Two melobesioid coralline algae (Rhodophyta, Corallinales), *Mesophyllum erubescens* (Foslie) Lemoine and *Mesophyllum funafutiense* (Foslie) Verheij from Sodwana Bay, South Africa

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Two species of the coralline red algal genus *Mesophyllum* (Corallinaceae, Melobesioideae) are reported from the southernmost coral reefs in the western Indian Ocean at Sodwana Bay, Natal, South Africa. Specimens attributed to *Mesophyllum erubescens* (Foslie) Lemoine were compared with the type specimens of *Lithothamnion erubescens* Foslie and *L. erubescens* f. *madagascariensis* Foslie [= *M. madagascariensis* (Foslie) Adey]. The comparison showed that the local material and the type specimens are all conspecific, confirming previous suggestions that *M. madagascariensis* should be subsumed in *M. erubescens*. *Mesophyllum funafutiense* (Foslie) Verheij was also recorded. These species are distinguishable on the basis of the structure of the roof and the pore of the tetrasporangial conceptacles, and on the size of tetrasporangial conceptacles and tetrasporangia.

Verslag word gedoen oor twee spesies van die koraalagtige rooi-alg-genus *Mesophyllum* (Corallinaceae, Melobesioideae) afkomstig van die mees suidelike koraalriwwe in die westelike Indiese Oseaan by Sodwana, Natal, Suid-Afrika. Eksemplare wat aan *Mesophyllum erubescens* (Foslie) Lemoine toegeskryf word, is met die tipe-eksemplare van *Lithothamnion erubescens* Foslie en *L. erubescens* f. *madagascariensis* Foslie [= *M. madagascariensis* (Foslie) Adey] vergelyk. Die vergelyking het getoon dat die plaaslike materiaal konspesifiek met die tipe-eksemplare is. Dit het vorige voorstelle bevestig dat *M. madagascariensis* by *M. erubescens* ingesluit behoort te word. *Mesophyllum funafutiense* (Foslie) Verheij is ook opgeteken. Hierdie spesies is onderskeibaar op grond van die bou van die dak (boonste wand) en die opening van die tetrasporangiale vrugholte, asook die grootte van die tetrasporangiale vrugholtes en tetrasporangia.

Keywords: *Mesophyllum*, Melobesioideae, coralline algae, coral reef, South Africa, algal taxonomy.

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Introduction

Crustose coralline algae (Rhodophyta: Corallinales) are important in the structure and ecology of coral reefs (Adey & MacIntyre 1973; Adey 1979; Adey *et al.* 1982). The southernmost coral reef system in the western Indian Ocean, at Sodwana Bay, Natal Province, South Africa, is conserved as part of the St. Lucia Marine Reserve (Ramsay & Mason 1990). The crustose coralline algae of this system are largely unknown, and further, there is no documentation of the flora for any of the related reefs in southern Mozambique (Keats & Chamberlain 1993, 1994). Indeed, except for the recent publications of Chamberlain (1993) and Keats and Chamberlain (1993, 1994) giving details of six species which occur at Sodwana, no modern study of the coralline flora has been made for any area of the western Indian Ocean.

We have, therefore, undertaken to study the non-geniculate coralline algal flora of Sodwana Bay National Park (Keats & Chamberlain 1993), and in this paper we report on two species of the genus *Mesophyllum*.

Materials and Methods

All collections were made by SCUBA diving at Sodwana Bay, Natal, South Africa, and are held in the herbarium of the University of the Western Cape (UWC). Specimens were removed from old coral and bedrock by using a sledge hammer and cold chisel. Specimens were sorted as well as possible in the field using a hand lens, and were air-dried or fixed in 10% formalin in sea water and transferred to 70% ethanol with 5% glycerol.

Data were obtained for type specimens of *Lithothamnion erubescens* Foslie and *L. erubescens* f. *madagascariensis* Foslie housed at the Kongelige Norske Videnskabers Selskab Museet, Trondheim, Norway (TRH). The types of *L. philippii* f. *funafutiensis* and its synonyms were not examined because they are documented in the literature.

For scanning electron microscopy, air-dried material was fractured using either finger nails, forceps, 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), and stored in a desiccator for at least 24 h prior to examination, then coated with gold for 2 – 3 min in a 5000-V Edwards S150B sputter coater, and examined with a Hitachi X650 scanning electron microscope, equipped with a Mamiya 6×7 camera.

For light microscopy, formalin-preserved specimens were decalcified in 10% nitric acid, and 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 either aniline blue in 40% Karo syrup, or lactophenol blue with glycerol and made permanent with glycerine jelly.

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

Mesophyllum erubescens (Foslie) Lemoine 1928: 252

Basionym: *Lithothamnion erubescens* Foslie 1900: 9 – 10

Synonyms: *Lithothamnion erubescens* f. *madagascariensis* Foslie 1901a: 3; *Lithothamnion madagascariensis* Foslie 1906: 19; *Mesophyllum madagascariensis* (Foslie) Adey 1970: 25

Habit and vegetative structure

Thallus non-geniculate, firmly adherent on rock and dead coral (Figure 1), usually not exceeding 5 – 8 cm in diameter, initially flat, but soon producing small, short branches (Figure 1) which may become extensive, flat portion of thallus up to 1 mm thick. Protuberances initially finger-like to slightly flattened, mostly 1 – 3 mm diameter and 2 – 7 mm long, exceptionally 12 mm long, frequently fused along their length, sometimes producing short branches, thallus lobes often regenerating over old protuberances. *Margin* adherent, entire, lacking orbital ridges. *Surface* smooth, texture silky, often with loose sheets of sloughing epithallial cells (Figures 5, 14), cell surface (SEM) *Phymatolithon*-type. Colour: Methuen violet brown.

Tetra/bisporangial conceptacles raised, measuring 350 – 500 μm in outside diameter (Figures 10, 18), usually crowded on protuberances but sometimes occurring on flat parts of thalli or on thalli that lack protuberances.

Thallus monomerous. *Medulla* strongly coaxial (Figures 2, 15), comprising arching tiers of cells when viewed in radial vertical section, occupying up to 75% of the thallus thickness (Figure 15) at the crust margin but less than 25% of thallus thickness in older regions (Figure 2), cells rectangular with rounded corners (Figures 3, 17), 7 – 22 μm long × 5 – 8 μm in diameter; medulla of protuberances faintly layered. *Cortex* fairly thick, comprising up to 75% of the thallus thickness in older areas (Figure 2), cells squarish to rectangular with rounded corners (Figures 3, 16), 5 – 10 μm long, 4 – 7.5 μm in diameter. Difference in cell size between cortex and medulla striking in sections (Figure 3) and under the SEM (Figure 15). Individual trichocytes sporadic (Figure 4), measuring 12 – 14 μm long × 8 – 9 μm diameter. *Subepithallial initials* markedly elongate (Figures 3, 16), rectangular with rounded corners, measuring 7 – 10 μm long × 5 – 7 μm in diameter. *Epithallial cells* single, with fairly wide cell lumen, showing epithallial concavities in surface view (Figure 13), in section flattened-oval, or domed (Figures 3, 16), 2 – 3 μm long × 6 – 7 μm in diameter, often shed in large sheets (Figures 5, 14).

Cell fusions abundant in cortical and medullary filaments (Figures 3, 16, 17), wide — often taking up most of the lateral wall of adjacent cells. Elongated and rounded initials, which stain deeply with aniline blue and lack epithallial cells, are common in protuberances and evidently regenerate thallus margin (Figure 6).

Reproduction

Gametangial plants monoecious. *Male conceptacles* uniporate, slightly raised; chamber flattened flask-shaped (Figure 21), measuring *ca.* 320 μm in diameter × *ca.* 80 μm high, with the roof *ca.* 60 μm thick; spermatangial systems simple (Figures 22, 23) on the floor walls and roof of the chamber, but more prolific on the floor, pore canal lined by papillae which project into the canal, spermatia on the floor borne at the tip of a small sausage-shaped cell that arises from a somewhat conical cell (Figure 23), spermatia on the roof borne on sausage-shaped cells without the conical cell subtending them (Figure 22). *Carpogonial conceptacles* not seen. *Carposporangial conceptacles* uniporate (Figures 24, 25), markedly raised, conical; chamber flask-shaped, measuring *ca.* 340 – 425 μm in diameter × *ca.* 140 – 200 μm high, with the roof *ca.* 120 μm thick; gonimoblast developing around the periphery of the chamber from a fusion cell that appears discontinuous in section (Figure 25), gonimoblast filaments consisting of 4 – 6 cells with a terminal carpospore (Figure 25); carpospore triangular to elliptical, but becoming spherical just prior to

