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Lithothamnion prolifer Foslie: A Common Non-geniculate Coralline Alga (Rhodophyta: Corallinaceae) from the Tropical and Subtropical Indo-Pacific

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A little-known, but ecologically important non-geniculate coralline, *Lithothamnion prolifer*, is recorded from a number of tropical Indo-Pacific sites, including Fiji, Australia, Kiribati and Indonesia. The species occurs primarily on vertical walls of caves and overhangs in Fiji and Australia, but was also found as rhodoliths in Kiribati. *Lithothamnion prolifer* is characterized by the combination of characters which follow. The thallus is extremely glossy, smooth, and rosy coloured. Thalli usually produce complanate protuberances, but protuberances become terete when growing on well lit, horizontal substrata, when unattached, or when growing on loose substrata. Conceptacles occur mainly on the tips of protuberances, and tetra/bisporangial conceptacles are large (to 1300 µm external diameter, with chambers up to 1100 µm diameter). The tetra/bisporangial conceptacles are flush or only slightly raised, and often extensive and irregularly shaped (resembling small sori). They lack a raised rim, and have flattened pore plates. The rosette cells surrounding the tetra/bisporangial pore appear somewhat sunken below the surrounding roof cells in SEM, and the cells of filaments lining the pore canals of tetra/bisporangial conceptacles do not differ from the cells of filaments making up the rest of the roof. Old conceptacles persist and become buried in the thallus, and are then usually completely filled in by irregularly arranged calcified cells.

Introduction

The non-geniculate coralline algae of the tropical Indo-Pacific region are poorly known at present, particularly as far as regional floras are concerned. For example, Chapman (1971) reported only 8 non-geniculate coralline species from Fiji. South and Kasahara (1992) recorded the 8 species reported by Chapman (1971) with an additional 4 species reported by Chapman (1977). None of these species have been studied in a modern context, and all must be treated as unconfirmed records. The only detailed studies of the non-geniculate coralline algae of any site in the tropical Indo-Pacific within the past 30 years were those of Gordón *et al.* (1976) who reported 15 species from Guam, Adey *et al.* (1982) who reported 27 species from Hawaii, and Verheij (1993 a, 1994) who reported 16 species from Indonesia. A study of the non-geniculate coralline algae of Fiji has therefore been undertaken by the first author to improve our knowledge of the taxonomy of the group in this region.

During the course of this study, a species of *Lithothamnion* was found that seemed concordant with *Lithothamnion prolifer* Foslie. It also conformed to specimens collected on the Great Barrier Reef, and which had been suspected of being a new species, but for which no description had been published. Specimens

of this species were also examined from Kiribati (coll. by G. Yeo), and Indonesia (coll. by E. Verheij). Therefore, this species was studied from material collected in Fiji, Kiribati, Indonesia, and the Great Barrier Reef.

Until recently, generic concepts for non-geniculate coralline algae were based on characters that have since been shown to be unstable or untenable (e.g. *Porolithon*, Penrose and Woelkerling 1988; *Fosliella*, Penrose and Chamberlain 1993). Recent studies by Woelkerling and co-workers have altered many of our generic concepts within this group, and have incorporated reproductive characters into the criteria used for generic delineation [e.g. May and Woelkerling (1988), Penrose (1992), Penrose and Chamberlain (1993), Penrose and Woelkerling (1988, 1992), Townsend *et al.* (1994), Woelkerling (1983, 1988), Woelkerling and Harvey (1993)]. As a result of these recent changes, it is often not possible to tell to which genus a particular species described in older literature belongs without reference to the type specimen. Ongoing studies in many parts of the world, however, are beginning to correct this situation [e.g. Chamberlain (1990, 1993, 1994), Chamberlain and Keats (1994), Chamberlain and Norris (1994 a, b), Keats and Chamberlain (1993, 1994 a, b, 1995), May and

Woelkerling 1988, Penrose (1991, 1992), Penrose and Chamberlain (1993), Penrose and Woelkerling (1991, 1992), Townsend *et al.* (1994, 1995), Verheij (1993 a, b, 1994), Woelkerling and Foster (1989), Woelkerling and Harvey (1993)].

To make studies of the non-geniculate corallines useful in the long-term, the approach has been adopted of describing all aspects of non-geniculate coralline algae in sufficient detail to enable future workers to assess species without having to resort to an analysis of type collections. Type material is, therefore, described and illustrated in detail. New or otherwise taxonomically interesting or ecologically important species will be dealt with first, with the aim of ultimately producing a guide to the non-geniculate coralline flora of the tropical Indo-Pacific that will also include taxonomic and field keys.

