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Three species of *Hydrolithon* (Rhodophyta, Corallinaceae): *Hydrolithon onkodes* (Heydrich) Penrose and Woelkerling, *Hydrolithon superficiale* sp. nov., and *H. samoënse* (Foslie) comb. nov. from South Africa

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Three species of *Hydrolithon* are reported from South Africa. *Hydrolithon onkodes* occurs on the southernmost coral reefs in the western Indian Ocean at Sodwana Bay, Natal. *Hydrolithon superficiale* sp. nov. is described on the basis of a distinctive layer of conceptacles that occur in a superficial layer of lightly calcified filaments with long, thin cells, that are sharply differentiated from the filaments of short cells in the thallus below. This species has been found only in the Sodwana Bay area of Natal Province. *Lithophyllum samoënse* Foslie is transferred to *Hydrolithon* on the basis of the anatomy of the tetrasporangial pore. It was also determined that *H. samoënse* (Foslie) comb. nov. is conspecific with *Spongites wildpretti* Afonso-Carrillo and *Neogoniolithon illitus* (Lemoine) Afonso-Carrillo. *Hydrolithon samoënse* is known to occur throughout South Africa.

Drie spesies van *Hydrolithon* is uit Suid-Afrika gerapporteer. *Hydrolithon onkodes* kom voor op die mees suidelike koraalriwwe in die westelike Indiese Oseaan by Sodwanabaai, Natal. *Hydrolithon superficiale* sp. nov. is beskryf, gebaseer op 'n onderskeidende laag van konseptakels wat voorkom in 'n oppervlakkige laag van ligte verkalkte filamente met lang dun selle wat duidelik verskil van die filamente van kort selle in die onderliggende tallus. Hierdie spesie is slegs in die Sodwanabaai gebied van Natal gevind. *Lithophyllum samoënse* Foslie is oorgedra na *Hydrolithon* gebaseer op die anatomie van die tatrasporangiale porie. Daar is ook vasgestel dat *H. samoënse* (Foslie) comb. nov. konspesifiek is met *Spongites wildpretii* Afonso-Carrillo en *Neogoniolithon illitus* (Lemoine) Afonso-Carrillo. *Hydrolithon samoënse* kom regdeur Suid-Afrika voor.

Keywords: Coralline algae, coral reef, *Hydrolithon*, *Lithophyllum*, *Neogoniolithon*, South Africa, *Spongites*, taxonomy.

Introduction

The coralline algae are an ecologically important group of marine plants in South Africa (Chamberlain 1993; Keats *et al.* 1993) and throughout the world (Woelkerling 1988), yet their ecology has been poorly studied. Part of the reason for this is the lack of modern taxonomic treatments for most regions of the world, including South Africa (Chamberlain 1983; Woelkerling 1988). Therefore, a study is being made of the taxonomy of South African non-geniculate coralline algae based on collections made by Yvonne Chamberlain, Richard Norris, Derek Keats and other colleagues. Priority is being given to studying ecologically significant species [e.g. *Spongites yendoi* (Foslie), Chamberlain (1993)], and new or otherwise taxonomically interesting species [e.g. *Spongites amplexifrons* (Harvey), Chamberlain & Norris, in press].

Three species attributable to the mastophoroid genus *Hydrolithon* Foslie are considered in the present paper. No previously described species has been found to agree with one species which is now described as new to science. Two other species are compared with type specimens and published records.

Materials and Methods

Subtidal collections were made by SCUBA diving. All specimens were removed from the substrate using a hammer and cold chisel. Data were obtained from type collections housed at C (Botanical Museum, Copenhagen) and TRH (Kongelige Norske Videnskabernes Selskab Museet, Trondheim). For scanning electron microscopy, air-dried material was fractured using either finger nails, forceps, diagonal cutters, or a small hammer and cold chisel. Wherever possible, a fracture perpendicular to a leading edge was used to determine internal anatomy. The fractured pieces were mounted on stubs, using adhesive tabs (Agar Scientific, 66a Cambridge Rd., Stanstead, Essex CM24 8DA, UK), stored in a desiccator for at least 24 h prior to examination, coated with gold for 2 – 3 min in an Edwards S150B sputter coater, and examined with an Hitachi X650 scanning electron microscope, equipped with a Mamiya 6×7 camera. Accelerating voltage was 20 kV initially, but was later increased to 25 kV for improved resolution.

For light microscopy, formalin-preserved specimens were first decalcified in 10% nitric acid, and then sectioned at 10 – 30 μm thickness using a Leitz CO_2 freezing microtome. Each individual section was removed from the microtome blade using a fine sable hair brush, and transferred to a slide containing aniline blue in 50% Karo syrup. Drawings were made directly from prepared slides using a Zeiss microscope equipped with a drawing tube.

Conceptacle outside diameter was measured directly from the SEM. All other measurements were made using a calibrated eyepiece micrometer. 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 the system of Adey and Adey (1973). Thallus terminology follows that of Chamberlain (1990, 1993).

Observations

Hydrolithon onkodes (Heydrich) Penrose & Woelkerling 1992: 3

BASIONYM: *Lithothamnion onkodes* Heydrich 1897: 6

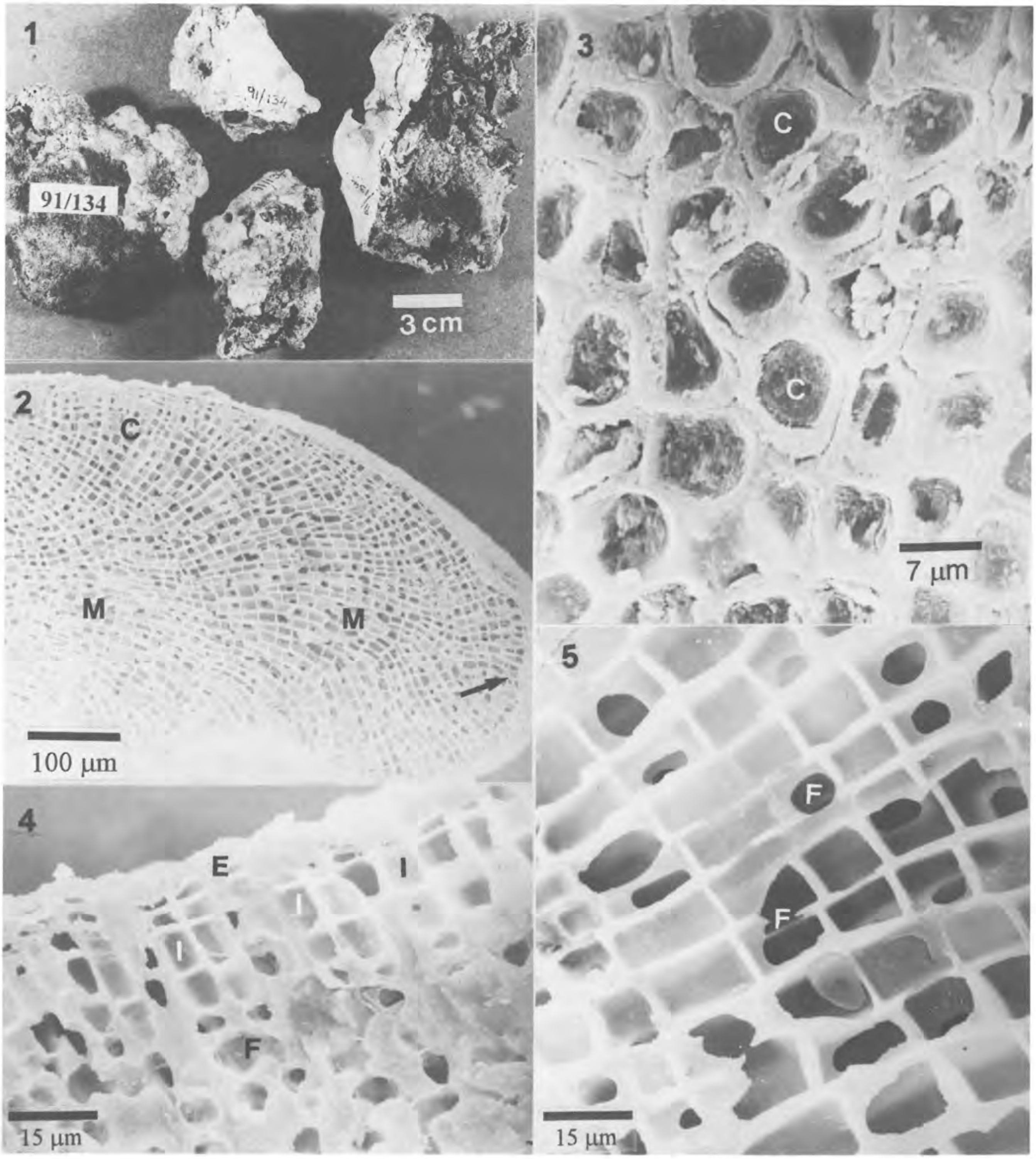
SYNONYMS: *Goniolithon onkodes* Foslie 1898: 8; *Lithophyllum onkodes* (Heydrich) Heydrich 1901: 533; *Porolithon onkodes* (Heydrich) Foslie 1909: 57; *Spongites onkodes* (Heydrich) Penrose & Woelkerling 1988: 173.

LECTOTYPE: TRH. Tawi Island, north-west edge of Huon Gulf, New Guinea, Heydrich No. 97 (see Penrose & Woelkerling 1988: 162; 1992: 83).

ETYMOLOGY: *onkodes* means swollen.