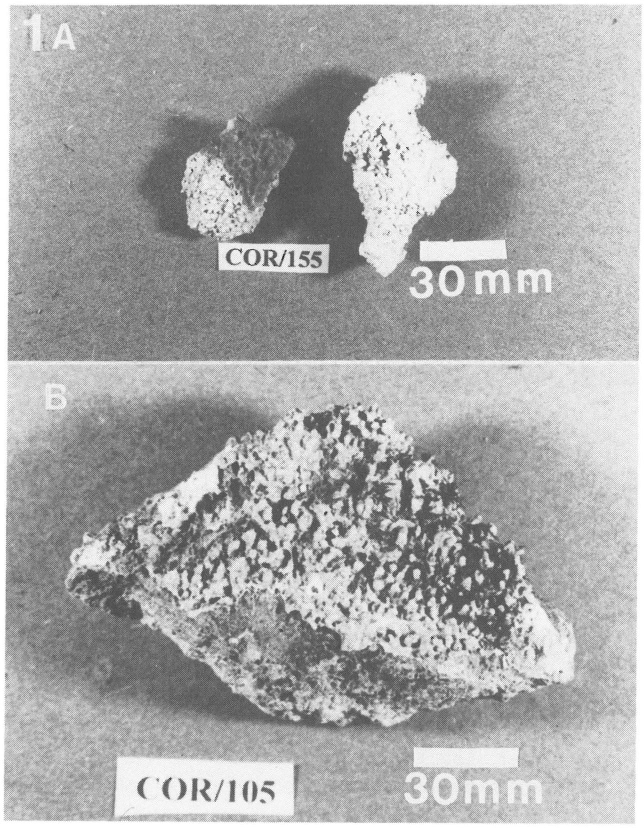
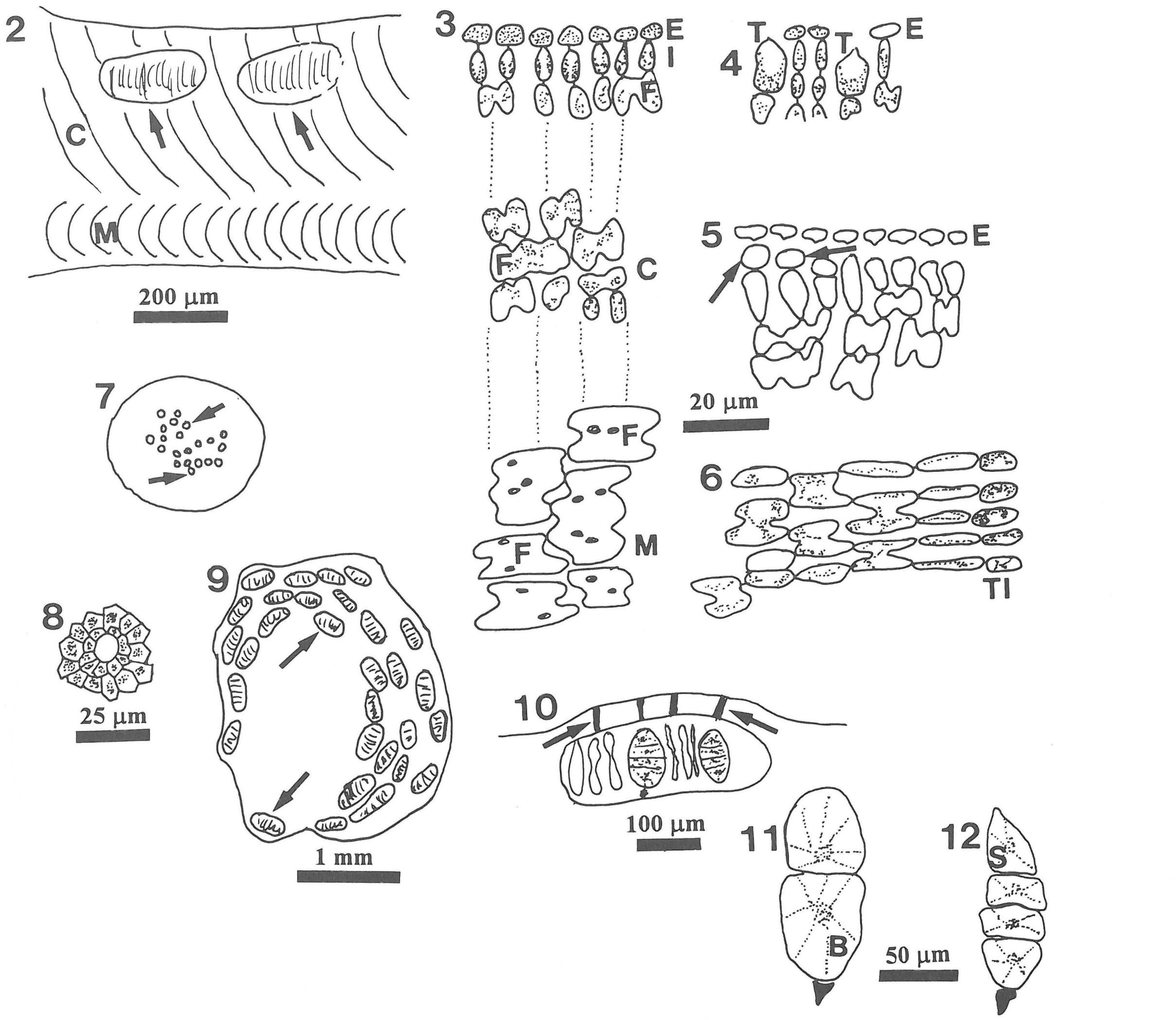


Figure 1 Specimens of *Mesophyllum erubescens* from Sodwana Bay (A, UWC: COR/105) and Uvongo (B, UWC: COR/105), Natal, South Africa.

release, measuring *ca.* 100 μm in diameter (Figure 25). *Sporangial conceptacles* tetrasporic or bisporic (Figures 10 – 12), raised, rounded to somewhat squarish (Figures 7, 10, 18), tops flat; chambers elliptical, measuring 210 – 300 μm in diameter × 85 – 125 μm high; conceptacle roof with 21 – 30 pores (Figures 7, 18); pore plugs present (Figure 10), densely staining with aniline blue; pore diameter 8 – 13 μm, pore surrounded by 10 – 13 cells visible in SEM that are flush with the surrounding roof (Figure 19). However, in light microscope view of the surface of excised roof, the pore appears surrounded by 7 – 9 rosette cells that are deeply sunken well below the surrounding roof (Figure 64), and that terminate the pore canal filaments (Figure 63). Filaments which line the pore canal composed of 3 – 4 cells, pore canal 27 – 33 μm long, pore filaments differ from normal roof filaments in having elongate, often banana-shaped, cells at their bases and in having fewer cells (4 – 7 in normal roof filaments) (Figure 63), cells of these filaments of a similar diameter to the cells of the rest of the roof filaments; roof 27 – 38 μm thick. Tetrasporangia and bisporangia 130 – 170 μm long × 55 – 94 μm in diameter, across the floor of conceptacle, separated by uncalcified filaments. Old conceptacles usually buried within the thallus and filled in with elongated, densely-staining, calcified sterile cells (Figures 9, 20).

Habitat and phenology

Mesophyllum erubescens is common on the reefs, but is nowhere very abundant. It is most often mixed with other crustose corallines overgrowing dead *Acropora* spp., both plate-like and staghorn varieties. It also occurs on vertical rock faces in somewhat dim light, and appears to be most abundant at depths of 18 – 25 m. A single specimen was found in a shallow rock pool in the intertidal zone at Uvongo, in southern Natal.



Figures 2 – 12 Vertical sections of *Mesophyllum erubescens* from Natal. **2.** Diagrammatic drawing of thallus showing buried tetrasporangial conceptacles (arrows), cortex (C) and coaxial medulla (M) (UWC: COR/105). **3.** Thallus showing epithallial cells (E), subepithallial initial (I), cortical (C) and medullary (M) cells with cell fusions (F) (UWC: COR/309). **4.** Outer thallus showing epithallial cells (E) and trichocytes (T) (UWC: COR/155). **5.** Outer thallus showing sloughing epithallial layer (E) and newly regenerated epithallial cells (arrows) (UWC: 91/168). **6.** Terminal initials (TI) in regenerating margin on protuberance (UWC: COR/105). **7.** Surface view of sporangial conceptacle showing pores (arrows) (scale as in Figure 2) (UWC: COR/105). **8.** Detail of sporangial pore (UWC: COR/105). **9.** Cross-section of protuberance showing buried sporangial conceptacles (arrows) (UWC: 91/119B). **10.** Diagrammatic drawing of a vertical section of a tetrasporangial conceptacle showing pore canals with pore plugs (arrows) (UWC: COR/309). **11.** Bisporangium with bispores (B) (UWC: COR/105). **12.** Tetrasporangium with tetraspores (S) (UWC: 91/119).

Distribution

South Africa: Sodwana Bay and Uvongo, Natal. World: Brazil, Cap Verd, Caribbean, Indonesia, Kenya, Korea, Guam, Hawaii, Japan, Madagascar, South Africa, Sri Lanka.

Specimens examined

—3030 (Port Shepstone): Uvongo Beach, Natal Province, on rock in tide pool, mid-eulittoral zone, *D. Keats* (UWC: COR/105) (–CD).

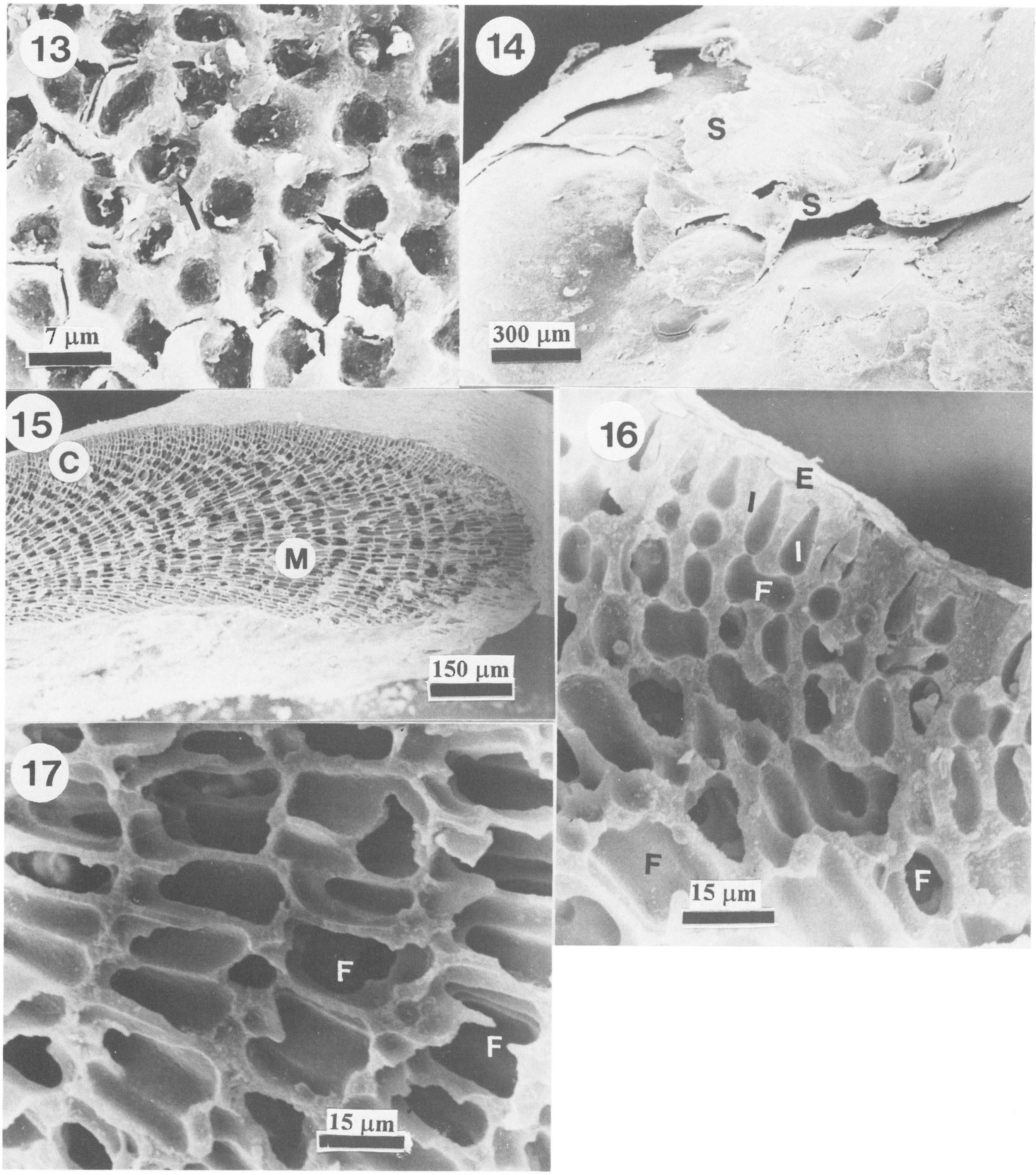
—2732 (Ubombo): Two-Mile Reef, Sodwana Bay, Natal Province, on rock in crevice under overhang, *D. Keats* (UWC: COR/121); Five-Mile Reef, Sodwana Bay, Natal Province, on staghorn *Acropora* thicket and vertical rock wall, 12 – 14 m depth, *D. Keats* (UWC: COR/155); Five-Mile Reef, Sodwana Bay, Natal Province, on rock face on coral reef, 12 – 14 m depth, *D. Keats* (UWC: COR/309); Seven-Mile Reef, Sodwana Bay, Natal Province, on dead coral, rock, and coral rubble, 25 m depth, *D. Keats & Y. Chamberlain* (UWC: 91/114, 91/118, 91/119); Two-Mile Reef, Sodwana Bay, Natal Province, dead coral and rock, 12 – 14 m depth, *D. Keats & Y. Chamberlain* (UWC: 91/40); Two-Mile Reef, Sodwana Bay, Natal Province, dead coral and rock, 15 – 18 m depth, *D. Keats & Y. Chamberlain* (UWC 91/168); Mbibi, Natal Province, walls of surge channel in big tide pool, *D. Keats* (UWC: 92/14) (–DA).