Materials and Methods

All material was collected by either SCUBA or snorkel diving. Study areas in Fiji include Suva Lagoon and its barrier reef, Beqa Lagoon, and Great Astrolabe Reef, while Australian study areas include Lizard Island, Palm Isles, Whitsundays and Capricorn Group. Dried specimens were also provided by Gary Yeo (University of the South Pacific) from Kiribati, and by Eric Verheij (L) from Indonesia (Verheij 1993 a). Fijian specimens were either air dried, or fixed in 10% Formalin and transported to the University of the South Pacific (USP), where they were decalcified in 10% nitric acid, and then sectioned at 10–30 µm thickness using a Reichert CO₂ freezing microtome. Each section was removed from the microtome blade using a fine sable hair brush, and transferred to a slide containing either methylene blue in glycerin jelly or aniline blue in 50% Karo syrup. Drawings were made directly from prepared slides using a Zeiss microscope equipped with a drawing tube. Australian specimens were transported to the Smithsonian Institution, Washington, where they were decalcified in Susa's fixative and processed using standard paraffin embedding regime (O'Brien and McCully 1978). Sections were cut to 10–15 µm thickness, and stained with phosphotungstic haematoxylin.

Specimens from Fiji are deposited in the herbarium of the University of the Western Cape, Bellville, South Africa (UWC) with duplicates also located in the South Pacific Regional Herbarium of the University of the South Pacific (SUVA). The Australian specimens are deposited in USNC, MELU, SYD and MURU [Herbarium abbreviations follow Holmgren *et al.* (1990) except MURU: The Herbarium, School of Biological and Environmental Sciences, Murdoch University, Murdoch, W. A., Australia].

For scanning electron microscopy, air or oven dried material was fractured using either finger nails, forceps, diagonal cutters, or a small hammer and cold chisel. Wherever possible a fracture perpendicu-

lar 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, U.K.), 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 a Hitachi X650 scanning electron microscope, equipped with a Mamiya 6X7 camera at an accelerating voltage of 20 kV.

Conceptacle outside diameter and pore diameter were 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 Chamberlain (1990), while morphological terminology follows Woelkerling *et al.* (1993). Typification data follow Woelkerling (1993). ! denotes type specimen examined. SEM = scanning electron micrograph.

Observations

Lithothamnion prolifer Foslie 1904: 18 (Figs 1–36)

Homotypic synonym: *Mesophyllum prolifer* (Foslie) Adey 1970: 25.

Nomen nudum: *Lithothamnion pseudosorum* (Johnson *et al.* 1991 a, b).

Lectotype: L!943.7–40 (Siboga Expedition collection 146), designated by Verheij and Woelkerling (1992). The L box 943.7–40 also contains two slides and the L! isotype (Siboga Expedition collection 139).

Etymology: Foslie (1904) did not mention the etymology, other than saying 'scantly prolificating', but '*prolifer*' means 'producing offsets; bearing progeny as offshoots' (Stearn 1983).

Published illustrations: *Lectotype:* Foslie (1904, pl. 1, figs 17–20), Printz (1929, pl. 8, fig. 13), Verheij (1993 a, figs 72, 74). *Other material:* Verheij (1993 a, figs 73, 75–82).

Representative specimens examined

Fiji: Suva Barrier Reef, 10–15 m depth, crevices and holes on vertical slope, (*D. Keats*, 1994, v. 10, UWC: 94/1005); Suva Barrier Reef, 10–15 m depth, crevices and holes on vertical slope, (*D. Keats*, 1994, v. 12, UWC: 94/1015); Suva Barrier Reef, crevices and holes on vertical slope, (*D. Keats*, 1994, v. 18, UWC: 94/1017); Great Astrolabe Reef, Osborne Passage, caves and holes, 2–30 m depth, (*D. Keats*, 1994, vi. 02, UWC: 94/1034, paratype); Great Astrolabe Lagoon, Dravuni patch reef, caves and holes, 5–15 m depth, (*D. Keats*, 1994, vi. 02, UWC: 94/1040); Great

Astrolabe Reef, outside of Usborne Passage, caves and holes, 2–30 m depth, (*D. Keats*, 1994. vi. 09, UWC: 94/1056); Great Astrolabe Reef, Herald Passage, caves and holes, 3–20 m depth, (*D. Keats*, 1994. vi. 10, UWC: 94/1075); North Astrolabe Reef, leeward side, caves and overhangs, 4–20 m depth, (*D. Keats*, 1994. vi. 11, UWC: 94/1111); Suva Barrier Reef, 2–25 m depth, crevices and holes, (*D. Keats*, 1994. vi. 21, UWC: 94/1113); Beqa Barrier Reef, leeward side, crevice ca. 12 m depth (*D. Keats*, 1994. vii. 16, UWC: 94/1129); Suva Barrier Reef, cave walls on vertical slope, (*D. Keats*, 1994. ix. 28, UWC: 94/1222).

