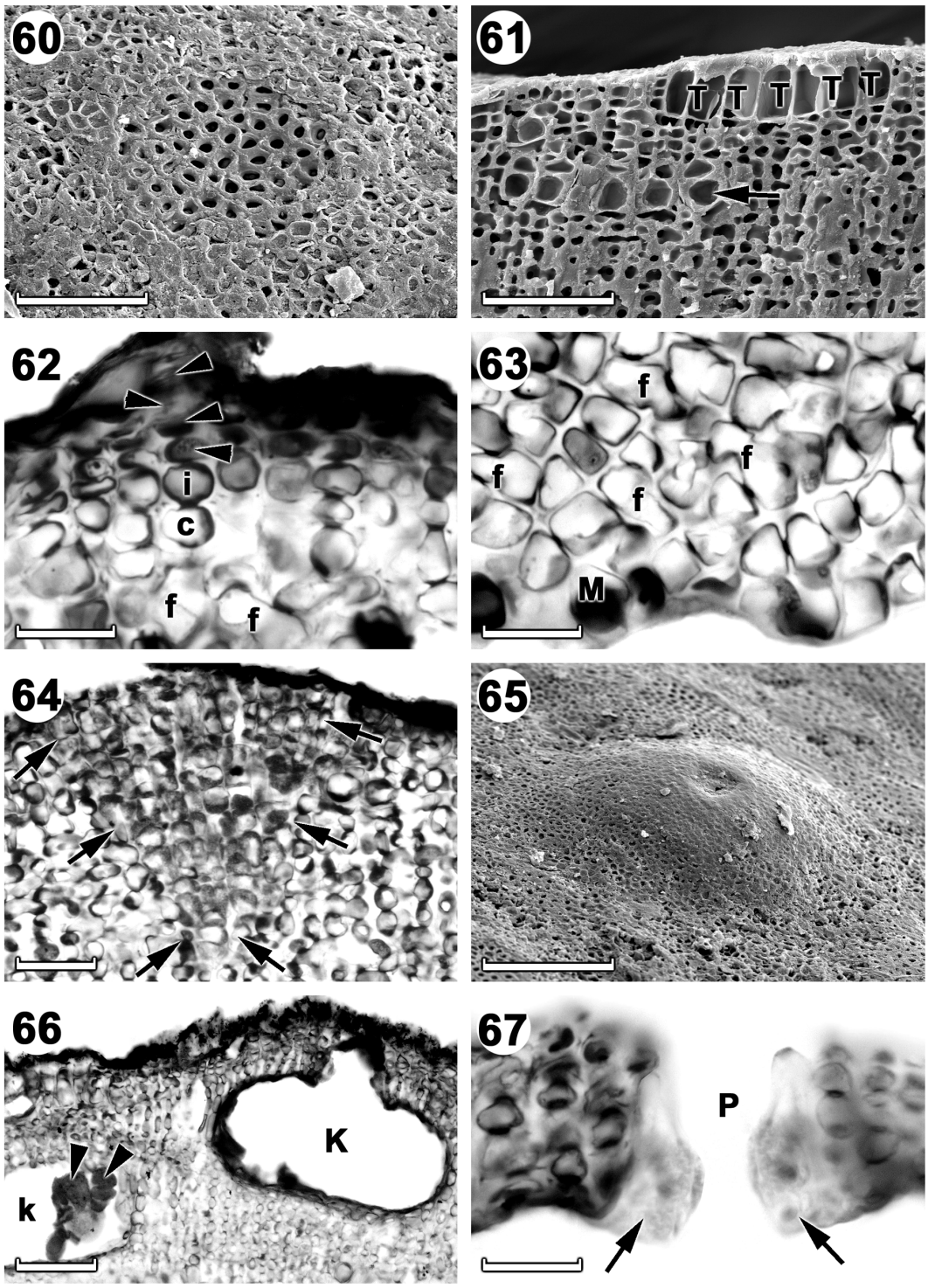
The holotype collection comprises of an upright, hugely foliose, lobed "honeycombed" structure, measuring roughly 60 mm in height and 65 mm in diameter along its longest axis (see Printz 1929; Pl. 70, Fig. 6). The fragment sent on lone was from a single lobe. Grazing scars are a very obvious feature of the surface. The thallus measures up to at least 225 μm thick, is generally encrusting, smooth and has adherent margins that are entire to lobed, but lack orbital ridges. The surface appears granular due to the presence of numerous tightly packed, pustulate, horizontally arranged trichocyte fields (Fig. 60).