Structure of type material

Lithothamnion erubescens Foslie 1900: 9 – 10 (see Woelkerling 1993: 85 – 86)

The holotype specimen comprises a lump of totally branched thallus, measuring *ca.* 3 cm in diameter and 2.5 cm thick. Branches interweave, and have blunt apices 1 – 2 mm across. There is very little basal crust present in the holotype, so no crust medulla was sectioned. Foslie slide 340 is present with the specimen, and was examined here.

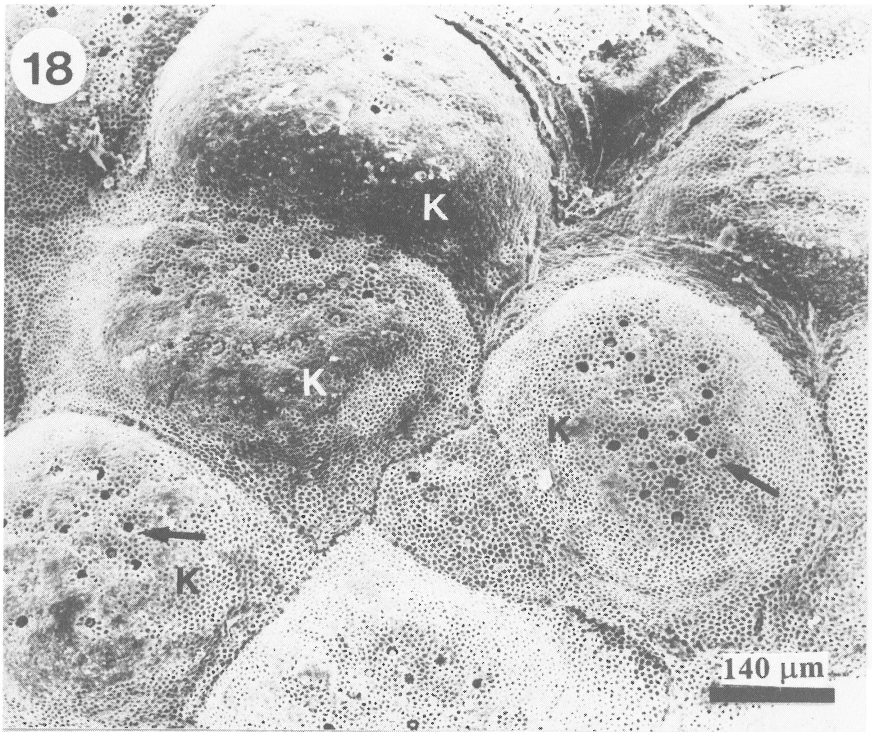
The protuberance medulla is faintly to strongly layered (Figures 28, 29), with cells measuring 4 – 15 µm long × 3 – 5 µm in diameter. Single, rounded epithallial cells occur at the thallus surface (Figures 26, 31), measuring 2.5 – 4 µm long × 4 – 7 µm in diameter, often peeling in sheets (Figure 27). The subepithallial initial is elongate, measuring 5 – 9 µm long × 4.5 – 6 µm in diameter. The cortical cells are squarish to

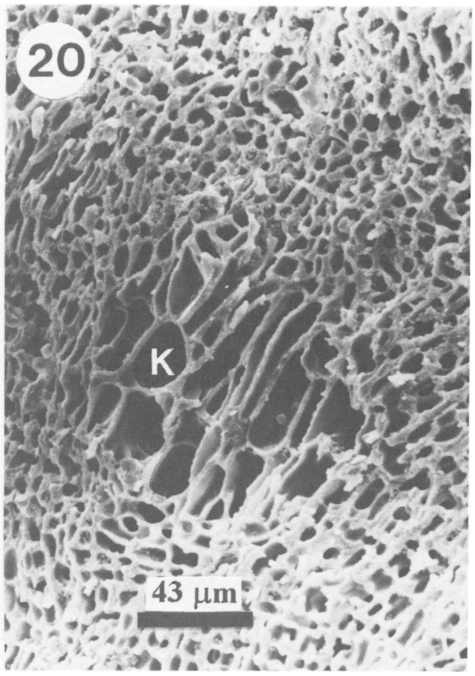


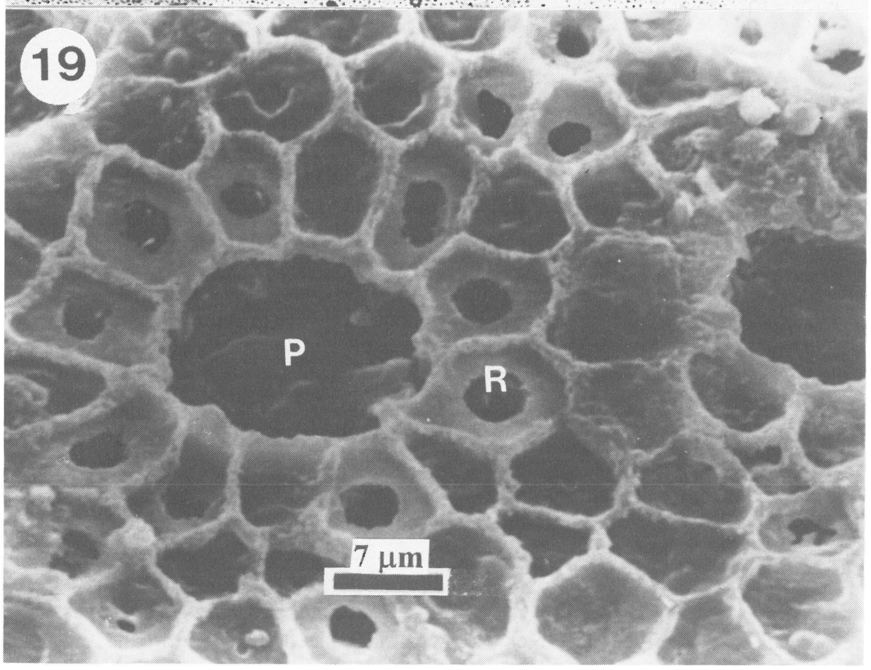
Figures 13 – 17 Scanning electron micrographs of *Mesophyllum erubescens* from Natal. **13.** Surface view of vegetative thallus; note epithallial concavities (arrow) (UWC: COR/105). **14.** Surface of vegetative thallus showing sloughing epithallial scales (S) (UWC: COR/121). **15.** Vertical section of thallus near leading margin showing coaxial medulla (M) and thin layer of cortical filaments (C) (UWC: COR/105). **16.** Cortical filaments showing epithallial cells (E), subepithallial initials (I), and cell fusions (F) (UWC: COR/121). **17.** Medullary cells showing cell fusions (F) (UWC: COR/105).

rectangular with rounded corners, measuring 5 – 10 µm long × 4.5 – 8 µm in diameter. The crust medulla was not seen in material sectioned, but cells appear rectangular in SEM fracture (Figure 32), measuring *ca.* 8 – 20 µm long × 4 – 11 µm in diameter. The regeneration of thallus margin was observed at the thallus surface (Figure 30).

The tetrasporangial conceptacles are squarish (Figure 33), raised, predominantly located on protuberances, measuring 266 – 380 µm outside diameter. The chambers are elliptical, measuring 219 – 246 µm in diameter × 113 – 130 µm high. The conceptacle roof has 14 – 20 pores measuring 5 – 11 µm in diameter, with each pore surrounded by 7 – 9 rosette cells that appear deeply sunken below the surrounding roof cells in a light microscope view of the surface of excised roof (Figure 60), and that terminate the pore canal filaments (Figure 59). The filaments which line the pore canal are composed of 3 – 5







Figures 18 – 20 Scanning electron micrographs of sporangial conceptacles of *Mesophyllum erubescens* from Natal. **18.** Sporangial conceptacles (K) showing pores (arrow) (UWC: COR/105). **19.** Detail of sporangial pore (P), showing apparent rosette cells (R); the cells which terminate the pore canal filaments are hidden below the surface of the pore (UWC: COR/105). **20.** Old sporangial conceptacle (K) buried within cortical filaments (UWC: COR/105).

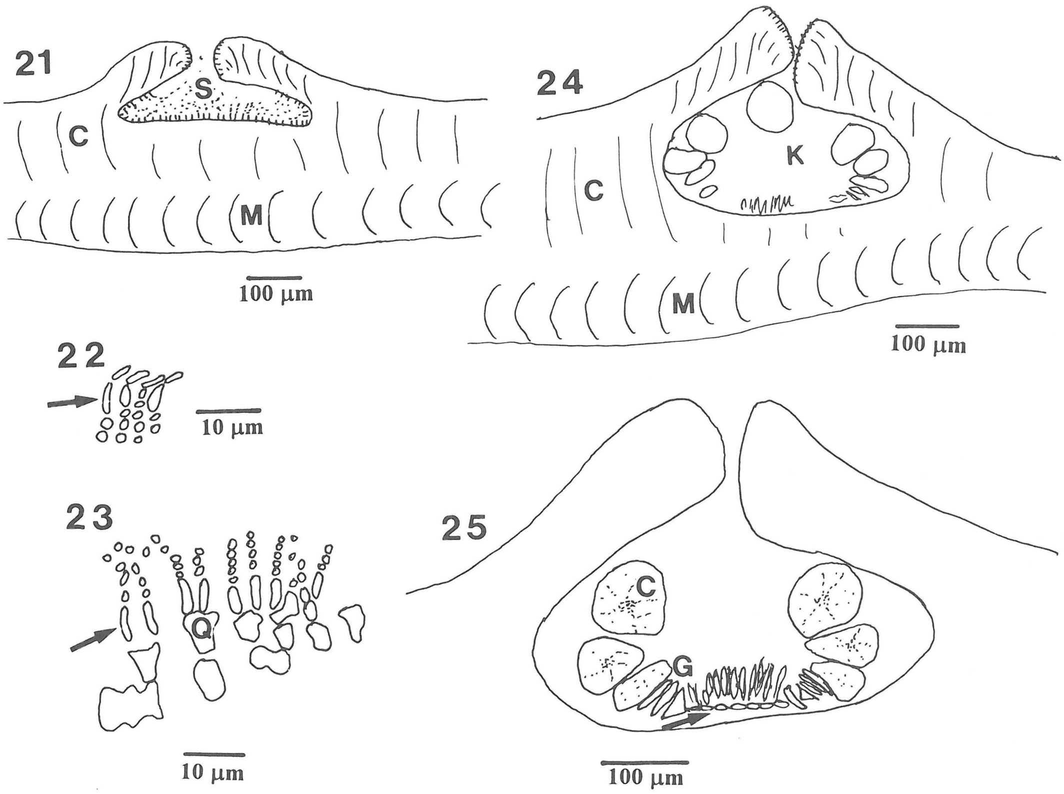
cells that are of a similar diameter to the cells of the rest of the roof filaments, but each of which differs from the surrounding roof filaments in having an elongate cell at its base (Figure 59). The roof is 27 – 33 µm thick (Figure 34), with old sporangial conceptacles becoming buried in the thallus, and in-filled with calcified filaments.