Kiribati: Tarawa Atoll, rhodoliths (*G. Yeo*, 1994 ix, UWC: 94/1279).

Indonesia: Langleai, South Western Sulawesi, 0–5 m depth (*E. Verheij*, 1985. vii. 24, L: B182, B200).

Great Barrier Reef, Australia: Lizard Island, lagoon, 20 m depth, (*R. Steneck and M. Borowitzka*, 1978. iv, USNC 78-12-20); Lizard Island, Granite Head, 15–20 m depth, (*R. Steneck and M. Borowitzka*, 1978, iv, USNC7 8-14-1), Lizard Island, Chinaman Reef, 0–2 m depth, (*R. Steneck and M. Borowitzka*, 1978. iv. 23, USNC7 8-16-1, UWC: 95/21); Palm Isles, Great Palm Island, Elk Cliff, (*R. Steneck and M. Borowitzka*, 1978. iii. 08, USNC 78-1-17); Palm Isles, Bramble Reef, 10 m depth (*R. Steneck and M. Borowitzka*, 1978. iii. 05, USNC 78-3-26, USNC 78-3-5); Whitsundays, Hazelwood Is., 6–7 m depth, (*C. O'Brien*, 1977. xii. 03, MELU GBR 7701); Whitsunday, Is., Peters Head, (*C. O'Brien*, 1977. xii. 07, MELU GBR 7702); Capricorn Group, Wistari Reef, lee, 10 m depth, (*R. Townsend*, 1978. v. 05, SYD GBR 7802, MURU GBR 7801, MURU GBR 7802).

Habitat and phenology

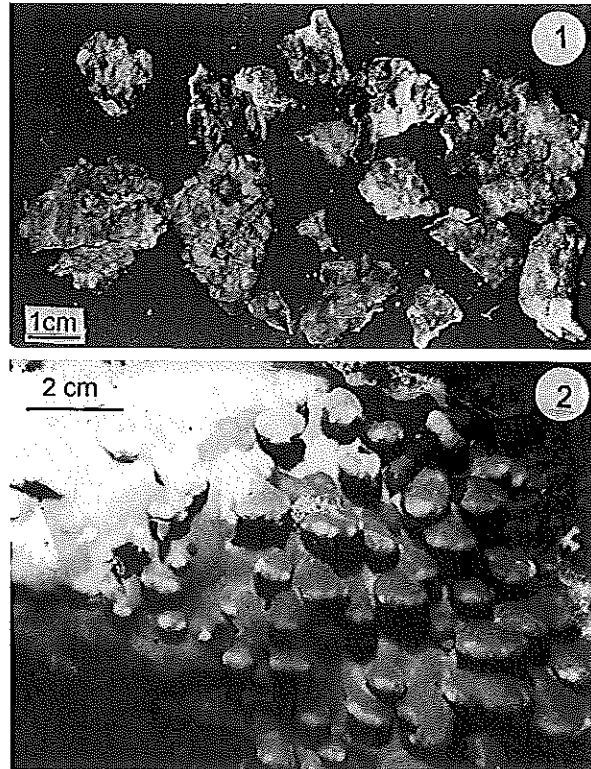
Lithothamnion prolifer occurs mainly on vertical surfaces in caves, crevices and under overhangs from the immediate subtidal area of the reef to at least 30 m. Between 30 and 40 m, it occurs in scattered patches on open substratum. It is most abundant, and branches are most well developed, in small caves, overhangs, and cryptic spaces between 10 and 25 m. It tends to occur in distinctive, conspicuous, rose-coloured patches which seldom exceed 30–40 cm in diameter. In Fiji, this species is common in all reefs sampled. On the east coast of Australia, it is a common member of the reef flora all along the Great Barrier Reef. In Kiribati, it forms extensive rhodolith beds at moderately sheltered sites at Tarawa Atoll. Male, carposporangial and tetra-bisporangial conceptacles were found in February–November, but no collections were made in December or January.

Distribution

Australia, Fiji, Kiribati, Indonesia.