Habit and vegetative structure

Thallus non-geniculate, adherent on rock and dead coral



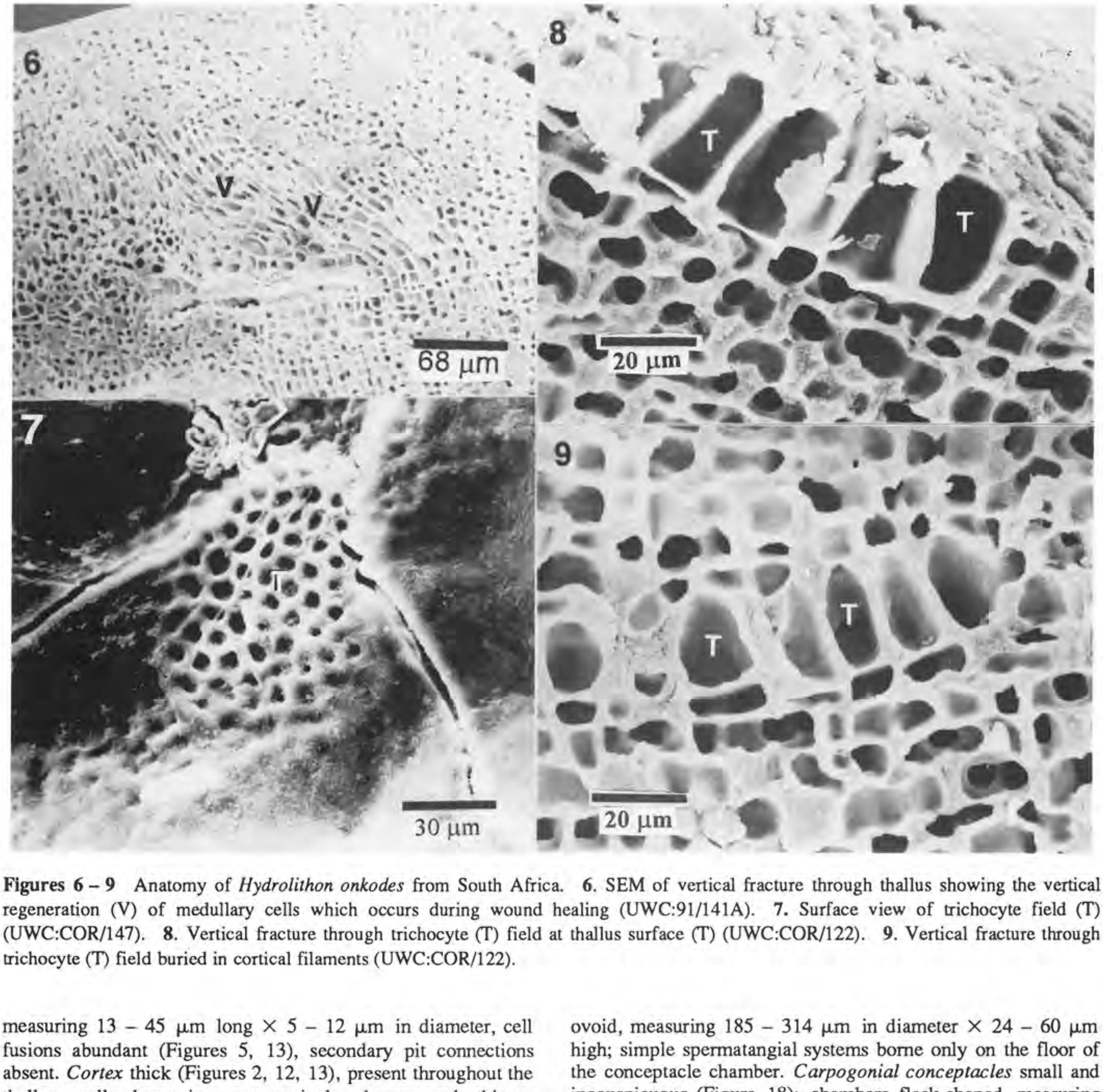
Figures 1 – 5 Habit and vegetative anatomy of *Hydrolithon onkodes* from South Africa. **1.** Habit photographs of representative specimens (UWC:91/134). **2.** Vertical fracture through thallus margin, showing medulla (M), cortex (C), and terminal initials at thallus margin (arrow) (UWC: 91/141A). **3.** Thallus surface showing calcified rims surrounding epithallial concavities (C) (UWC:91/141A). **4.** Vertical fracture near thallus surface, showing epithallial cells (E), subepithallial initials (I), and cell fusions (F) (UWC:91/141A). **5.** Vertical fracture through medulla showing cell shape, and cell fusions (F) (UWC:91/141A).

skeletons (Figure 1), to at least 100 mm in diameter, 1 – 10 mm thick, flat to low lumpy when conforming to substratum, lacking protuberances (Figure 1), thalli orbicular becoming confluent. *Margin* adherent, entire to lobed, lacking orbital ridges. *Surface* smooth, but frequently grazed by sea urchins or deeply bitten by parrotfish, cell surface (SEM) *Phymatolithon*-type (Figure 3); colour pale greyish pink in well-lit situations; texture granular owing to the presence of abundant trichocyte fields (Figure 7) that measure 63 – 131 µm in diameter and are easily visible with a hand lens.

Conceptacles slightly raised (Figure 10), all types measuring up to *ca.* 130 µm in external diameter; when conceptacles are densely crowded, trichocyte fields are entirely absent.

Thallus overgrowing *Neogoniolithon* spp., *Hydrolithon* spp., *Mesophyllum erubescens.*

Thallus monomerous. *Medulla* consists of a thick, central plumose core of filaments (Figures 2, 5, 12, 13), with cells that are approximately 1.6 – 4 times as long as they are wide,



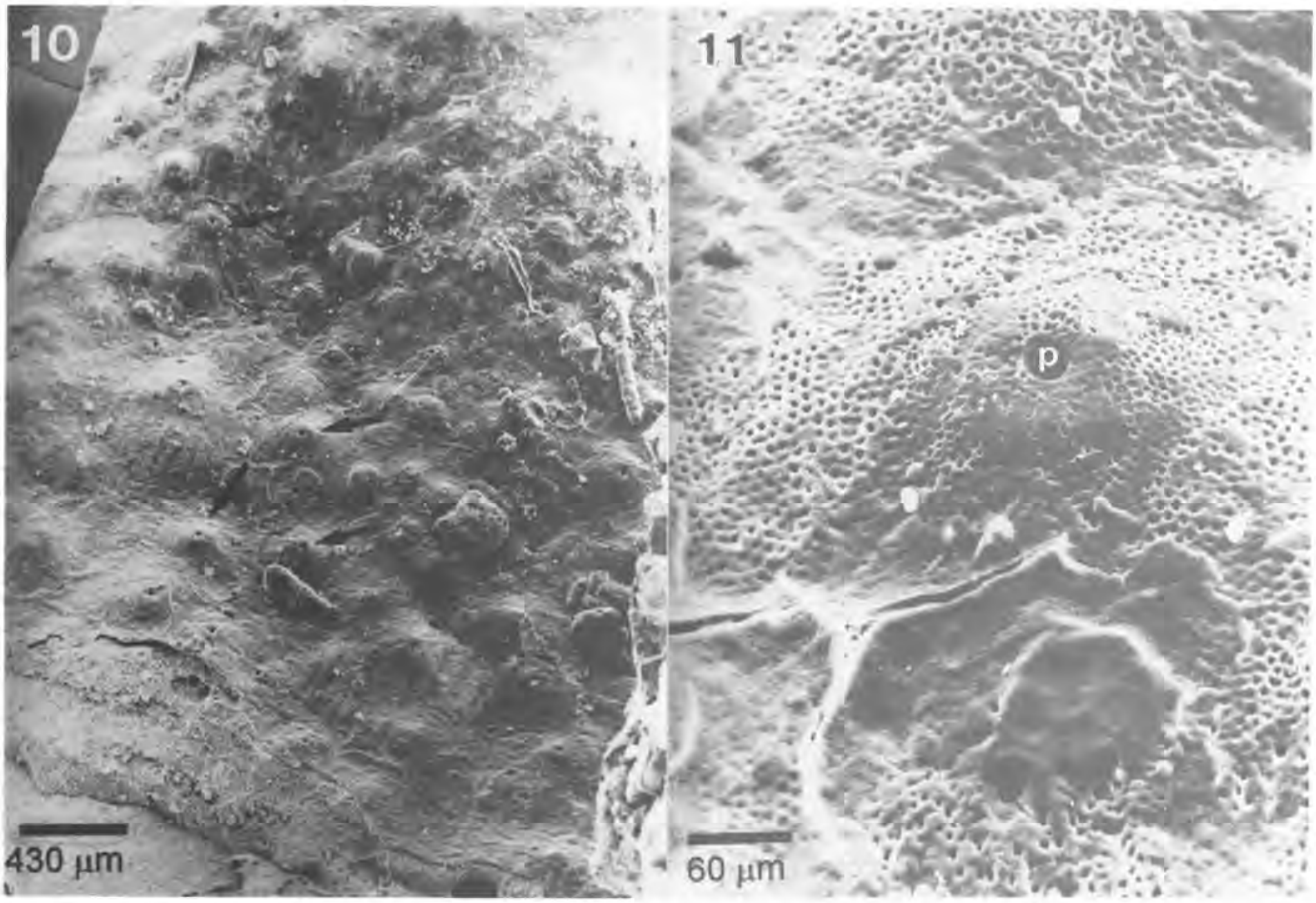
Figures 6 – 9 Anatomy of *Hydrolithon onkodes* from South Africa. **6.** SEM of vertical fracture through thallus showing the vertical regeneration (V) of medullary cells which occurs during wound healing (UWC:91/141A). **7.** Surface view of trichocyte field (T) (UWC:COR/147). **8.** Vertical fracture through trichocyte (T) field at thallus surface (T) (UWC:COR/122). **9.** Vertical fracture through trichocyte (T) field buried in cortical filaments (UWC:COR/122).

measuring 13 – 45 µm long × 5 – 12 µm in diameter, cell fusions abundant (Figures 5, 13), secondary pit connections absent. *Cortex* thick (Figures 2, 12, 13), present throughout the thallus, cells becoming progressively shorter and thinner towards the thallus surface (Figures 2, 13), measuring 5 – 15 µm long × 4 – 10 µm in diameter, cell fusions abundant (Figures 4, 13), secondary pit connections absent; buried trichocyte fields frequent (Figure 9). *Subepithallial initial* squarish to elongate (Figures 4, 13), measuring 4 – 11 µm length × 4 – 7 µm in diameter. *Epithallial cells* (Figures 2, 4, 13), domed when young but flattening with age, measuring 2 – 5 µm length × 3 – 7 µm diameter, 1 – 3 cell layers, outer layer frequently sloughed to reveal primary pit connections (Figure 3), having a thin outer wall that is often collapsed into the cell lumen in air-dried specimens (Figure 3). Fields of elongate trichocytes (Figures 8, 14) occurring commonly at thallus surface, individual trichocytes measuring 21 – 43 µm long × 9 – 21 µm in diameter.