Lithothamnion erubescens f. *madagascariensis* Foslie 1901a: 3 (see Woelkerling 1993: 142)

The holotype specimen comprises a small, warty lump measuring 13 × 15 mm across, and *ca.* 8 mm thick. Foslie's slide 689, which is a vertical section of a protuberance, is present with the holotype, and was examined.

The protuberance medulla is faintly to strongly layered (Figure 36), with cells measuring 8 – 15 µm long × 3 – 5 µm in diameter. Single, rounded epithallial cells occur at the thallus surface (Figure 35), measuring 2.5 – 4 µm long and 3 – 6 µm diameter, often peeling in sheets. The subepithallial initial is somewhat elongate, measuring 6 – 10 µm long and *ca.* 5 µm in diameter. The cortical cells are squarish to rectangular with rounded corners (Figure 37), measuring 5 – 13 µm long and 3.5 – 7 µm in diameter. The crust medulla is strongly coaxial, and composed of cells that are rectangular with rounded corners (Figure 38), and which measure 15 – 27 µm long and 5 – 8 µm in diameter.

Tetrasporangial conceptacles are squarish (Figure 39), raised, predominantly located on protuberances, and measure 210 – 350 µm outside diameter. The chambers are elliptical (Figure 40), and measure 250 – 276 µm in diameter and 143 – 158 µm high. The conceptacle roof has less than 30 pores (Figure 41) that are blocked by pore plugs. Pores measure 11 – 15 µm in diameter, and are surrounded by 11 – 12 cells that appear flush with the surrounding roof cells in SEM (Figure 41). However, in a light microscope view of the surface of excised roof it is evident that each pore is surrounded by 7 – 9 rosette cells that appear deeply sunken below the surrounding



Figures 21 – 25 Gametangial plants of *Mesophyllum erubescens* (UWC: 92/14). **21**. Diagrammatic drawing of vertical section through region of gametophyte thallus bearing a spermatangial conceptacle (S). Note medulla (M) and cortex (C). **22**. Spermatangial branches from conceptacle roof. Note elongated spermatangial initial (arrow). **23**. Spermatangial branches from conceptacle floor. Note elongated spermatangial initial (arrow), subtended by subconical cell (Q). **24**. Diagrammatic drawing of vertical section through region of gametophyte thallus bearing a carposporangial conceptacle (K). Note medulla (M) and cortex (C). **25**. Diagrammatic drawing of an outline of a carposporangial conceptacle, showing gonimoblast filaments (G) with carposporangium (C) arising from discontinuous fusion cell (arrow).

roof cells (Figure 62), and that terminate the pore canal filaments (Figure 61). The filaments which line the pore canal are composed of 3 – 5 cells that are of a similar diameter to the cells of the rest of the roof filaments, but each of which differs from the surrounding roof filaments in having an elongate cell at its base (Figure 63), and in having fewer cells. The conceptacle roof is 32 – 38 µm thick (Figures 40, 61), with old sporangial conceptacles becoming buried in the thallus, and infilled with calcified filaments (Figure 42).

Remarks

Foslie (1900) described *Lithothamnion erubescens* from Brazil, and later (1901a), *L. erubescens* f. *madagascariensis* from Madagascar. The latter taxon differed from the former in having less regular branches and frequently shorter cells (Foslie 1901b). Foslie (1904) considered the Indo-Pacific and Atlantic forms to belong to the same species, *L. erubescens*, with the reservation that only a few specimens were available for study. However, Foslie (1906) later assigned species status to the form *madagascariensis*. Recently there has been inconsistent use of these epithets. Masaki (1968) used *L. erubescens* f. *madagascariensis* based on Foslie (1904). Adey (1970) transferred *L. madagascariensis* to *Mesophyllum madagascariensis* (Foslie) Adey, a genus erected by Lemoine (1928). However, Gordon *et al.* (1976) continued to apply the epithet *erubescens* to the Indo-Pacific entity in Guam. Adey *et al.* (1982) implied that there is no real basis for distinguishing *M. madagascariensis* from *M. erubescens*. Verheij (1993a) examined both types and accepted *M. erubescens* as the correct epithet, but in neither case described or illustrated the type material. Until now, no detailed modern study of the types had been published, so there was no formal basis for synonymizing the two entities.

We found no discernable difference between the two type specimens, except for slight differences in branching pattern. Our field material encompasses the range of branching patterns shown by both types, and we regard this as an unreliable taxonomic character in this instance. The purported difference in protuberance anatomy between the two entities (Foslie 1901b) is refuted (Figures 28, 29, 36). Internal banding within the protuberance medulla is present in both types, although it is weaker in the type of *L. erubescens* f. *madagascariensis*. Both type specimens show similar sized cells within the protuberance medulla.

Woelkerling and Harvey (1993) questioned the validity of many of the characters traditionally used to distinguish among species of *Mesophyllum*, and noted that characters associated with sporangial conceptacle roofs appear to be stable and useful for distinguishing among species of *Mesophyllum* in Australia. The structure of the conceptacle pore was particularly significant. The conceptacle pore structure for our recently collected material of *M. erubescens* was identical to the pore structure of the type specimens of *M. erubescens* and *M. madagascariensis*, and with *M. erubescens* as documented by Verheij (1993a), and further, there was little or no variation in pore structure among the populations sampled during the present study. We therefore apply the epithet *erubescens* to our material as this has historical priority over *madagascariensis*. Several other species of *Mesophyllum* have been described with protuberances, and further studies are needed to clarify the taxonomy of this group.

The combination of characters which we regard as diagnostic of *M. erubescens* is (Table 1):

Table 1 A comparison of recently documented *Mesophyllum* species based on selected characters or tetra/bisporangial plants (+ denotes presence, – denotes absence, +/– denotes a character that may be either present or absent; ND: data not available)

	erubescens (Verheij 1993a)	*erubescens* This study	*funafutiense* (Verheij 1993a)	*funafutiense* This study	*engelhartii* (Wlk. Hrv. 1993)	*incisum* (Wlk. Hrv. 1992)	*lichenoides* (Wlk. Hrv. 1993)	*macroblastum* (Wlk. Hrv. 1993)	*printzianum* (Wlk. Hrv. 1993)	*syrphetodes* (Verheij 1993a, Adey *et al.* 1982)
Protuberances	+/–	+/–	–	–	+/–	+/–	–	+/–	+/–	+/–
Trichocytes	+/–	+/–	–	–	+	+	ND	–	+/–	–
Cortical cell length	5–10 µm	5–10 µm	5–10 µm	5–14 µm	9–14 µm	7–20 µm	ND	5–12 µm	6–14 µm	5–15 µm
Cortical cell diameter	5–11 µm	4–7.5 µm	5–10 µm	5–10 µm	3–9 µm	6–12 µm	ND	4–9 µm	4–7 µm	5–9 µm
Conceptacle chamber diameter	350–475 µm	210–300 µm	450–600 µm	500–575 µm	160–500 µm	340–655 µm	ND	145–270 µm	185–420 µm	250–350 µm
Conceptacles with raised rim	–	–	–	–	–	–	–	+	+	–
Tetra/bisporangium length	ND	130–170 µm	ND	186–225 µm	59–173 µm	130–220 µm	<221 µm	81–135 µm	121–150 µm	ND
Roof thickness	4–6 cells	4–7 cells	8–10 cells	7–10 cells	3–10 cells	4–7 cells	5–10 cells	4–5 cells	3–6 cells	4–6 cells
	ND	27–38 µm	ND	43–72 µm	24–68 µm	50–80 µm	ND	27–35 µm	40–54 µm	ND
Pore canal filaments number of cells	*ca.* 3–4 cells[a]	3–4 cells	8–10 cells	7–10 cells	3–10 cells	ND	ND	4–5 cells	ND	4–6 cells
cells same as rest of roof	–	–	+	+	+	–	–	+	–	+
elongate basal cells	+	+	–	–	–	–	–	–	–	–
shorter, more squat cells	–	–	–	–	–	–	+	–	–	–
distinct narrow filaments	–	–	–	–	–	+	–	–	+	–
Number of pores in conceptacle roof	>50	21–30	35–75	>100	ND	*ca.* 40[b]	ND	ND	ND	20–40
Conceptacles buried	yes	yes	yes	yes	sometimes	sometimes		yes	sometimes	yes
Pore cells (flush, raised, sunken)	ND	sunken[c]	ND	raised	ND	ND	ND	ND	ND	ND

[a] Data not given, but visible in Figure 86, p. 76, of Verheij (1993a).
[b] Data not given, but visible in Figure 16, p. 388, of Woelkerling & Harvey (1992).
[c] They are deeply sunken, but often not visible in SEM, so the surrounding roof cells may give the impression that they are flush.

(a) tetrasporangial or bisporangial conceptacles raised, lacking a raised rim;
(b) tetrasporangial or bisporangial pore surrounded by rosette cells that are deeply sunken below the surrounding roof, and often not visible in SEM;
(c) tetrasporangial or bisporangial pore canal lined by filaments composed of cells that are of a similar diameter to the cells of the surrounding roof filaments, but each of which differs from the surrounding roof filaments in having an elongate cell at its base (Figure 63), and in usually having fewer cells.

The elongate cells at the base of pore canal filaments that are of a similar diameter to the surrounding roof filaments provide the most characteristic feature of this species. *Mesophyllum incisum* sometimes has elongated cells at the base of pore canal filaments, but the cells of its pore canal filaments are markedly narrower than the cells of the surrounding roof filaments. Verheij (1993a) regarded 3 – 4-celled intersporangial filaments as diagnostic, but the significance of this character is uncertain, as data are not available for other species. The presence or absence of trichocytes, the number of pores in the tetrasporangial or bisporangial conceptacle roof, and the number of roof cells, as used by Verheij (1993a), do not appear to be reliable diagnostic characters (Table 1), although they may provide useful ancillary information. Although not diagnostic, the presence of protuberances is a useful field character for *M. erubescens*, as most thalli produce protuberances, even though a population may contain protuberant and non-protuberant plants. In addition, the tetrasporangial or bisporangial conceptacle chambers are always <475 µm in diameter, and old conceptacles become buried and filled in by calcified cells.