Habit and vegetative structure

Plants are non-geniculate, encrusting (Fig. 1) on dead coral, and moderately adherent except when heavily



Figs 1–2. Habit of *L. prolifer*.

Fig. 1. Fragments of typical specimen from Fiji (UWC: 94/1017). Fig. 2. Specimen photographed *in situ* in cave on Suva Barrier Reef. Note the complanate protuberances.

burrowed by invertebrates. On vertical substrata and in caves, thalli are often composed mainly of markedly flattened protuberances (Fig. 2) that usually emerge from the crustose portion of the thallus at an angle of ca. 45 degrees and often create partially overlapping layers. Thalli with terete or slightly flattened, vertically-oriented protuberances may also occur in some populations, especially when the plants are growing on horizontal substrata or as rhodoliths (Fig. 3). The margins and areas between protuber-

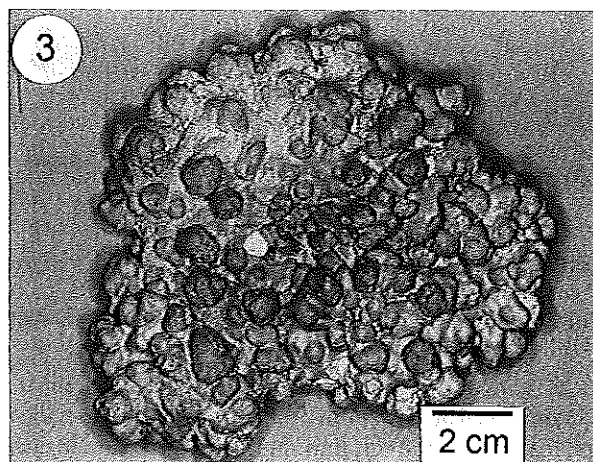
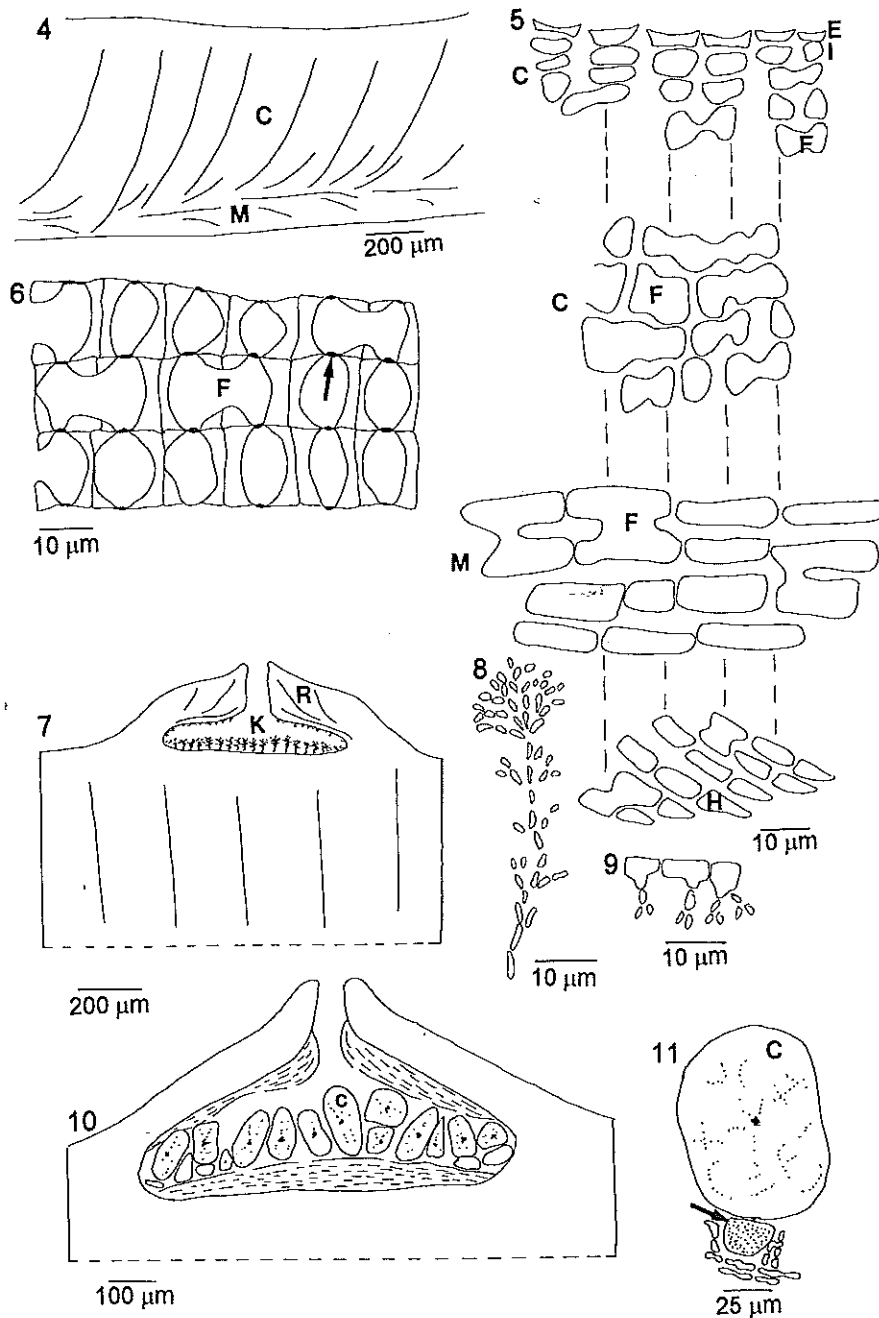