Reproduction

Gametangial plants monoecious or dioecious. *Male conceptacles* have a much larger chamber than sporangial conceptacles, but as they are often deep within the cortical layer, they usually appear to be of a similar size to sporangial conceptacles on the outer surface, chamber wide and shallow, or ovoid, measuring 185 – 314 µm in diameter × 24 – 60 µm high; simple spermatangial systems borne only on the floor of the conceptacle chamber. *Carpogonial conceptacles* small and inconspicuous (Figure 18); chambers flask-shaped, measuring 37 – 95 µm in diameter × 18 – 40 µm high with the roof *ca.* 18 µm thick, chamber flask-shaped, often near the surface but sometimes sunken to 170 µm deep, with a long pore canal (up to 130 µm) leading to the surface, carpogonia occurring centrally on the chamber floor (Figure 18), carpogonial branch 3-celled. Completely immersed conceptacles containing carpogonia occurring frequently. Carposporangia developing in carpogonial conceptacles after presumed karyogamy. *Carposporangial conceptacle* chambers elliptical, measuring 135 – 225 µm in diameter × 66 – 82 µm high with the roof up to 55 µm thick, pore canal (Figure 19) lined with small filaments, central fusion cell narrow and thick (Figure 19), gonimoblast filaments borne peripherally, 5 – 8 cells long including a terminal carpospore that measures 30 – 62 µm long × 50 – 63 µm in diameter, mature carpospores almost filling conceptacle chamber (Figure 19).

Tetrasporangial conceptable chambers (Figures 5, 15) elliptical, measuring 115 – 250 µm in diameter, 60 – 130 µm high, with the roof 40 – 55 µm thick, roof formed from filaments interspersed among the sporangia and pore canal lined by a ring of enlarged, domed cells. Small central columella (Figure 19) present. Tetrasporangia zonately divided (Figures 15, 16,



Figures 10 – 11 Tetrasporangial conceptacles of *Hydrolithon onkodes* from South Africa (UWC:COR/159). **10**. Surface view showing numerous conceptacles (arrows). **11**. A single conceptacle showing that it is slightly raised (p, pore).

17), measuring 25 – 50 µm long × 12 – 25 µm in diameter and densely staining when young (Figure 16), increasing to 90 – 120 µm long × 41 – 53 µm in diameter and weakly staining prior to release (Figure 17), mainly arranged at the conceptacle periphery (Figure 15). Bisporangial plants not seen.

Conceptacles of all types not shed, becoming buried in the thallus (Figure 12), and often containing apparently viable gametes or sporangia.

Habitat and phenology

Hydrolithon onkodes is one of the most common corallines in the shallower area of the reef (<10 m), where it occurs both on sandstone bedrock and old stony coral. It is most abundant on the area of the reef referred to by Ramsay and Mason (1990) as the reef crest. It is particularly common in sea urchin territories and among the bases of old staghorn coral [*Acropora bruggemanni* (Brook)]; it occurs to a depth of 20 m or more. The surface is frequently grazed by sea urchins and may show deep bites from parrotfish feeding. Thallus regeneration to repair this damage is commonly observed. It was found on all reefs sampled but is most abundant on Two Mile Reef at 10 – 14 m depth and Quarter Mile Reef at 6 – 8 m depth.

Conceptacles of all reproductive types were observed in January, February, July and November — no collections at other times.

Distribution

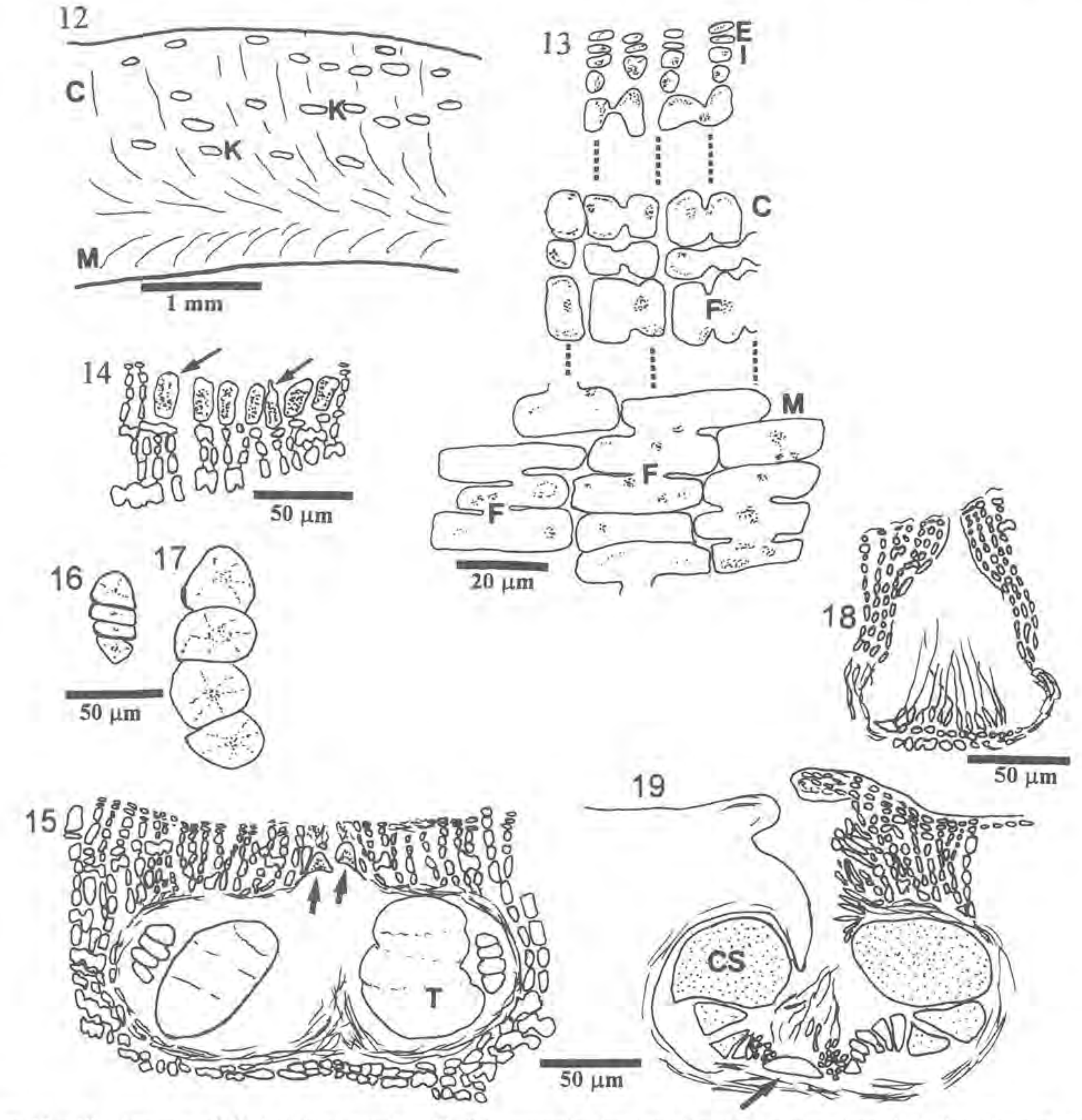
South Africa: Sodwana Bay, Natal Province. World: Throughout the tropical Indo-Pacific region.

Specimens examined

—2732 (Ubombo): Two-mile Reef, Sodwana Bay, on old dead coral in full light 9 – 12 m depth, *D. Keats* (UWC:COR/122); Anton's Reef, dead coral, rock edges and urchin territories, 10 m depth, *D. Keats* (UWC:COR/147); Five-Mile Reef, cementing dead coral, 18 – 22 m depth, *D. Keats* (UWC:COR/158); Two-Mile Reef, on dead coral, rock edges and in urchin territories, 10 – 12 m depth, *D. Keats* (UWC:COR/159); Five-Mile Reef, on rock in urchin territories, 15 – 20 m depth, *D. Keats* (UWC:COR/320); Two-Mile Reef, on old dead coral and rock, 12 m depth, *D. Keats* (UWC:COR/324); Two-Mile Reef, on old coral and rock, 12 m depth, *D. Keats* (UWC:COR/326); Two-Mile Reef, on rock, mainly in urchin territory, 12 – 14 m depth, *D. Keats & Y. Chamberlain* (UWC:91/148A); Five-Mile Reef, open rock surface, *ca.* 15 m depth, *D. Keats* (UWC:COR/314); Two-Mile Reef, rock and old coral, 15 – 18 m depth, *D. Keats & Y. Chamberlain* (UWC:91/169); Two-Mile Reef, on rock and old coral, especially abundant in territories of *Diadema* sp. and heavily grazed by sea urchins, *D. Keats & Y. Chamberlain* (UWC:91/134) (–DA).

Remarks

Hydrolithon onkodes is one of the most abundant shallow-water coralline algae throughout the tropical Indo-Pacific region (Adey *et al.* 1982; Gordon *et al.* 1976; Littler & Doty 1975). Its taxonomy has been well documented (Penrose & Woelkerling 1988, 1992), although detailed accounts and illustrations of the anatomy of freshly collected material are rare. Penrose and Woelkerling (1988) transferred *Porolithon onkodes* (Heydrich) Foslie to *Spongites* because it could not be distinguished at the generic level on the basis of previously used vegetative characters. Later, they recognized *Hydrolithon* on the basis of the sporangial pore structure described above, and moved *Spongites onkodes* (Heydrich) Penrose and Woelkerling to *Hydrolithon* (Penrose & Woelkerling 1992). Our observations confirm the inclusion of this species in the genus *Hydrolithon* on the basis of sporangial pore structure



Figures 12 – 19 Anatomy of *Hydrolithon onkodes*. **12.** Diagrammatic drawing of vertical section through thallus, showing medulla (M), cortex (C), and numerous buried conceptacles (K) (UWC:COR/324). **13.** Vertical section through thallus (M, medulla; F, cell fusion; C, cortex; I, subepithallial initial; E, epithallial cells) (UWC:COR/159). **14.** Vertical section through outer cortex, showing trichocytes (arrows) arranged in a field at thallus surface (UWC:COR/159). **15.** Tetrasporangial conceptacle showing sporangia (T). Arrows indicate large cells at the base of the sporangial pore (UWC:COR/122). **16.** Immature tetrasporangium (UWC:COR/159). **17.** Mature tetrasporangium just prior to release (UWC:COR/158). **18.** Vertical section of carpogonial conceptacle (UWC:COR/314). **19.** Vertical section through carposporangial conceptacle, showing single fusion cell (arrow) and gonimoblast filaments terminated by a large carpospore (CS) (UWC:COR/122).

(Penrose & Woelkerling 1992). This species is confined to the warmer subtropical waters off the Natal coast.

Hydrolithon onkodes is characterized as follows: thallus thick, adherent; thallus monomerous; medulla plumose; sporangial conceptacles that are only slightly raised or flush with the thallus surface; trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented fields which give the thallus a distinctive granular appearance when they occur at the surface.

Hydrolithon superficiale sp. nov. (Figures 20 – 30)

Type specimen

Mbibi, Natal, in large tide pool on vertical rocks in surge channel (*D. Keats*, 1991-07-01, UWC: COR/302); specimen deposited with Rijksherbarium, Leiden, The Netherlands.

Etymology

'superficiale' refers to the distinct superficial layer within which conceptacles develop.