The thallus is monomerous, and dorsiventrally organised. The medullary filaments comprise no more than 31 % of the thallus and consist of a central plumose (non-coaxial) core (Fig. 63), with cells that are square to rectangular, 6–26 μm in length and 4–15 μm in diameter. Medullary filaments in the lobe are generally coaxial. Cortical filaments make up the bulk of the thallus in crustose areas. Cells of cortical filaments are square to rectangular, 4–19 μm in length and 5–13 μm in diameter. Subepithallial initials are generally square, 6–11 μm in length and 5–10 μm in diameter. Epithallial cells are squat to elliptical, 3–6 μm in length and 5–11 μm in diameter, and occur in 1–3 cell layers (mostly 2–3 but up to 5 when shedding) (Fig. 62). Fields of squarish to rectangular trichocytes commonly occur at the thallus surface in tightly packed, pustulate horizontally arranged fields (Fig. 61). Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes are 14–31 μm in length and 9–25 μm in diameter. They are often overgrown and buried in the thallus in horizontal fields (Fig. 61). Cell fusions are abundant throughout the thallus; secondary pit connections were not seen. Wedge-shaped individuals of a species of coralline have been observed to occur in the thallus (Fig. 64). Data on measured characters in the holotype are summarized in Table 1.

Reproduction:—The holotype fragment lacked gametangial material, but did possess tetrasporangial material.

Tetrasporangial conceptacles are more-or-less flush with the thallus surface to only slightly raised above it, measuring 250–400 μm in external diameter (Figs 65, 66). Their chambers are elliptical to bean-shaped, 135–225 μm in diameter and 70–100 μm high, with the roof 22–37 μm (5–12 cells; incl. epithallial cell) thick. The conceptacle floor is located 12–18 cells below the surrounding thallus surface. No conceptacle primordia were found, but from the orientation of the conceptacle roof cells, it is presumed that the roof is formed from filaments peripheral to and interspersed among the tetrasporangial initials. A ring of enlarged, domed cells lines the base of the pore canal (Fig. 67). The pore-canal filaments are orientated more-or-less vertically and do not project into the pore. A small central columella is present (giving the conceptacle chamber its bean-shape) and zonately divided tetrasporangia are located peripheral to it. Tetrasporangia are 37–78 μm in length and 12–31 μm in diameter. Bisporangia were not seen. Tetrasporangial conceptacles often become buried in the thallus and often contain tetrasporangia (Fig. 66); infilled conceptacles have been observed although this is not common. Data on measured reproductive characters in the holotype are summarized in Table 2.

Remarks:—*Porolithon sandvicense* has not previously been studied in a modern context. Despite the fact that very little material was available for observation, the review of this species has led us to conclude that *P. sandvicense*, like *P. antillarum*, is the hugely upright foliose, lobed "honeycombed" form of *P. onkodes* which is commonly found in the South Pacific. Furthermore, a number of wedge-shaped individuals of another species of coralline algae have been observed to occur endophytically in the thallus of *P. sandvicense* (Fig. 64). These wedge-shaped individuals appear very similar to the wedge-shaped *Lithophyllum cuneatum* Keats that are characteristically



FIGURES 60–67. Vegetative and sporangial anatomy of the holotype of *Porolithon sandvicense* (TRH, A28-1605). **FIG. 60.** Thallus surface under SEM showing a single large, horizontally arranged trichocyte field (scale bar = 60 μm). **FIG. 61.** Vertical fracture of the thallus under SEM showing a single large pustulate, horizontally arranged trichocyte field at the surface (T) and buried in the thallus (arrow) (scale bar = 60 μm). **FIG. 62.** Vertical section of the dorsal region of the thallus showing multiple layers of epithallial cells (arrowheads), a subepithallial initial (i), a first cortical cell (c) and cell fusions (f) between adjacent cortical filaments (scale bar = 15 μm). **FIG. 63.** Vertical section of the ventral region of the thallus showing a thin monomerous, plumose medullary region (M) and extensive cell fusions (f) between adjacent filaments (scale bar = 15 μm). **FIG. 64.** Vertical section of the dorsal region of the thallus showing a wedge-shaped species of coralline (arrows) embedded in the thallus of *P. sandvicensis* (scale bar = 30 μm). **FIG. 65.** Magnified view under SEM of a single raised tetrasporangial conceptacle (scale bar = 120 μm). **FIG. 66.** Vertical section of the dorsal region of the thallus showing a raised tetrasporangial conceptacle (K) at the surface and a buried, un-infilled conceptacle (k) bearing peripheral tetrasporangia (arrowheads) (scale bar = 60 μm). **FIG. 67.** Vertical section through the pore canal (P) of a tetrasporangial conceptacle showing enlarged cells (arrows) lining the base of the pore canal (scale bar = 15 μm).

found to occur semi-endophytically on individuals of *P. onkodes* (as *H. onkodes*, Keats 1995). Whether this wedge-shaped coralline endophytic on *P. sandvicense* is indeed *L. cuneatum* could not be ascertained as there was insufficient material for a detailed analysis. Notwithstanding the gross morphology and the possible host-specific semi-endophyte described above, this species matches perfectly the description of *P. onkodes*. We therefore consider that *P. sandvicense* also is conspecific with *P. onkodes* and that it too is a heterotypic synonym thereof.