Fig. 3. Rhodolith form of *L. prolifer* from Kiribati (UWC: 94/1279).

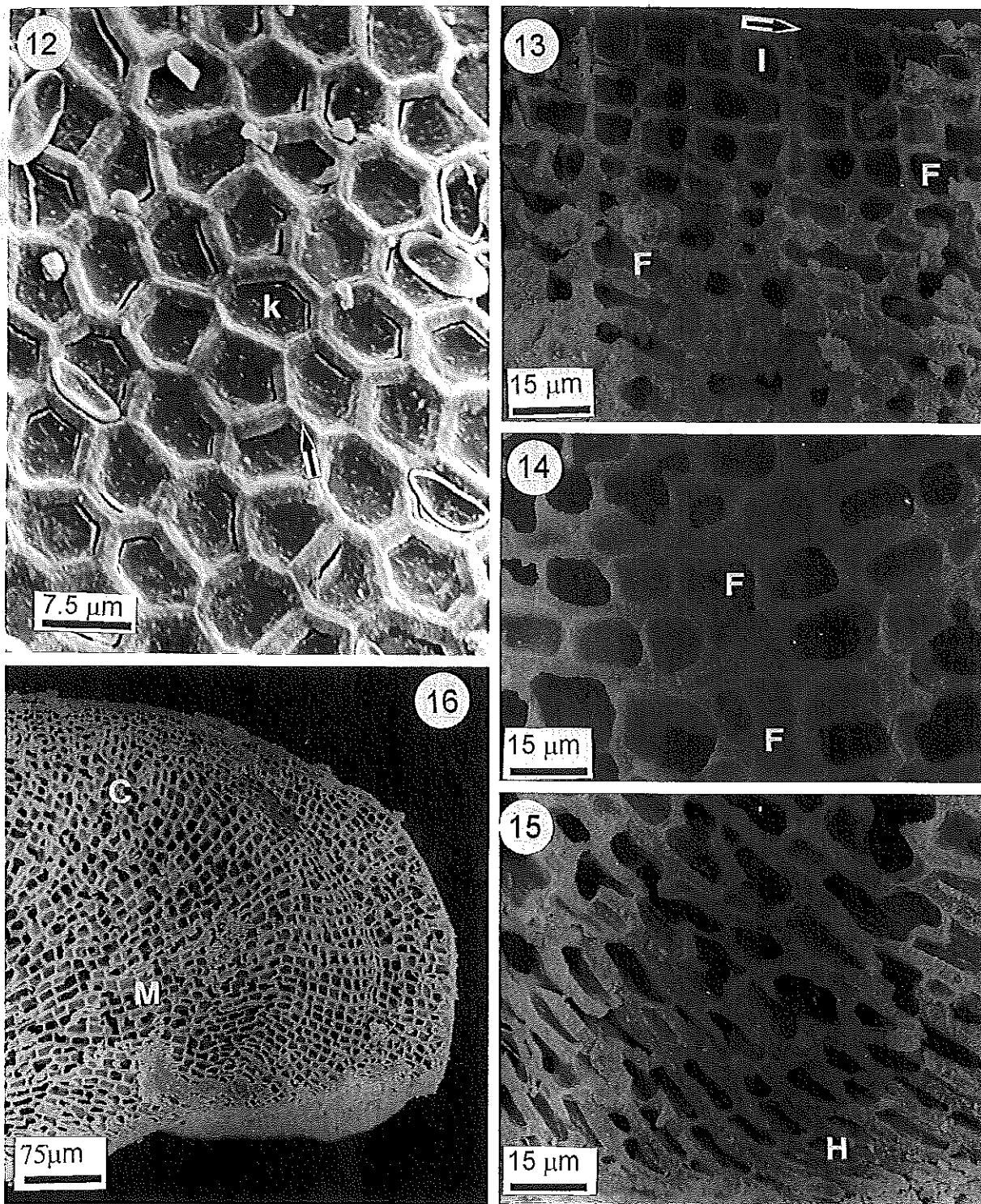


Figs 4–11. Vegetative and reproductive anatomy of *L. prolifer*.

Fig. 4. Diagrammatic drawing of VS of thallus showing medulla (M) and cortex (C) (UWC: 93/1017). Fig. 5. Drawing of VS of thallus showing epithallial cells (E), subepithallial initial (I), cells of cortical (C) and medullary (M) filaments with cell fusions (F). Medullary filaments curve downward and terminate in a hyaline cell (H) (UWC: 93/1017). Fig. 6. Strongly aligned cells from cortical filaments (F = cell fusion; arrow = primary pit plugs) (UWC: 93/1017). Fig. 7. Diagrammatic drawing of section of thallus with male conceptacles showing the shape of the chamber (K), and the roof (R) (UWC: 93/1017). Fig. 8. Branched spermatangial system from the floor of the male conceptacle (UWC: 94/1017). Fig. 9. Simple spermatangial systems from the roof of the male conceptacle (UWC: 94/1017). Fig. 10. Diagrammatic drawing of section of carposporangial conceptacle showing carposporangia (c) (UWC: 94–1278). Fig. 11. Detail of single carposporangium (c) with densely pigmented subtending cell (arrow) (UWC: 94/1278).