Diagnosis

Plants epilithic, crustose, flat; thallus dimerous; conceptacles borne on thallus surface and shed as a layer on senescence, conceptacle layer more lightly calcified than thallus, conceptacles hemispherical, tetrasporangial conceptacle chamber 72 – 91 µm diameter.

Plantae epiphyticae, crustosae, planae; thallus dimerus; conceptacula superficiei thalli insidentie et, quum senescentia, pro strato singulo, exuta; stratum conceptaculorum minus calcificatum quam thallus; conceptacula hemispherica, lumina conceptaculorum tetrasporangialium diametro 72 – 91 μm.

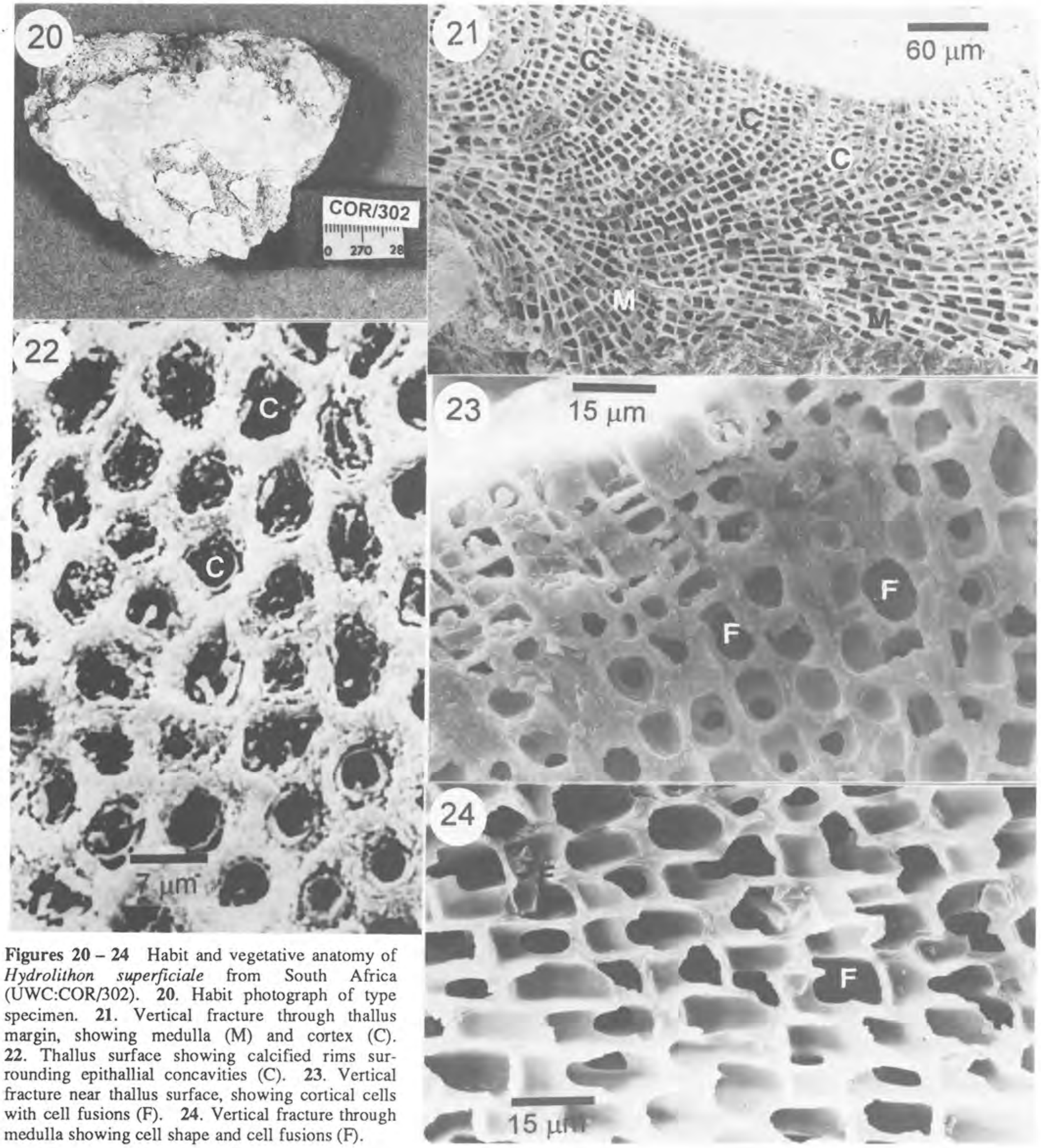
Habit and vegetative structure

Thallus non-geniculate, adherent, plants encrusting on rock, rubble or old coral (Figure 20), to at least 10 cm in diameter, 1200 μm thick; flat, with or without small protuberances up to 1 mm in diameter and 1 mm high; thalli orbicular becoming confluent, confluences flat. *Margin* adherent, entire to lobed, thin, without orbicular ridges. *Surface* smooth, cell surface (SEM) *Phymatolithon*-type (Figure 22), primary pit connections often visible; colour pale reddish pink, texture matt.

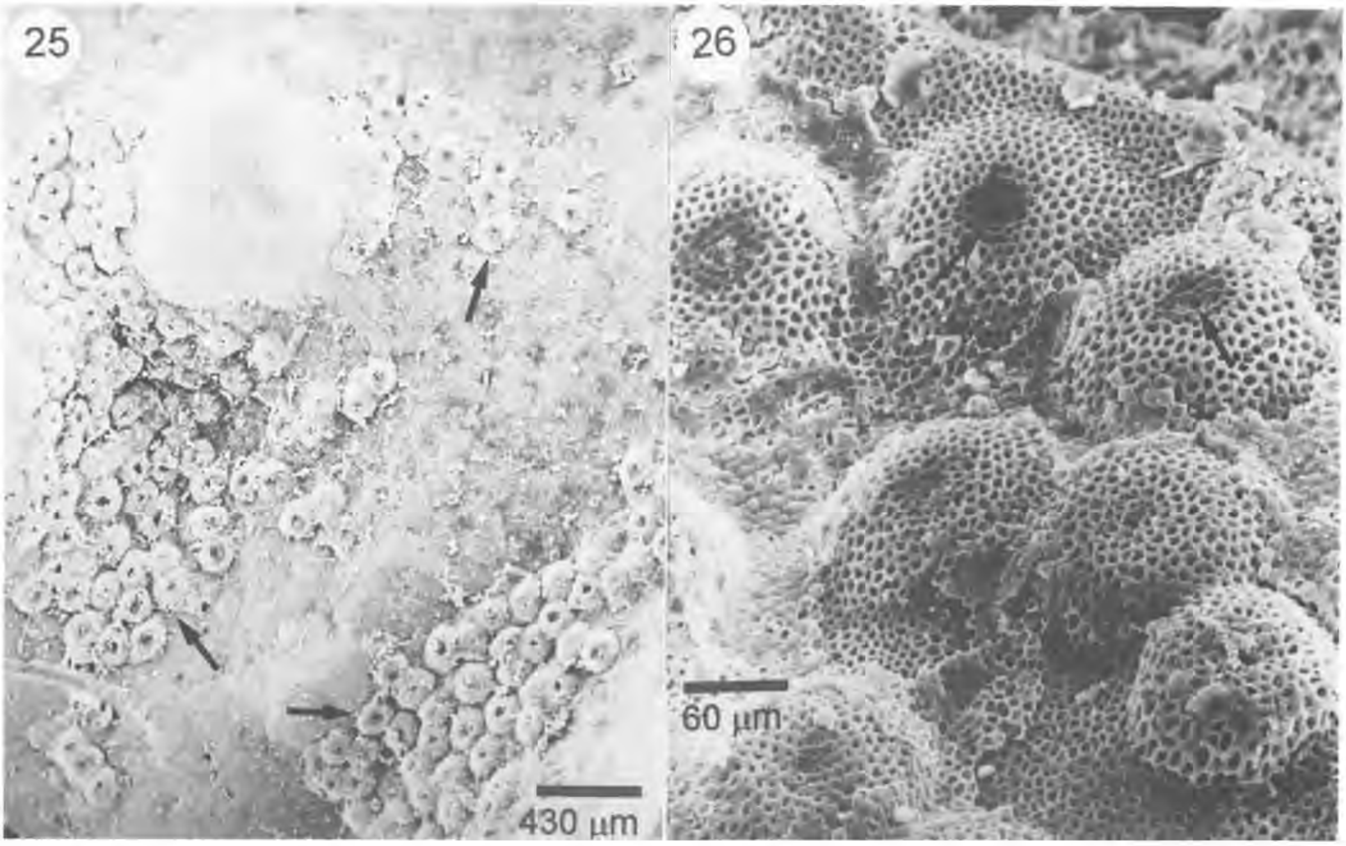
Conceptacles occur in patches (Figures 25, 26), confluent, densely crowded, translucent with pore slightly sunken (Figure 26), tetrasporangial conceptacles measuring 117 – 156 μm in diameter.

Thallus overgrowth data not recorded.

Thallus monomerous. *Medulla* up to 200 μm thick (Figures 21, 27), composed of filaments of elongate cells (Figures 24, 28), measuring 12 – 22 μm long × 8 – 12 μm diameter, cell fusions common (Figures 24, 28), secondary pit connections absent; terminal initial conspicuous, measuring 7 – 12 μm long × 3 – 6 μm in diameter. *Cortex* up to 650 μm or more thick (Figures 21, 23, 27), cells squarish to shorter than wide (Figures 23, 28), sometimes elongate, 4 – 5 (8) μm long × 4 – 8 μm in diameter, cell fusions abundant (Figures 23, 28), occupying most of adjacent walls; buried individual trichocytes



Figures 20 – 24 Habit and vegetative anatomy of *Hydrolithon superficiale* from South Africa (UWC:COR/302). **20**. Habit photograph of type specimen. **21**. Vertical fracture through thallus margin, showing medulla (M) and cortex (C). **22**. Thallus surface showing calcified rims surrounding epithallial concavities (C). **23**. Vertical fracture near thallus surface, showing cortical cells with cell fusions (F). **24**. Vertical fracture through medulla showing cell shape and cell fusions (F).