Mesophyllum funafutiense (Foslie) Verheij 1993b: 238

Basionym: *Lithothamnion philippii* f. *funafutiensis* Foslie 1899: 3 (see Woelkerling 1993: 100 – 101)

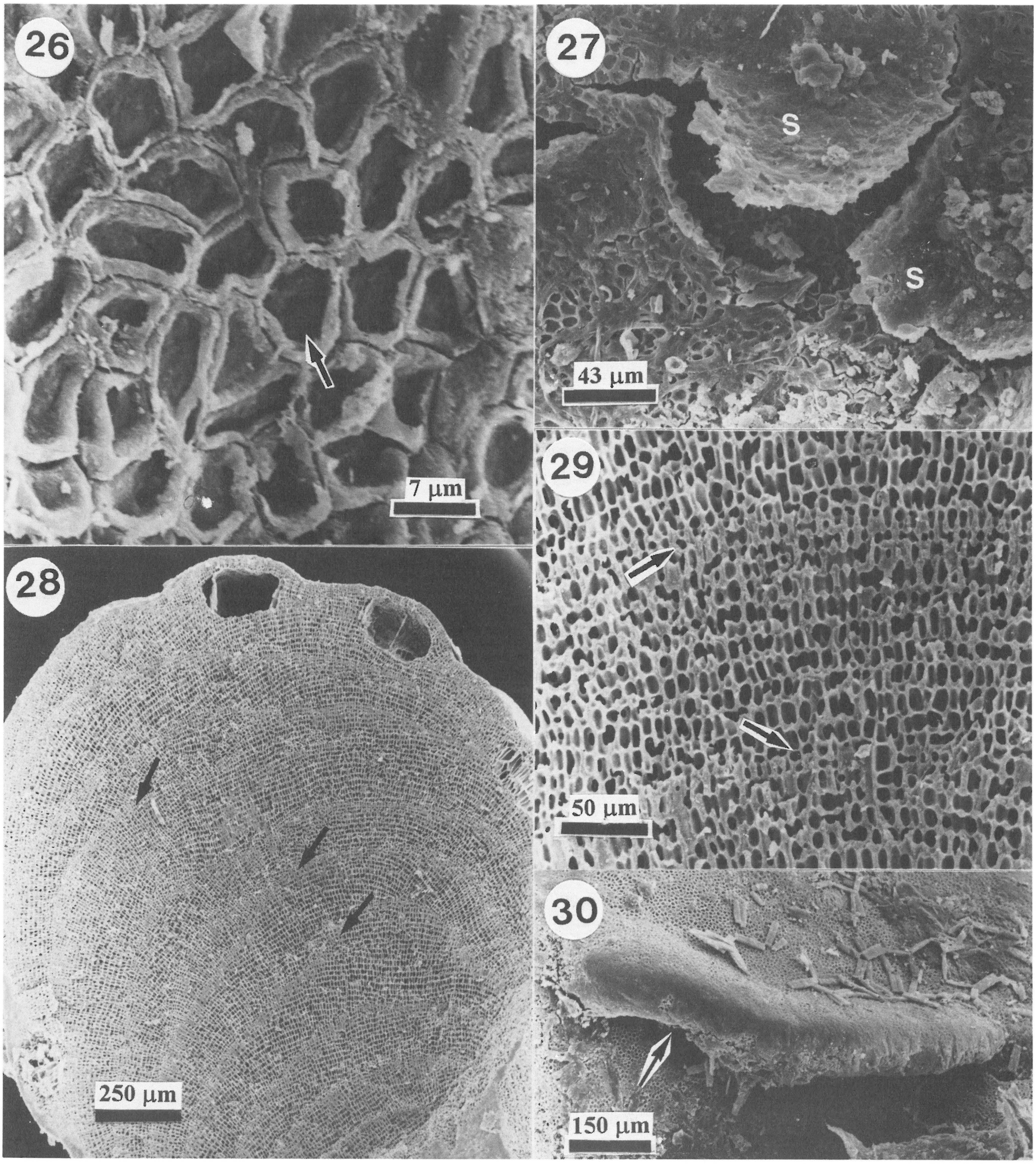
Synonyms: *Lithothamnion funafutiense* (Foslie) Foslie 1901a: 17; *Lithothamnion funafutiense* f. *purpurascens* Foslie 1901a: 18 (see Woelkerling 1993: 184 – 185); *Lithothamnion purpurascens* (Foslie) Foslie 1907: 182; *Mesophyllum purpurascens* (Foslie) Adey 1970: 26.

Habit and vegetative structure

Thallus non-geniculate, to at least 60 mm in diameter, encrusting on rock and dead coral, firmly adherent, lacking protuberances. *Margin* adherent, entire, with prominent orbital ridge. *Surface* smooth, glossy, with numerous centrally crowded bumps formed by sporangial conceptacles (Figure 43), small sheets of shedding epithallial cells common. Colour: Methuen reddish brown.

Tetra/bisporangial conceptacles strongly raised, 600 – 800 µm in outside diameter, dome-shaped and easily visible with the naked eye (Figure 43).

Thallus monomerous. *Medulla* coaxial, composed of arching tiers of cells when viewed in radial section (Figures 44, 52), occupying 30% of the thickness of older parts of the thallus, and up to 70% of the thallus thickness near a growing margin; medullary cells rectangular with rounded corners (Figures 45, 52, 54), but tending to be indistinct because of cell fusions and abundant starch grains (Figures 45, 55), measuring 12 – 28 µm long × 7 – 13 µm in diameter; cells at the lower surface smaller, often hyaline, terminating in a clear dome-shaped cell (Figure 45). *Cortex* comprising 30 – 70% of thallus thickness (Figures 44, 52), cortical cells rounded to oval, somewhat longer than broad, becoming larger and less distinct toward the

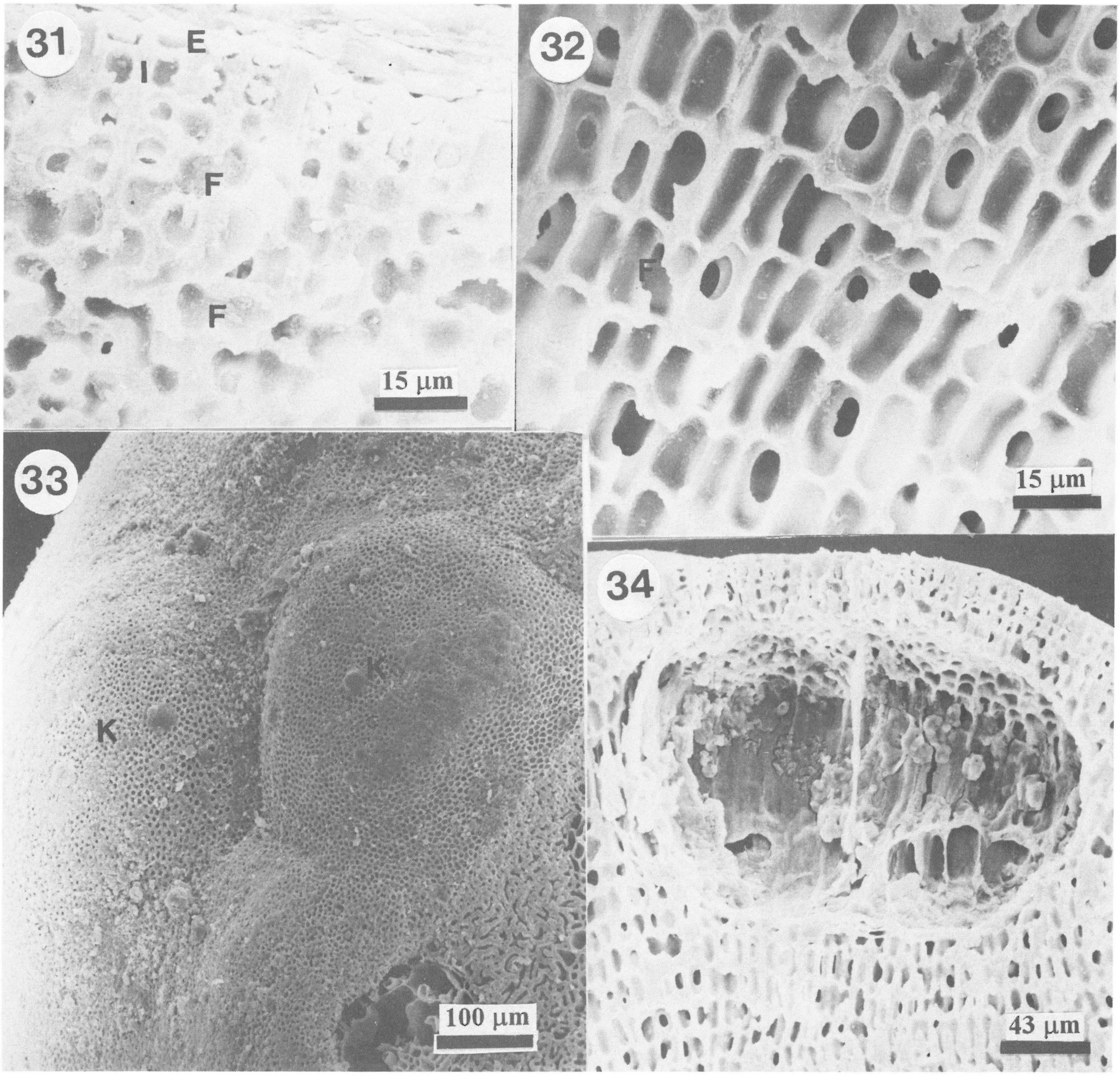


Figures 26 – 30 Scanning electron micrographs of the holotype of *Lithothamnion erubescens* Foslie. **26**. Surface view of vegetative thallus; note epithallial concavities (arrow). **27**. Surface of vegetative thallus showing sloughing epithallial scales (S). **28**. Vertical section of protuberance showing layering (arrows) within the protuberance medulla. **29**. Vertical section of protuberance medulla, showing shorter cells (arrows) which produce the layering pattern. **30**. Regenerated thallus margin (arrow) at base of protuberence.

medulla, 5 – 14 µm long × 5 – 10 µm in diameter. Lower cortical cells and medullary cells packed with starch bodies (Figures 45, 54, 55). Cell fusions abundant in cells of cortical and medullary filaments (Figures 45, 53, 54), wide, often taking up the entire wall of adjoining cells. *Subepithallial initial* elongate (Figures 45, 53), measuring 7 – 13 µm long × 4 – 8 µm in diameter. *Epithallial cells* single, ellipsoid, 4 – 6 µm long × 6 – 9 µm in diameter, sometimes being shed in small sheets (Figure 51), but evidently not as extensive as in the other species of *Mesophyllum* reported here. Surface of epithallial cells under the SEM appearing irregular and loosely connected, with an apparent gap between the walls of adjacent cells (Figure 50).

Reproduction

Gametangial plants: Not seen. *Sporangial conceptacles* centrally crowded, strongly raised and dome-shaped when mature (Figures 44, 56), but almost flush and flat-topped when



Figures 31 – 34 Scanning electron micrographs of the holotype of *Lithothamnion erubescens* Foslie. **31.** Cortical filaments showing epithallial cells (E), subepithallial initials (I) and cell fusions (F). **32.** Medullary cells showing cell fusions (F). **33.** Sporangial conceptacles (K). **34.** Recently empty sporangial conceptacle near thallus surface.

old and in the process of becoming buried, tetrasporic or bisporic (Figures 48, 49); chambers elliptical, measuring 500 – 575 µm in diameter × 210 – 230 µm high; roof often with >100 pores (Figures 46, 56), pore plugs present, densely staining with aniline blue. Pore surrounded by a crown of 7 – 9 very distinctive rosette cells which are noticeably (in SEM) raised above the epithallial cells of the surrounding roof (Figures 47, 57, 66); pore diameter 10.5 – 13.6 µm; filaments lining the pore not markedly different from normal roof cells (Figure 65), pore filaments 7 – 10 cells long, roof 43 – 72 µm thick. Sporangia measure 186 – 225 µm long × 50 – 100 µm in diameter (Figures 48, 49), uncalcified filaments among sporangia evidently degenerate during conceptacle maturation, and have not been seen in our specimens. Old conceptacles usually buried within the thallus and filled in with sterile cells (Figure 44).