ances measure 140–5000 µm thick. Protuberances measure 5–15(–30) mm long, 5–25 mm in widest dimension, and 2–5 mm in narrowest dimension. The surface is extremely glossy, resembling fine china, and has a smooth velvety texture (Fig. 2). Plants are generally rose to orange-pink, often with whitened

areas of sloughing epithallial cells. Uniporate conceptacles are mound-like, slightly apiculate, and occur mainly on the tips of protuberances. Multiporate conceptacles are flush with the surrounding roof to slightly raised above it (Fig. 22), and occur mainly on the tips of protuberances.



Figs 12–16. Vegetative anatomy of *L. prolifer* (SEM, UWC: 94/1017).

Fig. 12. Surface view of thallus showing broad epithallial concavities (k) and relatively thin lateral walls (arrow). Fig. 13. Fracture near thallus surface showing cell fusions (F) in cells of cortical filaments, subepithallial initials (i) and epithallial cells (arrow). Fig. 14. Cells of medullary filaments with cell fusions (F). Fig. 15. Medullary filaments at the ventral surface, showing their termination in cells with angular end walls (H). Fig. 16. Thallus margin showing medulla (M) and cortex (C).

The thallus is monomerous. The medulla is plumose (Figs 4, 16), and usually forms less than 15% of the thallus thickness. Cells of medullary filaments are narrowly to broadly oblong (Figs 5, 14, 15) and mea-