Figures 25, 26 Surface view of tetrasporangial conceptacles of *Hydrolithon superficiale*. **25**. Aggregations of uniporate conceptacles (arrows). **26**. Uniporate conceptacles showing hemispherical shape, and the pore sunken at the centre of a small depression (arrow).

occasional. *Subepithallial initial* in vegetative thallus squarish (Figure 28), measuring 4 – 8 µm long × 3.5 – 7 µm in diameter, in reproductive thallus markedly tall and thin, measuring 8 – 12.5 µm long × 3 – 6 µm in diameter. *Epithallial cells* in vegetative thallus domed (Figure 28), single, measuring 3 – 5 µm long × 5 – 7 µm in diameter; in reproductive thallus round to elongate (Figure 30), measuring 6 – 8 µm long × 5.5 – 9 µm in diameter; apparently fragile and often absent in vegetative thallus. Individual trichocytes present occasionally, flask-shaped (Figure 28), measuring *ca.* 13 µm long × 10 µm in diameter.

Reproduction

Gametangial plants not seen. *Tetrasporangial conceptacles* domed, borne in a distinct, superficial layer (Figures 25, 27, 29, 30) of thin-walled cells; the layer is differentiated in texture from the well-calcified cortex (Figure 23) below. Chambers domed, measuring 72 – 91 µm in diameter × 52 – 62 µm high, with the roof 26 – 31 µm thick, roof (Figures 29, 30) formed from filaments interspersed among the sporangia, composed of a rounded to elongate epithallial cell, a columnar cell, and 1 – 2 inner squarish cells (Figures 29, 30), pore canal with a ring of enlarged, elongate cells (Figures 29, 30) initiated by sterile cavity cells. Conceptacles always containing densely stained, immature sporangia (Figures 29, 30), some also having mature, lightly stained tetrasporangia (Figure 30). Tetrasporangia zonately divided (Figure 30), borne across conceptacle floor, deeply invaginate, measuring 24 – 26 µm in length × 12 – 20 µm in diameter. Bisporangial plants not seen. Entire conceptacle layer sloughed off after release of spores, never buried in the thallus.

Habitat and phenology

Found mainly in the upper sublittoral, in very large tide pools, and along the sublittoral fringe at fairly exposed sites, often in surge channels. Conceptacles of all types observed in November, January and July — no collections at other times.

Distribution

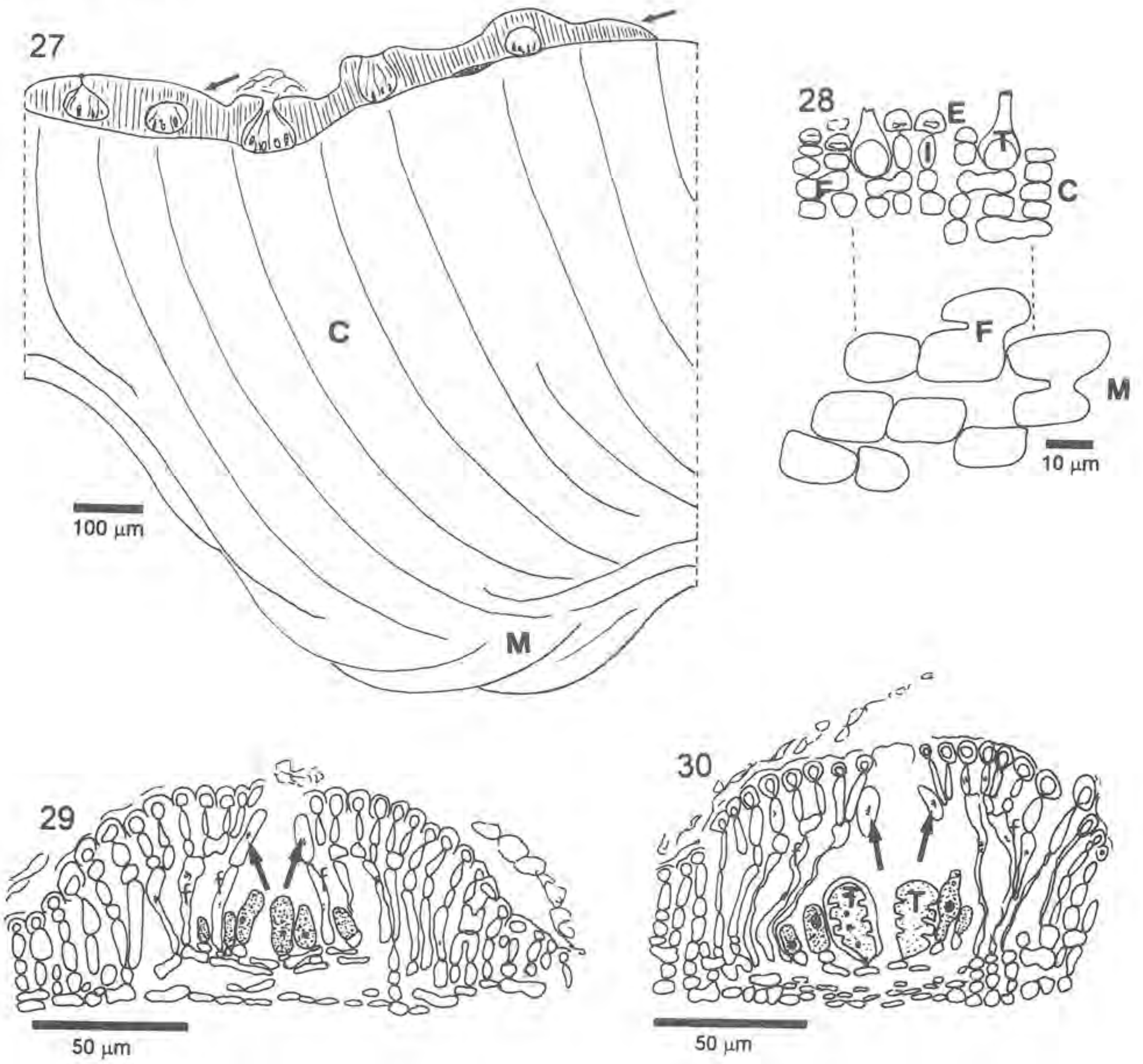
South Africa: Known only from the Sodwana Bay area of Natal Province. World: not reported outside of South Africa.

Specimens examined

—**2732** (Ubombo): Mbibi, in large tide pool on vertical rocks in surge channel, *D. Keats* (UWC:COR/302); Mbibi, large tide pool at 2 m depth along bottom of overhang at base of wall, *D. Keats* (UWC:COR/139); Mbibi, sides of surge channel, 1 – 2 m depth, *D. Keats* (UWC: 92/2) (–DA).

Remarks

Hydrolithon superficiale is very distinctive because no other recorded species of *Hydrolithon* has been found with a superficial development of conceptacle-bearing thallus. This species has only been recorded from the subtropical waters off northern Natal Province. It is of particular interest in the context of mastophoroid taxonomy. Until recently (Penrose & Chamberlain 1993), *Hydrolithon* and *Fosliella* have been regarded as distinct genera. However, Penrose and Chamberlain (1993) found that the distinctive *Hydrolithon* pore structure occurred in the type specimen of *Fosliella farinosa* (Lamouroux) Howe which is the type of the genus *Fosliella* Howe (1920). They also observed the same pore structure in plants pertaining to *Fosliella* as defined by Chamberlain (1983) collected in many parts of the world. They proposed therefore that *Fosliella* should be subsumed in *Hydrolithon*. They also proposed that the distinctive, thin, possibly neotenous plants, with 4-celled germination discs (Chamberlain 1983, 1984), previously referred to *Fosliella*, should be termed the *Fosliella*-state of *Hydrolithon* to draw attention to their



Figures 27 – 30 Vertical sections of tetrasporangial plants of *Hydrolithon superficiale* [UWC:COR/139 (= YMC:92/13)]. **27**. Diagrammatic drawing of a vertical section through thallus, showing medulla (M), cortex (C) and conceptacle-bearing layer at surface (arrow). **28**. Vertical section through thallus (M, medulla; F, cell fusion; C, cortex; E, epithallial cell; I, subepithallial initial; T, trichocyte). **29**. Immature conceptacle showing sporangial initials (shaded) interspersed among sterile filaments (f); conceptacle pore cells (arrows) are attached to sterile filaments. **30**. More mature tetrasporangial conceptacle in which two incompletely divided tetrasporangia (T) have developed, sterile filaments are senescing (f), and pore cells (arrows) have become detached.

characteristic features.

The ephemeral nature of the reproductive layer in *H. superficiale* recalls plants attributable to possibly neotenous, *Fosliella*-state species of *Hydrolithon* such as *H. farinosum* (Penrose & Chamberlain 1993). However, the robust crustose thallus is characteristic of other, presumably perennating, *Hydrolithon* species such as *H. onkodes*. This suggests that, like *H. cymodoceae* (Penrose 1992), *H. superficiale* may prove to have an associated, thin form. Culture experiments might elucidate the relationship among such species.

Hydrolithon superficiale differs from *H. cymodoceae* (Foslie) D. Penrose (1992) in having tetrasporangial conceptacles with numerous continuously produced tetrasporangia, not one, or sometimes two sporangia; from *H. farinosum* (Lamouroux) D. Penrose & Y. Chamberlain (1993) and *H. cruciatum* Bressan in Bressan, Miniati-Radin & Smundin, in having thick thalli with a distinct, ephemeral sporangial layer; from *H. onkodes*, *H. reinboldii* (Weber van Bosse & Foslie in Foslie) Foslie and *H. samoënse* in having a distinct, ephemeral sporangial layer.

The distinguishing features of *H. superficiale* are as follows: thalli thin, adherent, flat; thallus monomerous; individual, burying trichocytes occasional; tetrasporangial conceptacles borne in a superficial, lightly calcified layer; conceptacle-bearing layer shed as a unit on senescence.

Hydrolithon samoënse (Foslie) comb. nov.

BASIONYM: *Lithophyllum samoënse* Foslie 1906: 20

SYNONYMS: *Pseudolithophyllum samoënse* (Foslie) Adey 1970: 13; *Lithophyllum illitus* Lemoine 1929: 54; *Neogoniolithon illitus* (Lemoine) Afonso-Carrillo 1984: 133; *Spongites wildpretii* Afonso-Carillo 1988: 99.

LECTOTYPE: TRH! Satana on Savi Island, Samoa, *Reichinger*, July 1905, where a freshwater stream met the shore (see Woelkerling 1993). Printz 1929, pl. 53, Figure 19 (as *Lithophyllum*).

ETYMOLOGY: '*samoënse*' refers to the type locality in the Samoan island group.

Habit and vegetative structure

Thallus non-geniculate, strongly adherent, up to 10 cm or more in diameter, plants encrusting on rock and stones (Figures 31 – 33), up to at least 10 cm in diameter, 470 μm thick; flat, lacking protuberances; thalli orbicular becoming confluent, confluences flat, margin adherent, thin without orbital ridges. *Surface* covered with low humps (Figure 32), cell surface (SEM) *Phymatolithon*-type (Figures 35, 36), primary pit connections often visible; colour gleaming purplish-red, texture matt, craters of old conceptacles, white patches and swirls of sloughing epithallial cells common.