Habitat and phenology

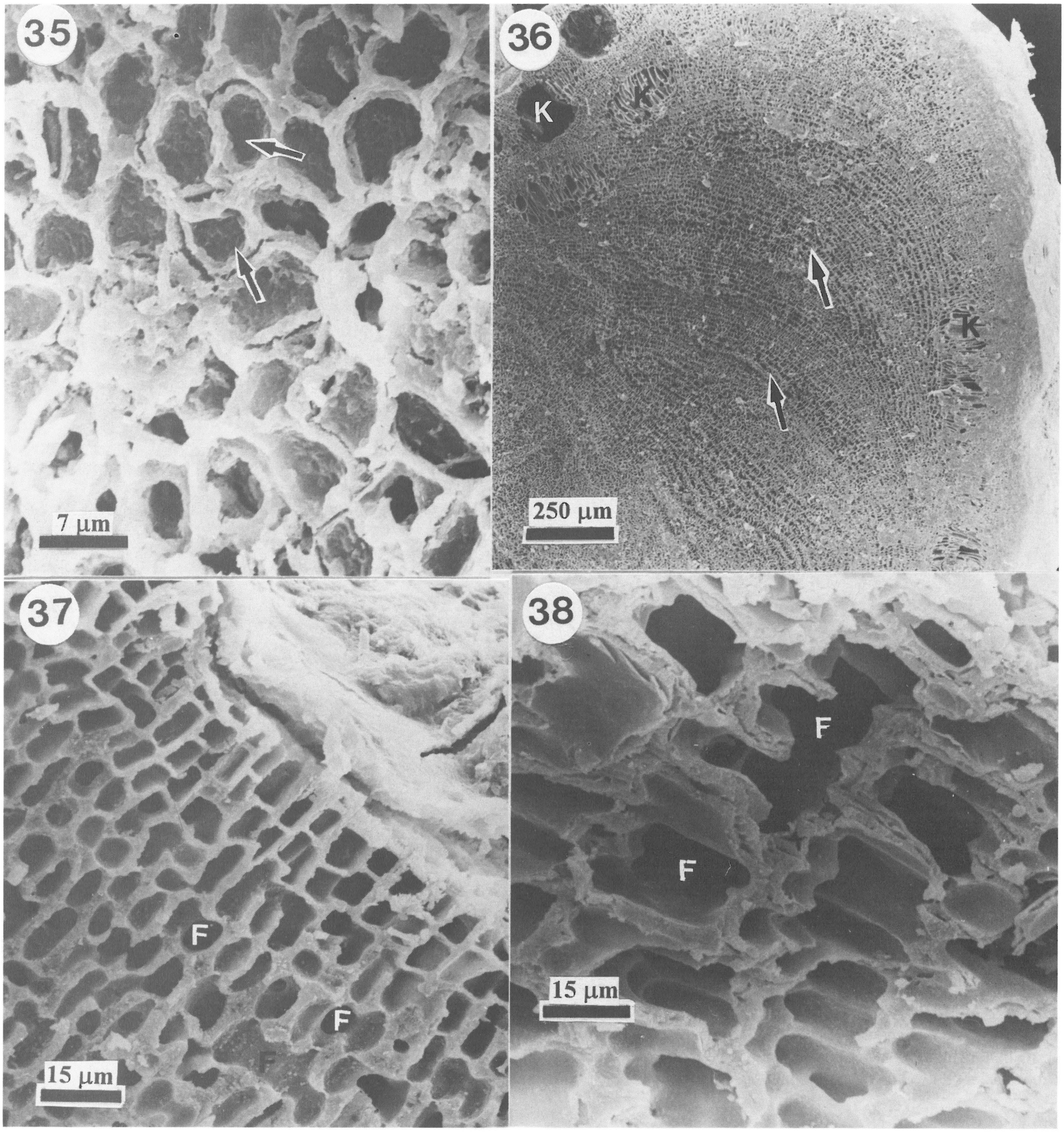
Only three specimens were collected, growing on old dead coral and rock at 12 – 17 m depth, suggesting that this species is relatively rare in the area. Sporangial conceptacles were recorded in July and November, the only months during which collections were made.

Distribution

South Africa: Sodwana Bay, Natal. World: Funafuti Atoll, Guam, Hawaii, Indonesia, Red Sea, South Africa.

Specimens examined

—2732 (Ubombo). Two-Mile Reef, Sodwana Bay, South Africa, on vertical walls under overhang, *ca.* 12 m depth, *D. Keats* (UWC: COR/325); Seven-Mile Reef, Sodwana Bay, Natal Province, on old coral on coral reef, 25 m depth, *D. Keats & Y. Chamberlain* (UWC: 91/117); Two-Mile Reef, Sodwana Bay, Natal Province, on old coral on reef, 12 – 14 m depth, *D. Keats & Y. Chamberlain* (UWC: 91/135) (–DA).



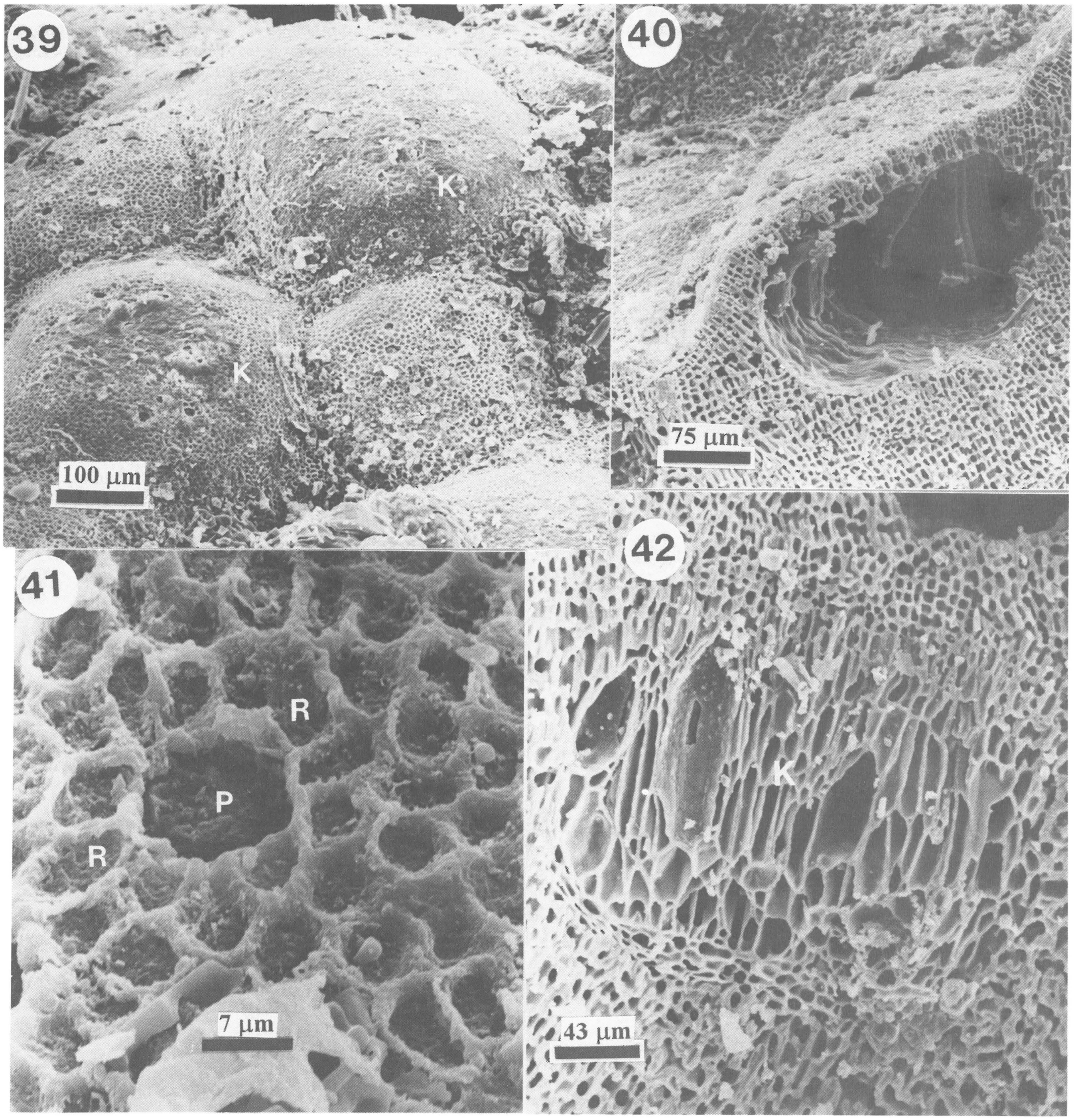
Figures 35 – 38 Scanning electron micrographs of the holotype of *Lithothamnion erubescens* f. *madagascariensis* Foslie. **35.** Surface view of vegetative thallus; note epithallial concavities (arrow). **36.** Vertical section of protuberance showing layering (arrows) within the protuberance medulla and old, buried conceptacles (K). **37.** Cortical filaments showing cell fusions (F). **38.** Medullary cells showing cell fusions (F).

Remarks

Mesophyllum funafutiense is a well-documented species, and our specimens conform well to the descriptions published, for example, by Adey *et al.* (1982) (as *M. purpurascens*) and Verheij (1993a). The characters which we regard as diagnostic of this species are:

(a) tetrasporangial or bisporangial conceptacles domed, lacking a raised rim;
(b) tetrasporangial or bisporangial conceptacle pores surrounded by rosette cells that are distinctly raised above the surrounding surface;
(c) tetrasporangial or bisporangial conceptacle pore canal lined by filaments that do not differ from the other roof filaments;
(d) tetrasporangial or bisporangial conceptacle chamber 450 – 600 µm in diameter;
(e) tetrasporangium or bisporangium 186 – 225 µm long.

The diagnostic value of character (b) above is uncertain, as its state has not been determined for any species listed in Table 1 other than *M. erubescens*. Characters (a) and (c) do not allow *M. funafutiense* to be distinguished from *M. engelhartii* (Foslie) Adey or *M. syrphetodes* Adey, Townsend et Boykins. Of the characters listed, only its larger conceptacles (d) and tetrasporangia (e) allow *M. funafutiense* to be distinguished



Figures 39 – 42 Scanning electron micrographs of the holotype specimen of *Lithothamnion erubescens* f. *madagascariensis* Foslie. **39**. Sporangial conceptacles (K). **40**. Recently empty sporangial conceptacle near thallus surface. **41**. Detail of sporangial pore (P), showing apparent rosette cells (R); the cells which terminate the pore canal filaments are hidden below the surface of the pore. **42**. Old sporangial conceptacle (K) buried within cortical filaments.

from *M. engelhartii* and *M. syrphetodes* (Table 1).

In *M. funafutiense*, the surfaces of epithallial cells tend not to collapse into the cell lumen in air-dried specimens as it does in most other species of *Mesophyllum* that we have examined, and this gives the surface a distinctive appearance in scanning electron micrographs. This character may become useful in defining species as more information becomes available. Verheij (1993a) used the number of cells in the uncalcified intersporangial filaments within tetrasporangial conceptacles as a diagnostic character, but noted that these cells were not seen in *M. funafutiense*. The potential diagnostic value of this character remains uncertain until all developmental stages of tetrasporangial conceptacles are available for study in *M. funafutiense*, and until its state is recorded for other species of *Mesophyllum*.

Useful field identification characters include a very glossy thallus that lacks protuberances; a strongly coaxial medula; fairly large, domed conceptacles (measuring 600 – 800 µm outside diameter), occurring in a densely crowded mass; and the roof of sporangial conceptacles penetrated by up to 100 or more pores.