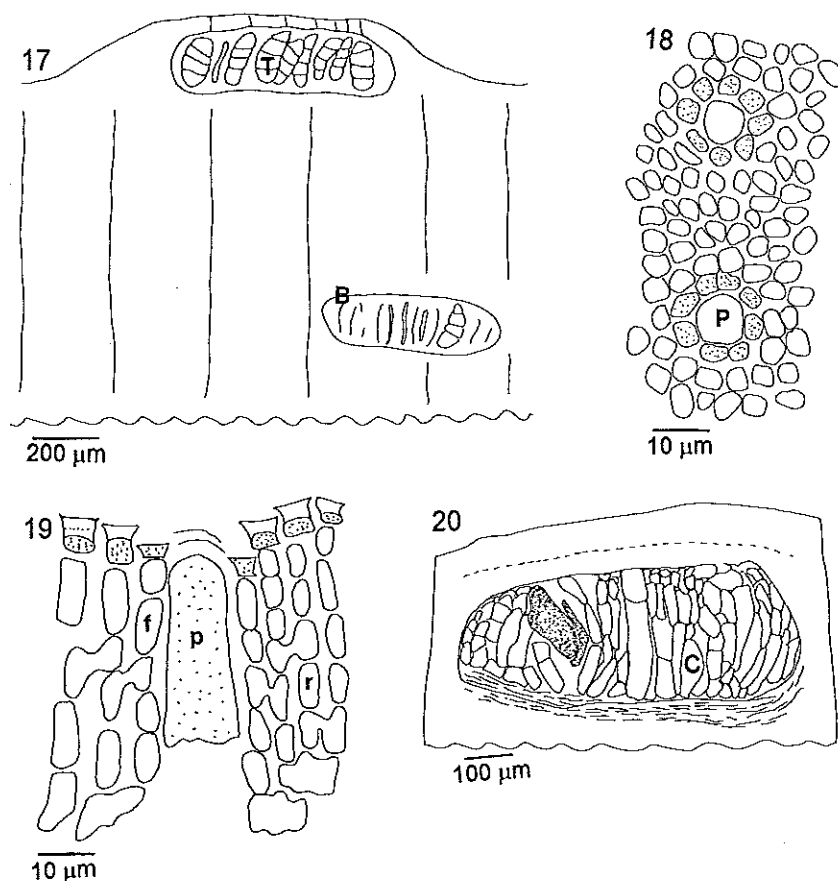
sure 17–30 μm long \times 7–11 μm in diameter. Cell fusions are abundant (Figs 5, 14, 15) but secondary pit connections were not seen. Ventrally situated medullary filaments curve downwards toward the

substratum and terminate in more-or-less triangular cells (Figs 5, 15). The cortex comprises more than 85% of thallus thickness in crustose portions (Figs 4, 5), except near the margin (Fig. 16). Cells of cortical filaments are ovoid, to pear-shaped, to rectangular near the thallus surface (Figs 5; 6, 13), but become more elongate towards the medulla and where protuberances are forming. They measure 5–15 μm long \times 5–9 μm in diameter. Cell fusions are abundant, frequently occupying most of the wall of adjoining cells (Figs 5, 6, 13), but secondary pit connections were not seen. Cells of cortical filaments are commonly strongly horizontally aligned (Fig. 6). Most cortical filaments have cells with fairly thick walls and relatively narrow lumens (Fig. 13). No trichocytes were observed. Subepithallial initials are squat to squarish when not dividing (Figs 5, 13), but elongate just prior to division. They measure 5–15 μm long \times 5–9 μm in diameter. Flared epithallial cells occur singly (Fig. 5) and measure 2.5–8 μm long \times 6–12 μm in diameter. In surface view (SEM) they have broad concavities, surrounded by relatively thin

calcified walls (Fig. 12). Epithallial sloughing as a few cells or in sheets is commonly observed.

Reproduction

Gametangial plants are apparently dioecious. Uniporate male conceptacles are slightly raised, mound-like and slightly apiculate. They measure up to 1300 μm in outside diameter. Their chambers are elliptical (Fig. 7), and measure 480–1000 μm in diameter \times 110–190 μm high, with the roof 118–155 μm thick. The roof (Fig. 7) is evidently formed from filaments peripheral to the fertile area that are oriented more-or-less parallel to the conceptacle surface at the lower surface and perpendicular to it dorsally. Spermatangial systems develop on the floor, walls and roof of the conceptacles (Fig. 7). Those spermatangial systems on the floor are strongly dendroid (Fig. 8), while on the walls and roof they are mainly simple (Fig. 9). Protective cells above spermatangial initials were not observed in young conceptacles. Carpogonial conceptacles were not seen. Carposporangial con-



Figs 17–20. Anatomy of tetrasporangial plants of *L. prolifer*.

Fig. 17. Diagrammatic drawing of section showing conceptacle with tetrasporangia (T) and buried conceptacle (B) that has not been infilled (UWC: 94/1017). Fig. 18. Surface view of pores (P) of tetrasporangial conceptacle showing rosette cells (stippled) (UWC: 94/1017). Fig. 19. Vertical section of pore plate showing filaments (f) lining the pore canal, pore plug (p), and intervening roof filaments (r) (UWC: 94/1017). Fig. 20. Diagrammatic drawing of section of buried tetrasporangial conceptacle that is infilled by calcified cells (C) (UWC: 94/1034).