Conceptacles crowded across thallus (Figures 31, 36), appearing as tiny, pale pin-points in fresh material, varying from slightly raised (Figure 40) to flush with, to sunken below thallus surface, measuring up to *ca.* 100 μm in diameter.

Thallus overgrowing *Spongites yendoi* (Foslie) Y. Chamberlain; overgrown by *Mesophyllum discrepans* (Foslie) Lemoine, *Leptophytum acervatum* (Foslie) Chamberlain & Keats, *Spongites discoideus* (Foslie) Y. Chamberlain, *Ralfsia verrucosa* (Areschoug) J. Agardh, *Lithophyllum* sp.

Thallus monomerous. *Medulla* (Figures 34, 38, 41, 44) composed of 2 – 5 filaments of elongate cells measuring 4 – 8 μm long × 2.5 – 9 μm diameter, cell fusions common (Figures 37, 42). *Cortex* (Figures 34, 37, 42 – 44) present throughout thallus and composing most of the thallus thickness, cells squarish or shorter than wide, sometimes elongate, measuring 4 – 9 μm long × 4 – 9 μm diameter, appearing haphazard in arrangement. Cell fusions abundant (Figures 37, 42), occupying most length of adjacent walls (Figures 37, 44). *Subepithallial initials* (Figure 44) varying from short to elongate, measuring 5 – 12 μm long × 3 – 6 μm diameter. *Epithallial cells* single (Figures 37, 42), short and wide, measuring 2 – 4 μm long × 4 – 6 μm diameter, with thin outer wall. Individual trichocytes (Figures 42, 43) present occasionally, bottle-shaped, measuring *ca.* 14 μm length × 9 μm diameter.

Reproduction

Gametangial plants dioecious. *Male conceptacle* chambers domed (Figure 45), measuring 52 – 72 μm in diameter × 26 – 33 μm high, with the roof *ca.* 13 μm thick, and composed of filaments running parallel to the conceptacle surface; simple spermatangial systems borne on conceptacle chamber floor only. *Carpogonial conceptacles* inconspicuous, chambers elliptical to domed, measuring 37 – 56 μm in diameter × 18 – 22 μm high, with the roof 10 – 14 μm thick; carpogonia occurring across the chamber floor. Carpogonia developing in *carposporangial conceptacles* after presumed karyogamy; chambers (Figures 47, 48) domed measuring 85 – 130 μm (fused pair 190 μm) in diameter × 52 – 98 μm high, with the roof 20 – 26 μm thick, roof composed of rounded epithallial cell, tall thin cell, and small inner cell, gonimoblast filaments borne around the periphery of a central fusion cell (Figure 48), central fusion cell narrow and thick, borne on layer of tall cells (Figure 48), gonimoblast filaments borne peripherally, up to four cells long including terminal carposporangium that measures 27 – 42 μm long × 23 – 32 μm in diameter.

Tetrasporangial conceptacle chambers (Figure 46), circular to elliptical measuring 65 – 117 μm in diameter × 49 – 78 μm high, with the roof 13 – 26 μm thick; roof 2 – 3 cells thick (Figure 46), comprising elongate epithallial cell, columnar cell, with or without a small inner cell; pore canal lined with enlarged, more or less vertically oriented cells (Figure 46), tetrasporangia borne peripherally, zonately divided (Figure 46), measuring 20 – 39 μm long × (7) 13 – 23 μm in diameter. Bisporangial conceptacles not seen.

Old conceptacles shed, not becoming buried in the thallus; shed conceptacles leaving craters that become infilled.

Habitat and phenology

Common in pools, forming gleaming red thalli on large stones and vertical rock surfaces along the sublittoral fringe at exposed sites. Tetrasporangial conceptacles recorded in January, May, June and October. Gametangial conceptacles seen only once, in November.

Distribution

South Africa: Sodwana Bay to Yzerfontein. World: Canary Islands, Spain (Atlantic), France (Atlantic), British Isles, Tahiti, Hawaii(?).

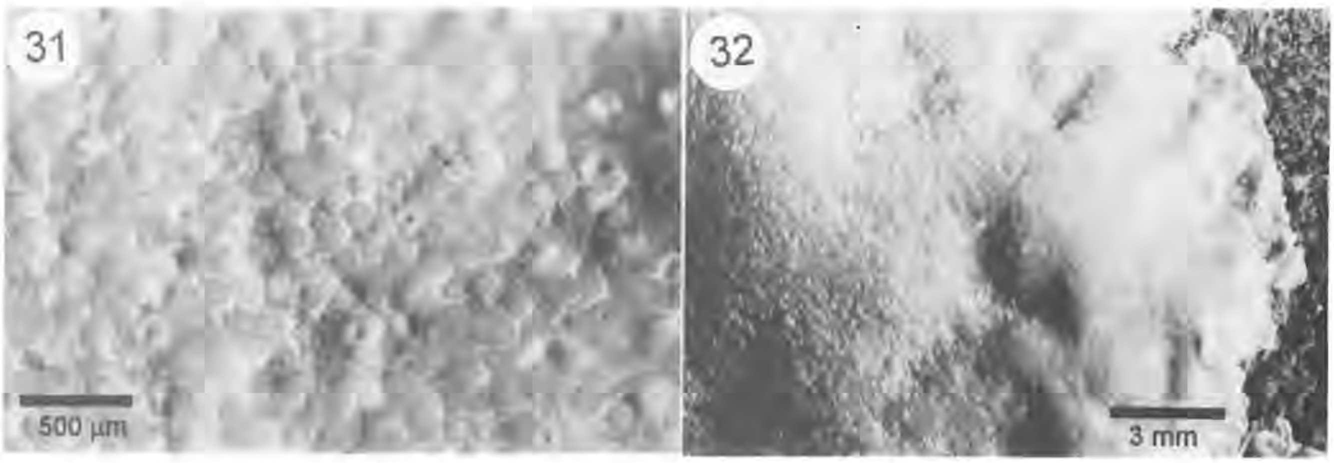
Specimens examined

—**3418** (Simonstown): Cape of Good Hope, *Y.M. Chamberlain* (YMC:89/248); Holbaaipunt, sublittoral fringe on bedrock (*D. Keats*, 1992-05-05, UWC:92/93); Holbaaipunt, low shore on wave exposed bedrock (*D. Keats*, 1992-05-18, UWC:92/98, and *D. Keats*, 1992-06-01, DWK:92/146); Chalumna, Eastern Cape (*Y.M. Chamberlain*, 1989-10-29, YMC:89/159); Betty's Bay (*Y.M. Chamberlain*, 1989-10-02, YMC:89/61A).

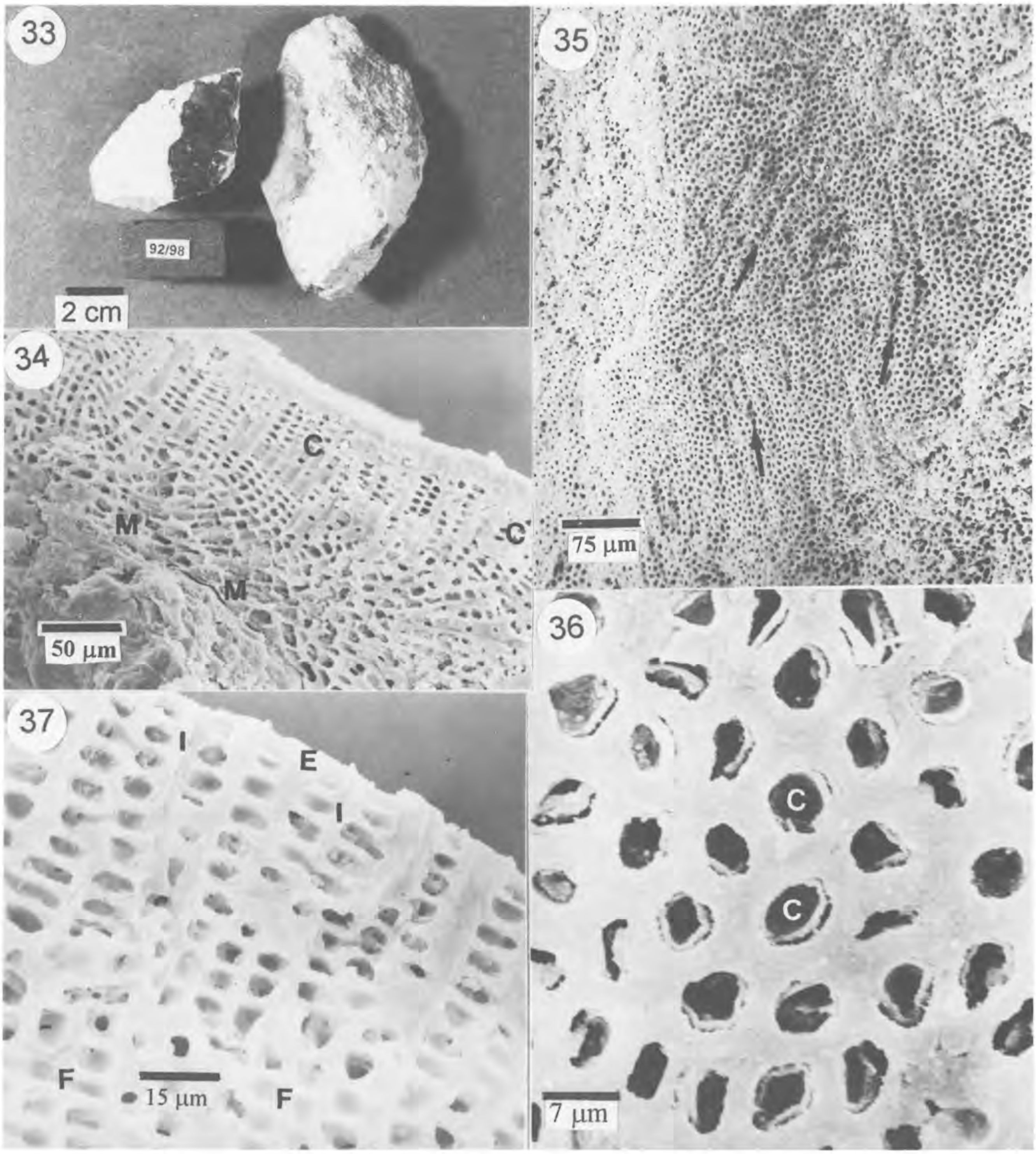
—**2732** (Ubombo): Jesser Point, on layers of old dead coralline algae, 2 – 3 m depth in surge area, *D. Keats & Y. Chamberlain* (UWC:91/179 & YMC:91/179) (–DA).