Discussion

The genus *Mesophyllum* was established by Lemoine (1928) for melobesioid species with a coaxial medulla. Woelkerling and Harvey (1992, 1993) questioned the validity of this character for generic delineation because several species combine coaxial and non-coaxial areas in the same thallus. Instead,

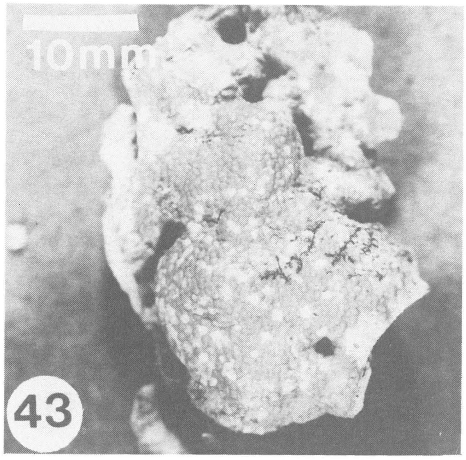
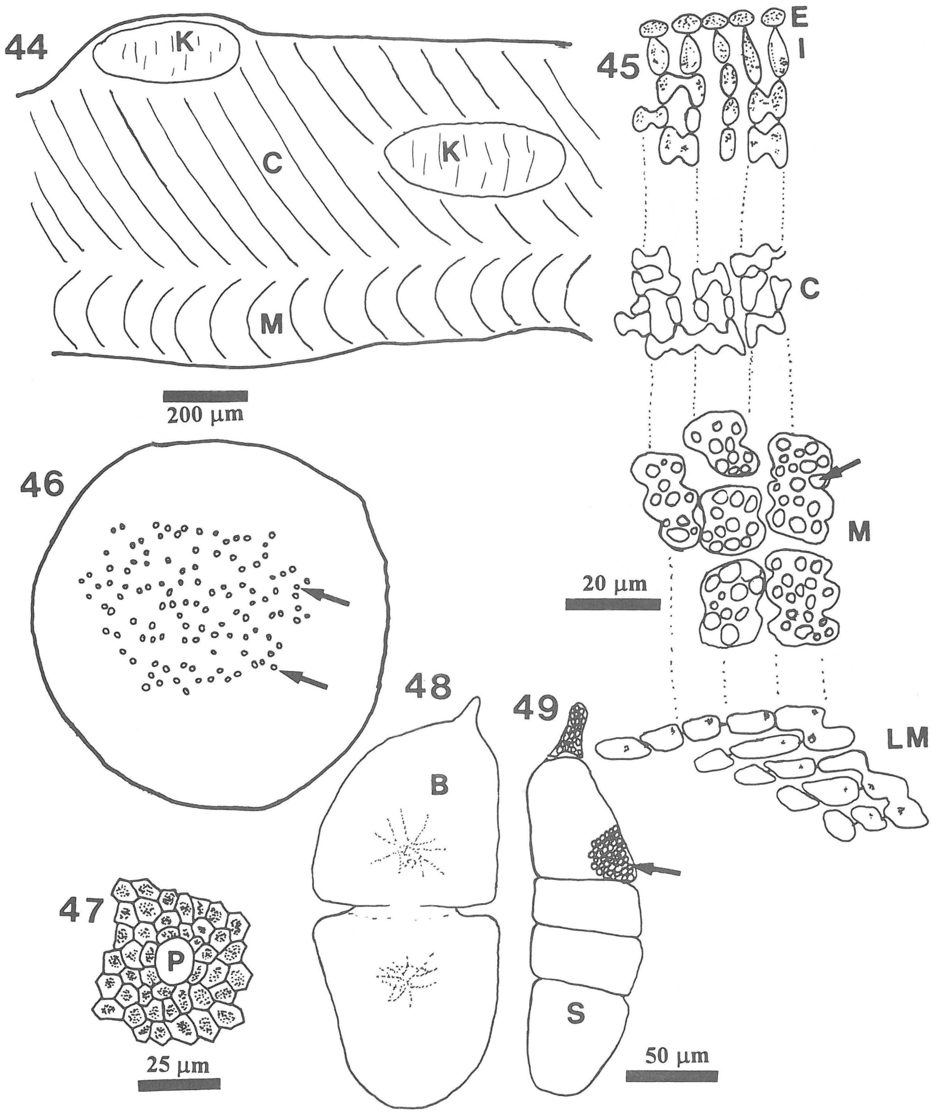


Figure 43 Specimens of *Mesophyllum funafutiense* from Sodwana Bay, Natal, South Africa (UWC: COR/325).

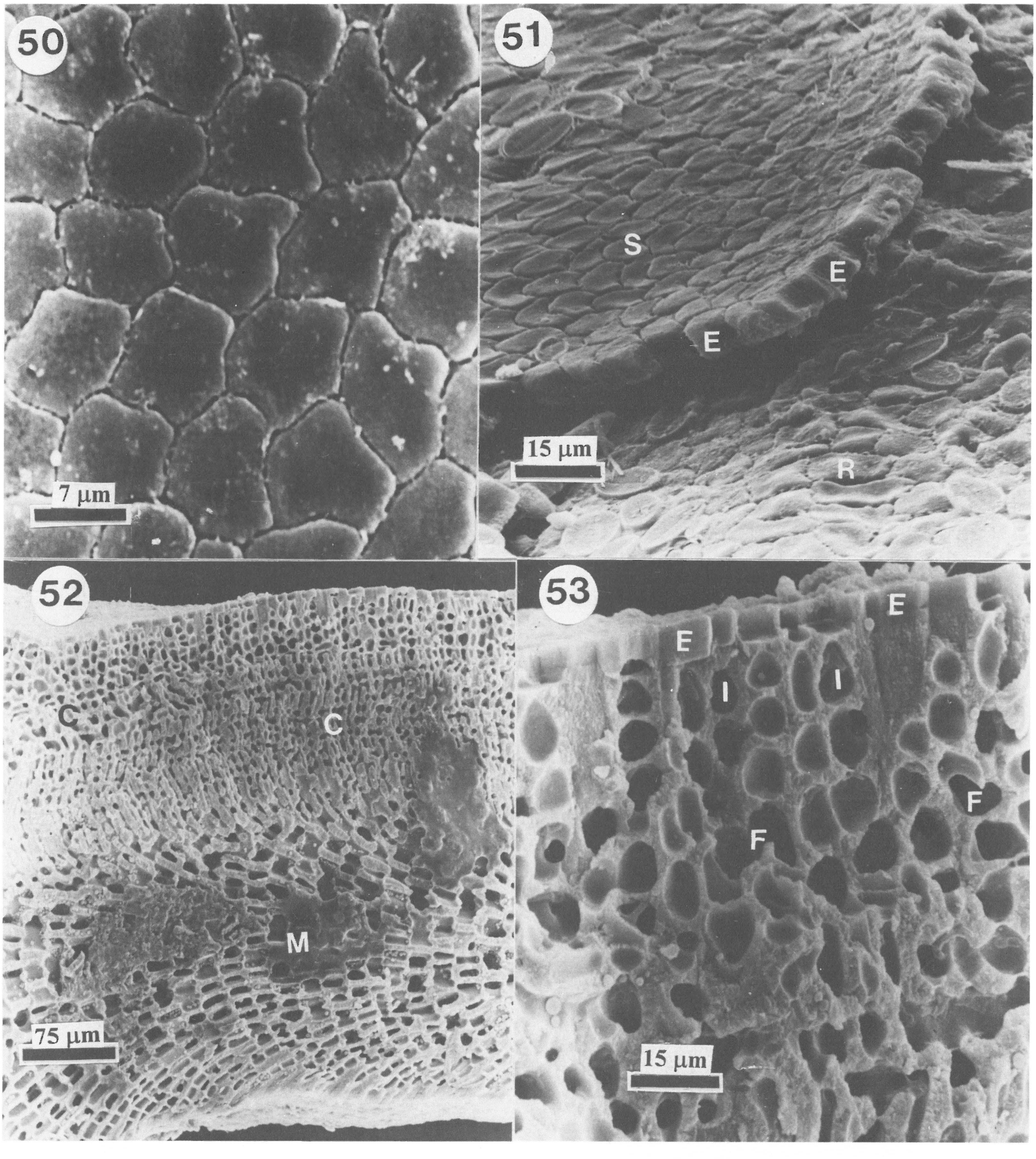
Woelkerling and Harvey (1992, 1993) delimited *Mesophyllum* from other melobesioid genera on the basis of the anatomy of spermatangial conceptacles, as suggested by Suneson (1937), Lebednik (1978) and Townsend (1979), including the following combination of characters:

(a) internal construction monomerous;
(b) haustoria absent;
(c) outermost walls of terminal epithallial cells rounded or flattened but not flared;
(d) vegetative intitials usually as long as or longer than cells immediately subtending them;
(e) spermatangial initials formed directly from meristematic cells;
(f) spermatangial initials overlain by a layer of protective cells;
(g) spermatangial conceptacle roofs formed centripetally from groups of peripheral filaments;
(h) spermatangial branches simple;
(i) spermatangial branches occur on the floor, walls and roof of male conceptacles.

However, all melobesioid species that have been examined according to these new criteria, and which have had a predominance of coaxial medulla, have been ascribed to *Mesophyllum*.



Figures 44 – 49 Anatomy of *Mesophyllum funafutiense* from Natal. **44.** Diagrammatic drawing of a thallus showing buried tetrasporangial conceptacles (arrows), cortex (C) and coaxial medulla (M) (UWC: 91/117). **45.** Thallus showing epithallial cells (E), subepithallial initial (I), lower cortical (C), medullary (M) and lower medullary cells (LM) with cell fusions (F) (UWC: 91/117). **46.** Surface view of sporangial conceptacle showing pores (arrows) (UWC: 91/117). **47.** Detail of sporangial pore (P) (UWC: 91/117). **48.** Bisporangium with bispores (B) (UWC: 91/135). **49.** Tetrasporangium with tetraspores (S) and starch grains (arrow) (UWC: 91/117).