Discussion

Taxonomic implications:—Based on new morphological and anatomical studies of the type and of specimens from localities in the Indian (Comoros, South Africa, Tanzania) and Pacific (Fiji, Taiwan) Oceans, the placement of *P. onkodes* in *Porolithon* is reaffirmed. *Porolithon onkodes* possesses all the features of the genus *Porolithon* as delimited by Kato *et al*. (2011) (see Introduction section), which is characterised by having the following combination of features: 1) thalli unsegmented (i.e. non-geniculate); 2) lack of secondary pit connections; lateral cell fusions between contiguous filaments present; 3) absence of a basal layer of palisade cells; 4) trichocytes in large, tightly packed horizontal fields (that lack vegetative filaments between them); 5) tetrasporangial conceptacles formed by filaments peripheral to the fertile area and interspersed among the tetrasporangial initials; and 6) spermatangia that develop on the floor of the male conceptacle chamber. In addition, within tetrasporangial conceptacles the pore canals are lined by a ring of conspicuous, enlarged cells that arise from filaments interspersed among the sporangial initials. These pore canal cells do not protrude into the pore canal but are orientated more-or-less perpendicularly to the roof surface.

Within *Porolithon*, *P. onkodes* is reaffirmed as a distinct species, but of variable morphological appearance and is characterised by the following combination of features: 1) thallus thick, adherent, generally encrusting and lacking protuberances, but may be lumpy; in response to heavy chiton grazing pressure on some coral reefs, the coralline can become hugely foliose, appearing "honeycombed" and lobed; 2) thallus monomerous; 3) medullary filaments plumose; 4) trichocytes present, both at the surface and buried in the thallus, consisting of numerous horizontally orientated, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 5) within fields, trichocytes are not separated by the cells of normal vegetative filaments; 6) epithallial cells commonly in 1–3 layers (up to 5 when shedding); 7) tetra/bisporangial conceptacles predominantly flush to only slightly raised above the rest of the surrounding thallus surface; 8) tetra/bisporangial conceptacle roof commonly 5–12 cells thick; 9) tetrasporangial conceptacle floor more commonly 12–19 cells below the surrounding thallus surface; and 10) carposporangial conceptacles bearing a continuous, discoid fusion cell with peripheral gonimoblast filaments that are 5–11 cells long (incl. terminal caropospore).

The morphological variability found in *P. onkodes* is known to occur in a number of other species of non-geniculate corallines and notably grazing has been shown to be one of the primary causes for such variability. Steneck & Adey (1976) demonstrated that non-branching specimens of *L. congestum* from the Caribbean that were subjected to parrot fish grazing in the subtidal zone, became variably protuberant when transplanted to the edges of reef flats where fish feeding was reduced. Maneveldt & Keats (2008) demonstrated that grazing by the limpet *Scutellastra cochlear* is primarily responsible for the occurrences of encrusting (smooth), un-branched specimens of *Spongites yendoi* from South Africa. Several other studies (e.g. Steneck & Watling 1982, Steneck 1983, 1985, 1986, Steneck & Paine 1986, Steneck *et al*. 1991) have also shown that grazing affects the thallus thickness and morphology of non-geniculate coralline algae.

Despite the suggested reproductive isolation of the taxa described here (see Lemoine 1964, 1966), there appears to be no valid taxonomic reason for their separation. The characters considered diagnostic of *P. onkodes* are variably present in all of the taxa described here. These species were originally distinguished on minor differences in external morphology, tetrasporangial conceptacle size and shape, and internal vegetative anatomy that vary to the extent that they are unreliable for distinguishing species. Foslie (1905) himself concluded that many of his earlier taxa were probably synonymous and alluded that "a considerable reduction was necessary" (see also Woelkerling 1984). Our studies of the types of *P. antillarum*, *P. cocosicum*, *P. pachydermum* and *P. sandvicense* have shown that they are all conspecific with and thus heterotypic synonyms of *P. onkodes*, which has nomenclatural priority.

Biogeographical and ecological implications:—*Porolithon onkodes* not only occurs throughout the Indo-Pacific and eastern Atlantic Oceans, but as a result of the present study, is now known to commonly occur throughout the tropical and subtropical regions of the western Atlantic Ocean. *Porolithon onkodes* is thus arguably one of the most widespread tropical to subtropical non-geniculate coralline algae.