Remarks

The lectotype of *Lithophyllum samoënse* comprises three lumps of shale (Printz 1929, pl. LIII, Figure 19) measuring up to 10 cm in diameter. These were collected by Reichinger in July 1905, at Satana on the Samoan island of Savii, and were

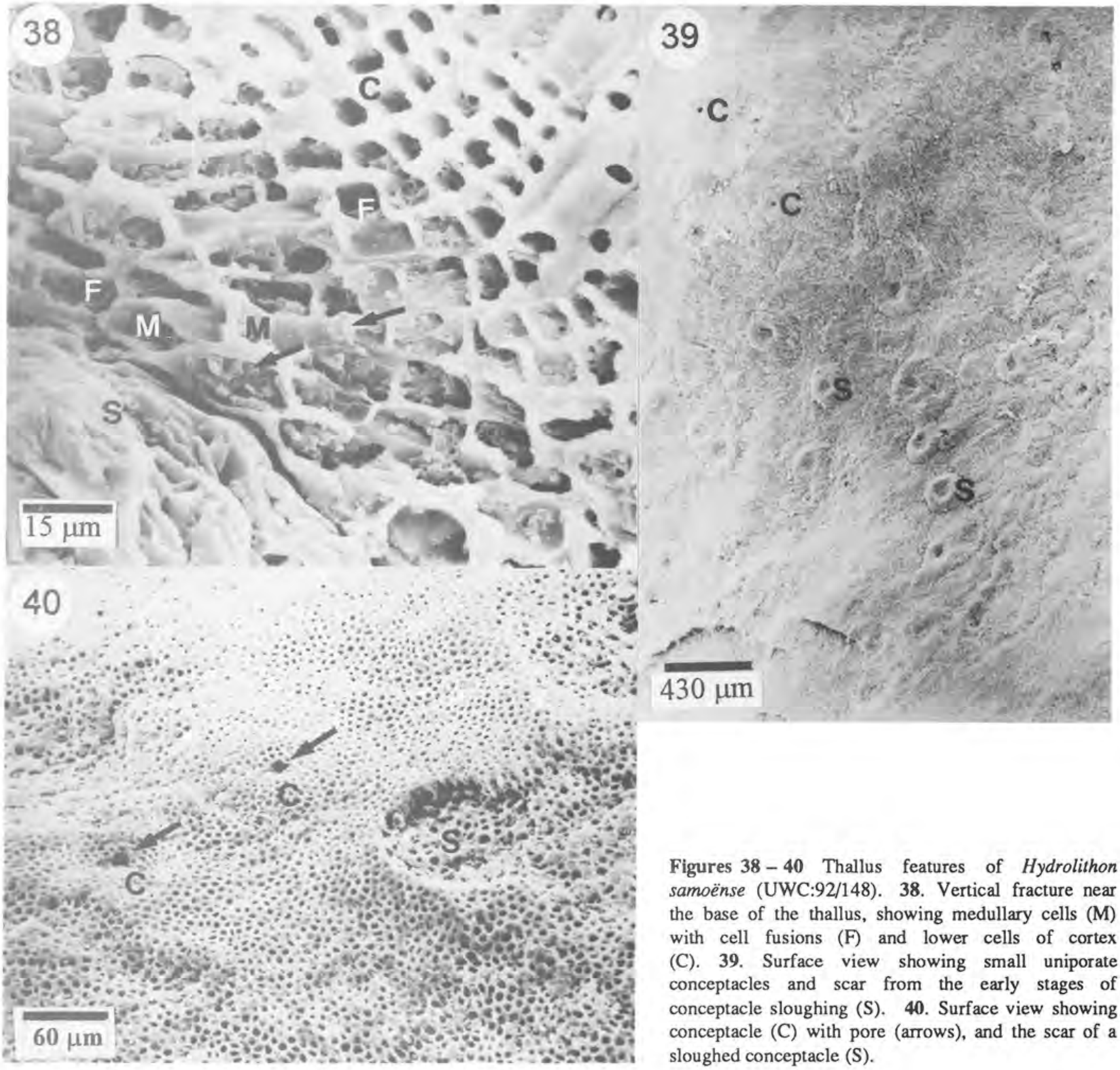


Figures 31, 32 Surface views of *Hydrolithon samoënse* (UWC:91/179). **31**. Typical pock-marked surface resulting from the sloughing of old conceptacles. 32. Densely crowded, small disc-like conceptacles at the surface.



Figures 33 – 37 Habit and vegetative anatomy of *Hydrolithon samoënse*. **33**. Habit photograph of typical specimen (UWC:92/98). **34**. Vertical fracture through thallus showing medulla (M) and cortex (C) (UWC:92/148). **35**. Thallus surface showing numerous scars from limpet grazing (UWC:92/148). **36**. Thallus surface showing calcified rims surrounding epithallial concavities (C) (UWC:92/148). **37**. Vertical fracture near thallus surface showing cortical cells with cell fusions (F), subepithallial initial (I), and epithallial cells (E) (UWC:92/148).

found where a freshwater stream met the shore. The upper surface of the shale had originally been covered with thin, adherent, confluent, flat crustose coralline thalli. The thalli that remain measure up to 20 mm in diameter and 350 μm thick, small ridges occur at confluences. All thalli are covered with small craters marking the position of conceptacles, tetrasporangial conceptacles measure up to at least 170 μm in diameter, male ones to 60 μm. A few circular, domed uniporate roofs are present but these have mostly been shed. The thallus is monomerous (Figure 49), measuring up to 350 μm thick, and sometimes young thalli regenerate on top of senescent parts of the same thallus. The medulla comprises up to 20% of the thallus thickness, but in most parts it is only one or two cells thick (Figure 50), cells measure 6 – 16 μm long × 3 – 6 μm in diameter, cell fusions occur. The cortex (Figure 50) is composed of loosely aggregated filaments of squarish, bead-like cells measuring 3 – 8 μm long × 3 – 8 μm in diameter, cell fusions (Figure 50) occur, subepithallial initials are not distinct



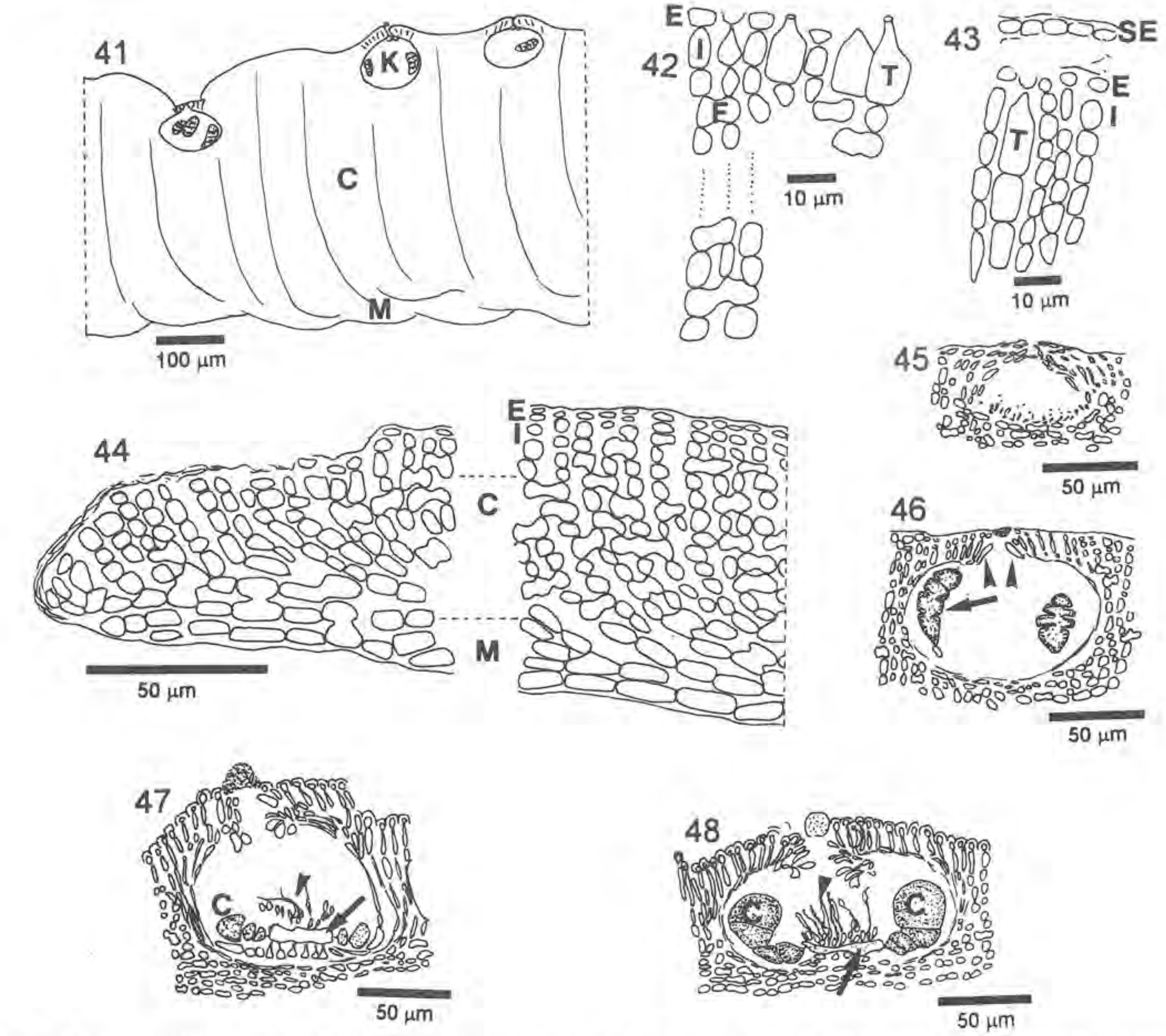
Figures 38 – 40 Thallus features of *Hydrolithon samoënse* (UWC:92/148). **38.** Vertical fracture near the base of the thallus, showing medullary cells (M) with cell fusions (F) and lower cells of cortex (C). **39.** Surface view showing small uniporate conceptacles and scar from the early stages of conceptacle sloughing (S). **40.** Surface view showing conceptacle (C) with pore (arrows), and the scar of a sloughed conceptacle (S).

from cortical cells, epithallial cells are small, often absent; individual trichocytes are sporadic (Figure 50), measuring *ca.* 15 µm long × 10 µm in diameter, not becoming buried in the thallus.