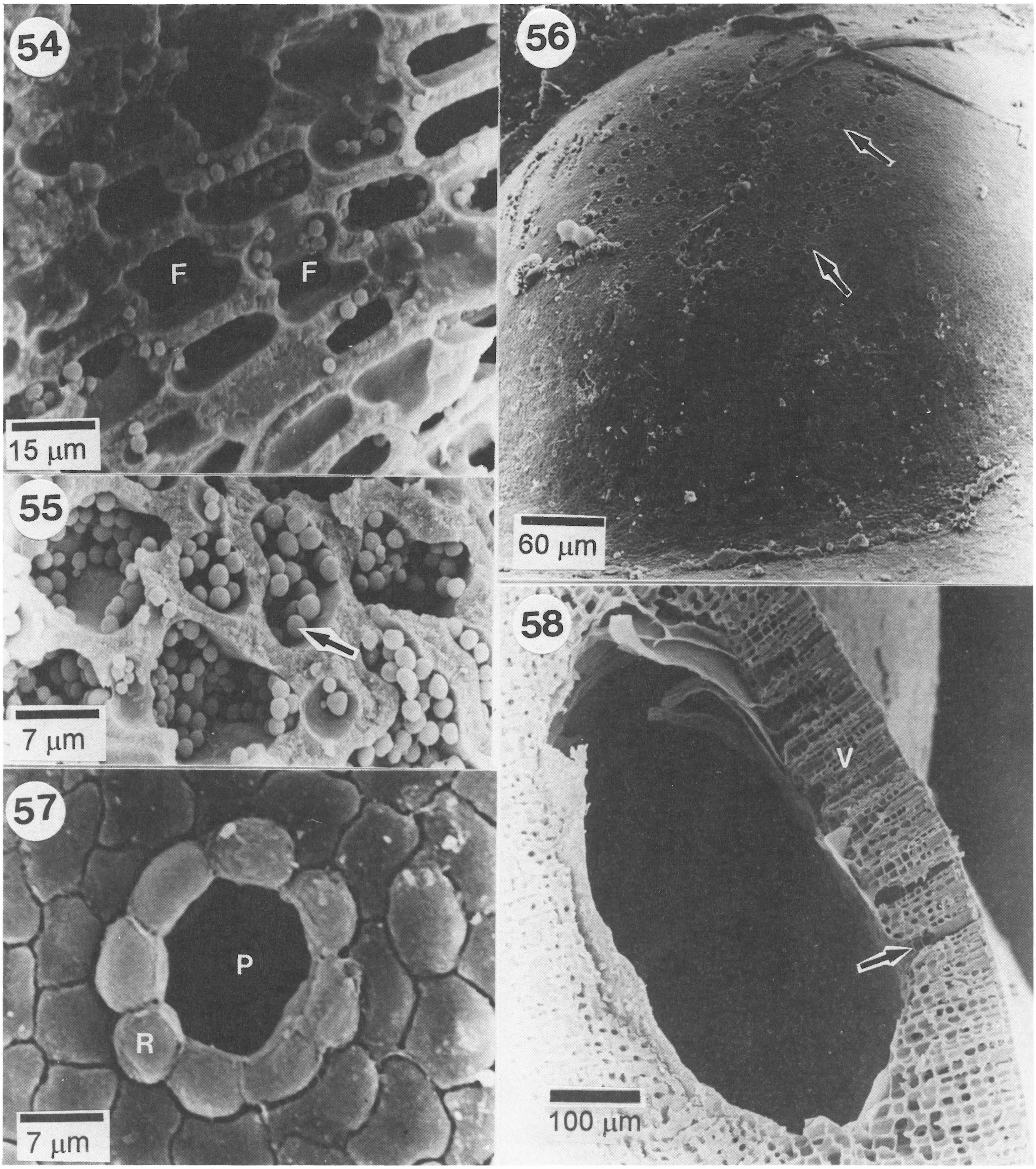


Figures 50 – 53 Scanning electron micrographs of *Mesophyllum funafutiense* from Natal (UWC: 91/117). **50.** Surface view of vegetative thallus. **51.** Surface of vegetative thallus showing sloughing epithallial scales (S), epithallial cells (E) and the surface of regenerated epithallial cells (R). **52.** Vertical section of thallus showing cortex (C) and coaxial medulla (M). **53.** Cortical filaments showing epithallial cells (E), subepithallial initials (I) and cell fusions (F).

This suggests that, while *Mesophyllum* may not be designated only on the basis of a coaxial medulla, this character is strongly associated with the genus, and may be useful for identification when sexual material is not available, as is often the case with populations of *Mesophyllum* species.

Gametangial conceptacles were not present on the type specimen of *M. erubescens* or *M. madagascariensis*, but we did find one plant of *M. erubescens* in South Africa with gametangial conceptacles. Spermatangial systems were simple and occurred on the floor, walls and part of the roof of the conceptacle, as recorded in Indonesian material by Verheij (1993a). However, Adey *et al.* (1982) reported simple spermatangial systems restricted to the conceptacle floor in Hawaiian specimens of *M. erubescens* (as *M. madagascariensis*), but did not illustrate a male conceptacle. On the basis of criteria (a) – (d) and (g) – (i), our material of this species conforms to *Mesophyllum*.

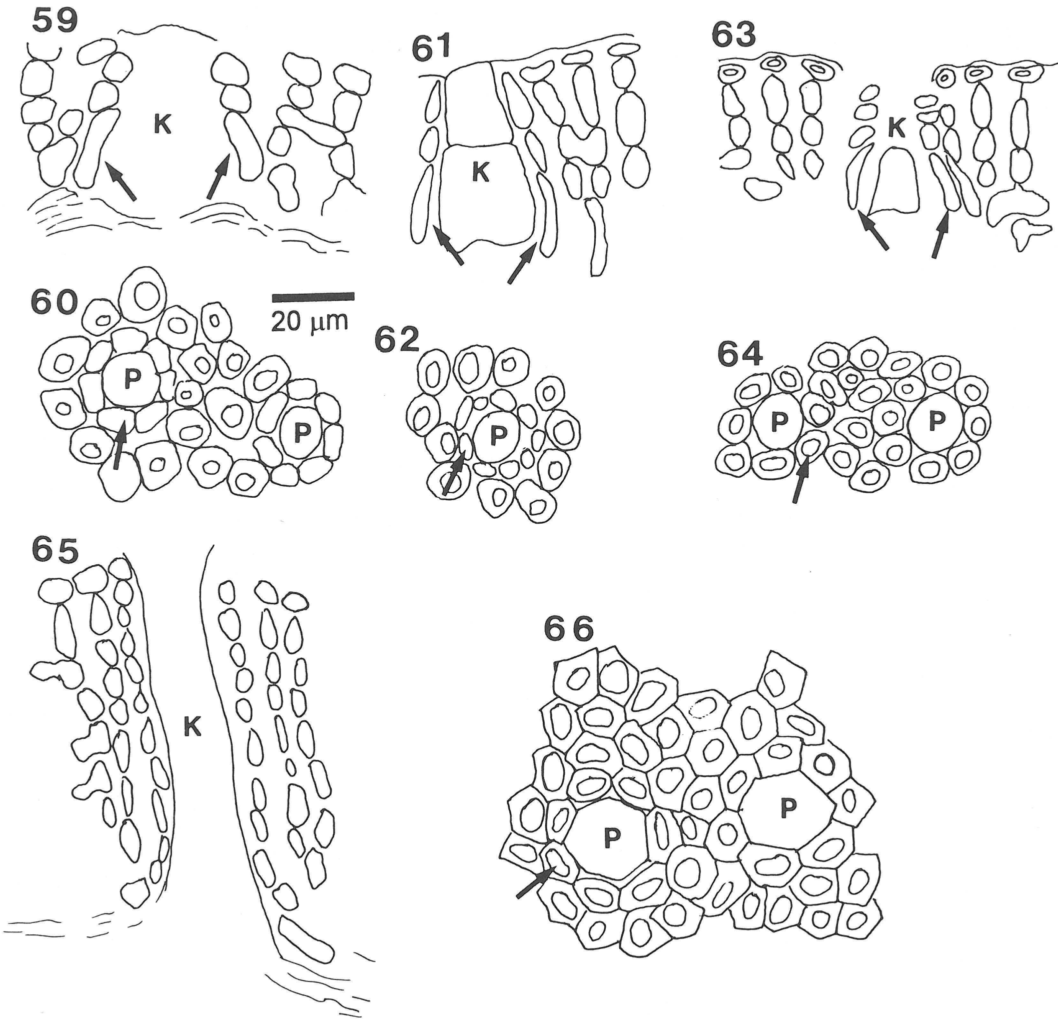
No spermatangial conceptacles of *M. funafutiense* were found during the present study, but simple spermatangial systems on the floor, walls and roof of the male conceptacle



Figures 54 – 58 Scanning electron micrographs of *Mesophyllum funafutiense* from Natal (UWC: 91/117). **54**. Medullary cells showing abundant starch grains (arrow) and cell fusions (F). **55**. Starch grains (arrow) in cortical cells. **56**. Sporangial conceptacle with numerous pores (arrow). **57**. Detail of sporangial pore (P), showing raised rosette cells (R). **58**. Recently empty sporangial conceptacle near thallus surface showing pore canal (arrow) and conceptacle roof (V).

were recorded from Indonesia by Verheij (1993a). This species therefore conforms to *Mesophyllum* on the basis of criteria (a) – (d) and (g) – (i) above, in combination with the presence of a strongly coaxial medulla.

A monograph on the genus *Mesophyllum* is urgently needed. At least 147 taxa have been attributed to the genus (Woelkerling 1988), and it seems unlikely that they are all good taxa. There is some uncertainty as to which characters are useful for delineating species, but those related to growth form, including the presence or absence of protuberances, the degree of leafiness, and the degree of adherence are probably unreliable (Woelkerling & Harvey 1992, 1993). Those characters associated with sporangial conceptacles, including outside diameter, chamber diameter, height, shape, number of pores, pore anatomy, and size of sporangia may also prove useful, and should be included in accounts of species wherever possible. Of particular taxonomic significance are the presence or absence of a raised rim on tetrasporangial and bisporangial



Figures 59 – 66 Comparative anatomy of tetrasporangial pore for *Mesophyllum erubescens* and *M. funafutiense*. **59.** Vertical section of tetrasporangial pore of holotype of *Lithothamnion erubescens* Foslie. Note elongate cells (arrow) at base of pore. **60.** Tetrasporangial pore plate of holotype of *Lithothamnion erubescens* Foslie with pore (P) and rosette cells (arrow). **61.** Vertical section of tetrasporangial pore of holotype of *Lithothamnion erubescens* f. *madagascariensis* Foslie. Note elongate cells (arrow) at base of pore. **62.** Tetrasporangial pore plate of holotype of *Lithothamnion erubescens* f. *madagascariensis* Foslie with pore (P) and rosette cells (arrow). **63.** Vertical section of tetrasporangial pore of *Lithothamnion erubescens* from Natal. Note elongate cells (arrow) at base of pore (UWC: COR/105). **64.** Tetrasporangial pore plate of *Lithothamnion erubescens* from Natal with pore (P) and rosette cells (arrow) (UWC: COR/105). **65.** Vertical section of tetrasporangial pore of *Lithothamnion funafutiense* from Natal (UWC: COR/325). **66.** Tetrasporangial pore plate of *Lithothamnion funafutiense* from Natal with pore (P) and rosette cells (arrow) (UWC: 91/117).

conceptacles, and the structure of the pore canal, and we agree with Woelkerling and Harvey (1993) that these characters are stable and reliable. Another character that should be emphasized is the position of the rosette cells that surround the pores of sporangial conceptacles; they may be raised above surrounding roof cells (e.g. *M. purpurascens*), flush with them (e.g. a species of *Mesophyllum* presently under study), or sunken below them (e.g. *M. erubescens*). Characters associated with sexual conceptacles are of little practical value, since sexual conceptacles are rare in members of this genus.

Mesophyllum erubescens is pan-tropical/subtropical, while *M. funafutiense* seems to be confined to the tropical Indo-Pacific region (Adey *et al.* 1982; Foslie 1904; Gordon *et al.* 1976; Masaki 1968). This supports the view that is emerging of the Sodwana Bay area of northern Natal as having a coralline flora typical of the tropical Indo-Pacific region, with some pan-tropical/subtropical elements (Keats & Chamberlain 1993, 1994).

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This paper is dedicated to the memory of Aldridge Groener, an exceptionally dedicated and capable student of phycology, who was killed in the pursuit of his M.Sc. research.

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