The ecological importance of non-geniculate coralline algae as cementers and primary reef frame-builders of the coral reef margin has been widely documented. Species ascribed to the genus *Porolithon* in particular, have been highlighted as being especially important (Lee 1967, Adey 1978, Littler 1973, Gherardi & Bosence 1999, 2001, Littler & Littler 2000, Villas Bôas *et al*. 2005, Figueiredo *et al*. 2008). In many tropical Indo-Pacific and tropical eastern Atlantic regions, *P. onkodes* has been reported to be one of the single-most important ecological species because of its wide distribution (Lee 1967, Littler 1973, Littler & Doty 1975, Gordon *et al*. 1976, Adey *et al*. 1982, Ballesteros & Afonso-Carrillo 1995, Payri *et al*. 2001, Littler & Littler 2003). Similarly, *P. pachydermum* has been documented as one of the single-most important ecological species in many areas of the tropical and subtropical western Atlantic (Adey 1978, Littler *et al*. 1995, Gherardi & Bosence 1999, 2001, Littler & Littler 2000, Villas Bôas *et al*. 2005, Figueiredo *et al*. 2008). As the two taxa are now shown to be conspecific, it seems logical to suggest that *P. onkodes* is arguably one of the most important cementers and primary reef frame-building algae of the world's tropical reefs. It is perhaps not difficult to understand the importance of this latter statement when one considers the remarkable ability of this species to photoacclimate to a wide range of ambient light regimes (Payri *et al*. 2001).

Thalli of *P. onkodes* have generally been described as encrusting to slightly lumpy (see Table 1). This study has, however, shown that the species is morphologically variable as a three-dimensional, hugely foliose, "honeycombed" form of the species also occurs in some shallow South Pacific coral reef areas in which upright lobes are produced (*pers*. *obs*., Fig. 14; see also Littler & Littler 1999, 2003). At the bases of these upright lobes are found the tubular burrows of the chiton *Cryptoplax larvaeformis*. Similarly, on some Caribbean reefs, the coralline (as *P. pachydermum*) has been reported to have the same "castle-like", "honeycombed" appearance (Littler *et al*. 1995, Littler & Littler 2000). At the bases of this latter coralline are found the tubular burrows of the chiton, *Choneplax lata*. These forms are evidently caused by growth in response to the grazing activities of the chitons (Littler *et al*. 1995, Littler & Littler 1999, 2000, 2003). Incidentally, both *P. antillarum* and *P. sandvicense*, which are characteristically "honeycombed" in appearance, occur within the distributional ranges of the chitons *C. lata* and *C. larvaeformis* respectively (see Littler *et al*. 1995, Ocean Biogeographic Information System 2013, continuously updated). It is thus not inconceivable that the "honeycombed" appearances of these taxa resulted from chiton grazing. In this coralline-herbivore interaction, the importance of *P. onkodes* as a source of food and refuge for the chitons is clearly evident. Similar interactions have been documented elsewhere (e.g. Steneck 1982, Maneveldt *et al*. 2006, Maneveldt & Keats 2008) and symbiont fidelity may be more common than previously assumed.

Conclusion

Arguably, the one gap in this study is the lack of molecular data to support our conclusions. However, until the challenge of DNA amplification of old type specimens is overcome, all we are left with are reviews based on phenotypes of type material for advancing taxonomic knowledge. Having said this, we are not discounting the importance of molecular analyses. On the contrary, we accept that such analyses are critical to fully understanding the distributions of all things biological.

In summary, the conspecificity of a number of taxa ascribed to the genus *Porolithon*, based here on morphological and anatomical data, will clearly have both biogeographic and biodiversity implications. While this study has increased the geographic range of *P. onkodes*, it has also resulted in the reduction of the number of real taxa and so many species checklists will need to be revised. Chamberlain (1991) had already concluded that after thorough study of types and modern material, a considerable reduction in the number of real species would occur. This has not only become true for a number of other coralline floras (e.g. Woelkerling 1997, Maneveldt *et al*. 2008), but also for the genera *Hydrolithon* and *Porolithon*.

Acknowledgements

We thank the Department of Biodiversity & Conservation Biology (BCB) at the University of the Western Cape for providing funding and research equipment, and the South African National Research Foundation (NRF) for research grants to GWM and DWK. We are most grateful to the following for providing invaluable discussion and input: Walter H. Adey, Julio Afonso-Carrillo, Alan Channing, Yvonne M. Chamberlain, Raphael Riosmena-Rodríguez, Paul C. Silva and William J. Woelkerling. Yvonne M. Chamberlain (BM), Sigurd M. Såstad and Tommy Prestø (TRH) and William J. Woelkerling (PC) greatly facilitated the loan of herbarium specimens. Special thanks to William J. Woelkerling, Paul W. Gabrielson and Adele Harvey for invaluable comments to an earlier draft of this manuscript. We also thank two anonymous reviewers for their valued comments.

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