Gametangial plants monoecious. Male conceptacles at thallus surface (Figure 51), conceptacle chambers *ca.* 55 µm in diameter, 25 µm high, with the roof 15 µm thick, roof composed of unpigmented cells, remains of spermatangial systems on conceptacle floor only; carpogonial conceptacles slightly raised above the thallus surface, chamber flask-shaped (Figure 52), carposporangial conceptacles not seen. Tetrasporangial conceptacle chambers elliptical (Figures 53, 54), *ca.* 130 µm in diameter, 60 µm high, with a roof composed of tall thin cells subtending squarish epithallial cells, inner small cells sometimes present, pore surrounded by a ring of enlarged, vertically oriented cells (Figure 53), conceptacles mostly empty, a few senescent tetrasporangia seen. Bisporangial conceptacles not seen. Old conceptacles are probably shed, but empty or infilled cavities are also seen in the thallus (Figure 49). The most complete roof structure was seen when conceptacles had been overgrown by new thalli that protected the roof from damage.

On the basis of examination of the type of *Hydrolithon samoënse*, South African plants, European plants identified as *Spongites wildpretii* by Dr. Afonso-Carrillo, and Tahitian plants (YMC, unpubl.), together with Masaki's (1968) description of Japanese plants of *Lithophyllum samoënse*, it is concluded that *L. samoënse* and *S. wildpretii* are conspecific. Examination of published descriptions of *Neogoniolithon illitus* (Lemoine 1929, as *Lithophyllum*; Afonso-Carrillo 1984) and slides of the type material provided by Dr. Afonso-Carrillo, shows that this species is also conspecific with *L. samoënse.* Published descriptions of plants from Japan (Masaki 1968, as *Lithophyllum*), India (Krishnamurthy & Jayagopal 1985, as *Lithophyllum*), Mexico (Dawson 1960) and Tahiti (Setchell 1926) are considered to pertain to *H. samoënse*.

South African specimens of *H. samoënse* agree well with the type specimen of *Lithophyllum samoënse* from Savii, Samoa. The species is transferred here to *Hydrolithon* on the basis of the anatomy of sporangial conceptacles as noted above (Penrose & Woelkerling 1992). Since *Hydrolithon samoënse*, *Spongites wildpretii* and *Neogoniolithon illitus* are conspecific, the older species epithet (*samoënse*) has nomenclatural priority. This species is widespread throughout South Africa.



Figures 41 – 48 Vertical sections of *Hydrolithon samoënse*. **41.** Diagrammatic drawing of thallus showing thin medulla (M), relatively thick cortex (C) and sporangial conceptacles (K) (YMC:89/248). **42.** Cortex showing epithallial cells (E), subepithallial initial (I), trichocytes (T), and cell fusions (F) (YMC:89/248). **43.** Outer cortex showing sloughing epithallial cells (SE), newly formed epithallial cells (E), subepithallial initials (I) and trichocytes (T) (YMC:89/248). **44.** Thallus near the margin showing medulla (M), cortex subepithallial initial (I), and epithallial cells (E) (YMC:89/159). **45.** Spermatangial conceptacle (YMC:89/248). **46.** Tetrasporangial conceptacle, showing tetrasporangia (arrow) and elongated pore cells (arrowheads). **47.** Early stage of gonimoblast development, showing maturing carpospores (C), fusion cell (arrow), and the remains of carpogonia (arrowhead) (UWC:91/179). **48.** Later stage of gonimoblast development, showing maturing carpospores (C), fusion cell (arrow), and the remains of carpogonia (arrowhead) (UWC:91/179).

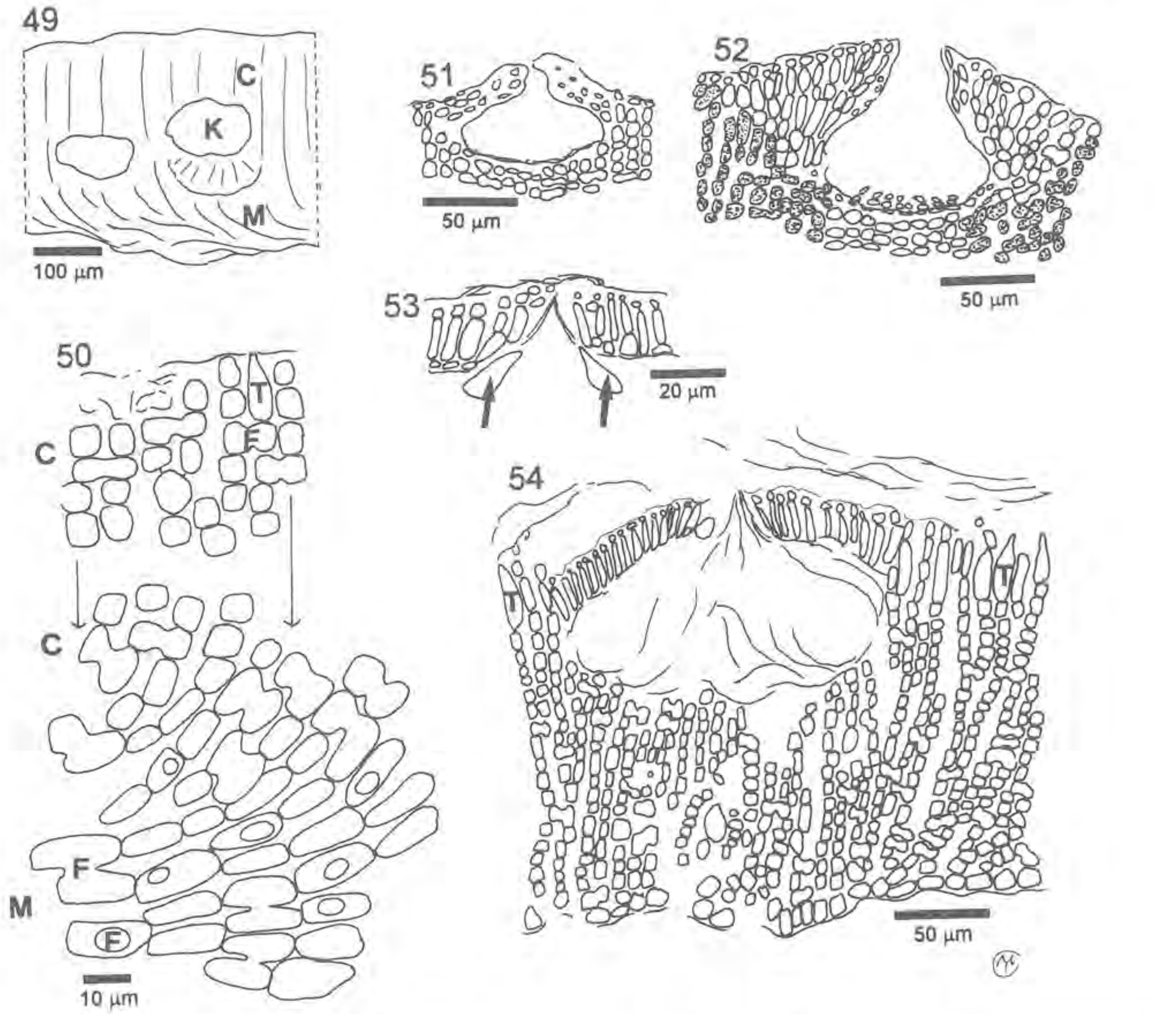
The description and illustrations of the Hawaiian species *Neogoniolithon rugulosum* Adey, Townsend and Boykins (1982: 17) suggest that it may also be conspecific with *H. samoënse*, but it has larger conceptacles (160 – 200 µm diameter), and conceptacle roof structure is not visible in the published description. The type specimen of *N. rugulosum* is therefore worthy of further study to determine its relationship with *H. samoënse*.

The distinguishing characters of *H. samoënse* are as follows: thalli thin, adherent, flat or slightly protuberant; thallus monomerous; cortex with small, squarish, bead-like cells; individual, non-burying trichocytes present; gametangial plants monoecious, conceptacles initially with slightly raised, circular roofs composed of unpigmented cells; tetrasporangial conceptacle roofs composed of tall, thin cells and epithallial cells, sometimes small inner cells present; tetrasporangial pore surrounded by a ring of enlarged, vertically oriented cells.

On the shore this species occurs as flat, gleaming, reddish thalli, with tiny pale, pin-point conceptacles. The thalli are often overgrown by more vigorous crustose algae.

Discussion

The delimitation of the genus *Hydrolithon*, as distinct from related mastophoroid genera, is based on recent publications by Penrose (1991, 1992), Penrose and Chamberlain (1993) and Penrose and Woelkerling (1991, 1992). The main characters distinguishing *Hydrolithon* from other mastophoroid coralline algae are: pore canals of sporangial conceptacles lined by a ring of conspicuous, elongate cells that arise from filaments interspersed among sporangial initials. These cells do not protrude into the canal, and are oriented more or less perpendicularly to the roof surface (Penrose & Woelkerling 1992). The three species discussed here belong to *Hydrolithon* on the



Figures 49 – 54 Vertical sections of *Lithophyllum samoënse* type specimen from TRH. **49**. Diagrammatic drawing of tetrasporangial thallus with buried conceptacle (K), medulla (M), and cortex (C). **50**. Thallus showing medulla (M), cortex (C), trichocyte (T) and cell fusions (F). **51**. Spermatangial conceptacle; spermatangial systems presumably occurred on the conceptacle floor but only small remnants are present. **52**. Carpogonial conceptacle; note that the roof is composed of unpigmented cells. **53**. Tetrasporangial conceptacle; note roof structure and enlarged pore cell (arrows). **54**. Tetrasporangial conceptacle pore.

basis of their mastophoroid characters, in combination with the above sporangial pore structure.

The key to the known species of *Hydrolithon* in South Africa is provided below. It is important to note that other species of *Hydrolithon* occur in South Africa, and are presently under study.

Key to *Hydrolithon* in South Africa

1a Plants thin, epiphytic, especially on *Gelidium pteridifolium* .... ***H. pellire*** Chamberlain & Norris

1b Plants not thin epiphytes **2**

2a Plants becoming very thick, surface granular due to trichocyte fields, trichocyte fields buried in thallus, tetrasporangial conceptacles flush to slightly raised .... ***H. onkodes***

2b Plants thinner, smooth, lacking obvious trichocyte fields, sporangial conceptacles raised **3**

3a Conceptacles produced in a superficial layer of elongated, lightly calcified cortical cells, shed as a layer on senescence .... ***H. superficiale***

3b Conceptacles evident as minute 'pinpricks' at thallus surface, tetrasporangial conceptacle roofs composed of tall thin cells with a single epithallial cell and sometimes a small inner cell, conceptacles shed individually or in groups on senescence leaving small scars at the thallus surface .... ***H. samoënse***

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