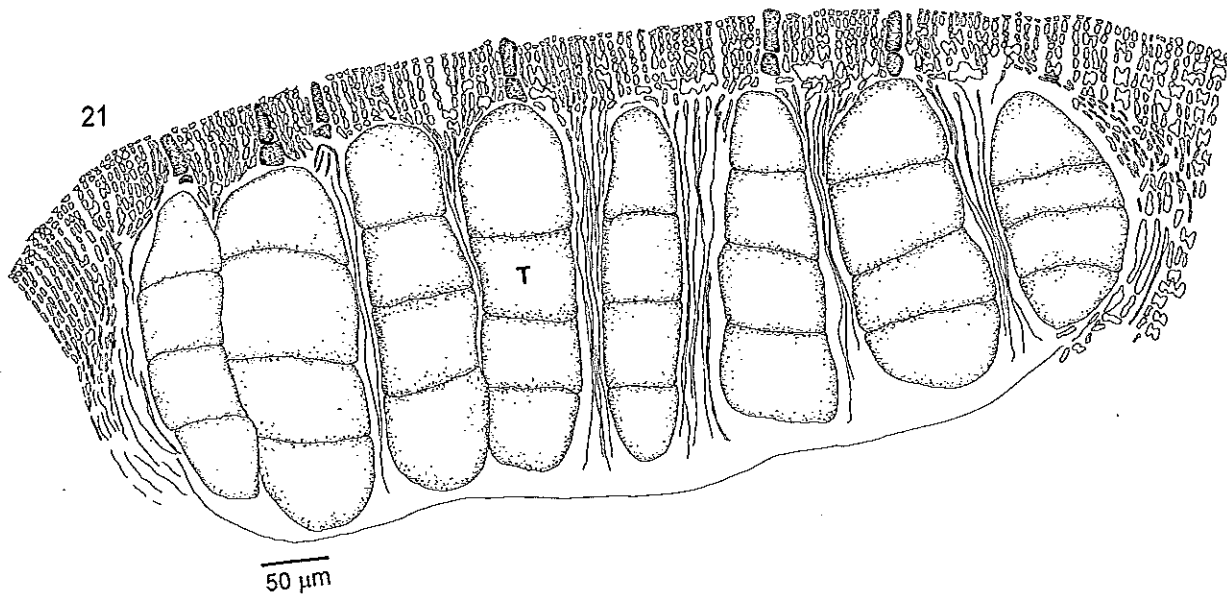


Fig. 21. Section of tetrasporangial conceptacle showing pores with pore plugs (stippled) and tetrasporangia (T) (UWC: 94/1017).

ceptacles are conical (Fig. 10) and measure 240–525 μm in external diameter. Their chambers are elliptical and measure 750–100 μm in diameter \times 290–325 μm high, with the roof ca. 125 μm (ca. 14 cells) thick. A fusion cell is apparently absent and gomimoblast filaments are borne across the conceptacle floor (Fig. 10). They comprise 1–2 cells including the carposporangium (Figs 10, 11). Carposporangia measure 85–125 μm in diameter \times 110–135 μm long, but round up to 125–135 μm diameter and almost fill the chamber when mature.

Tetrasporangial plants. Both tetrasporangial and bisporangial conceptacles were observed. The tetra/bisporangial conceptacles are flush to slightly raised with flattened, central pore plates (Figs 17, 21, 22, 23). They lack raised rims (Fig. 23) and measure up to 1300 μm in external diameter. Their chambers are elliptical (Figs 17, 26) and measure 320–1100 μm in diameter \times 160–304 μm high, with the roof ca. 50 μm thick. The roof is formed from filaments interspersed among the sporangia. The lower segments of these filaments degenerate (Fig. 21) leaving a roof composed of filaments of 5–9 cells (mostly 5–7) plus a flared epithallial cell (Figs 19, 21, 25). Pore plugs are present (Fig. 19) and are often visible under low magnification. The pore, which measures 12–15 μm in diameter, is surrounded by 7–9 rosette cells that are sunken below the level of surrounding roof cells (Figs 18, 24). The cells of the filaments lining the pore canals and those of the rims of tetra/bisporangial conceptacles do not differ from the cells of filaments making up the rest of the roof (Fig. 19). However, pore canal filaments are usually shorter (Fig. 19) than surrounding roof filaments with the result that their upper ends are slightly sunken into the pore (Fig. 24). These are the rosette cells seen in surface SEM (Fig.

24). Tetrasporangia and bisporangia measure 80–225 μm long and 30–115 μm in diameter (Fig. 21). As they mature, tetrasporangia and bisporangia swell considerably, and become weakly staining (with aniline blue). When they expand, all remaining intersporangial filaments are crushed between adjacent tetrasporangia (Fig. 21). Old conceptacles persist and become buried in the thallus and are generally completely filled in by irregularly arranged calcified cells (Figs 20, 26).

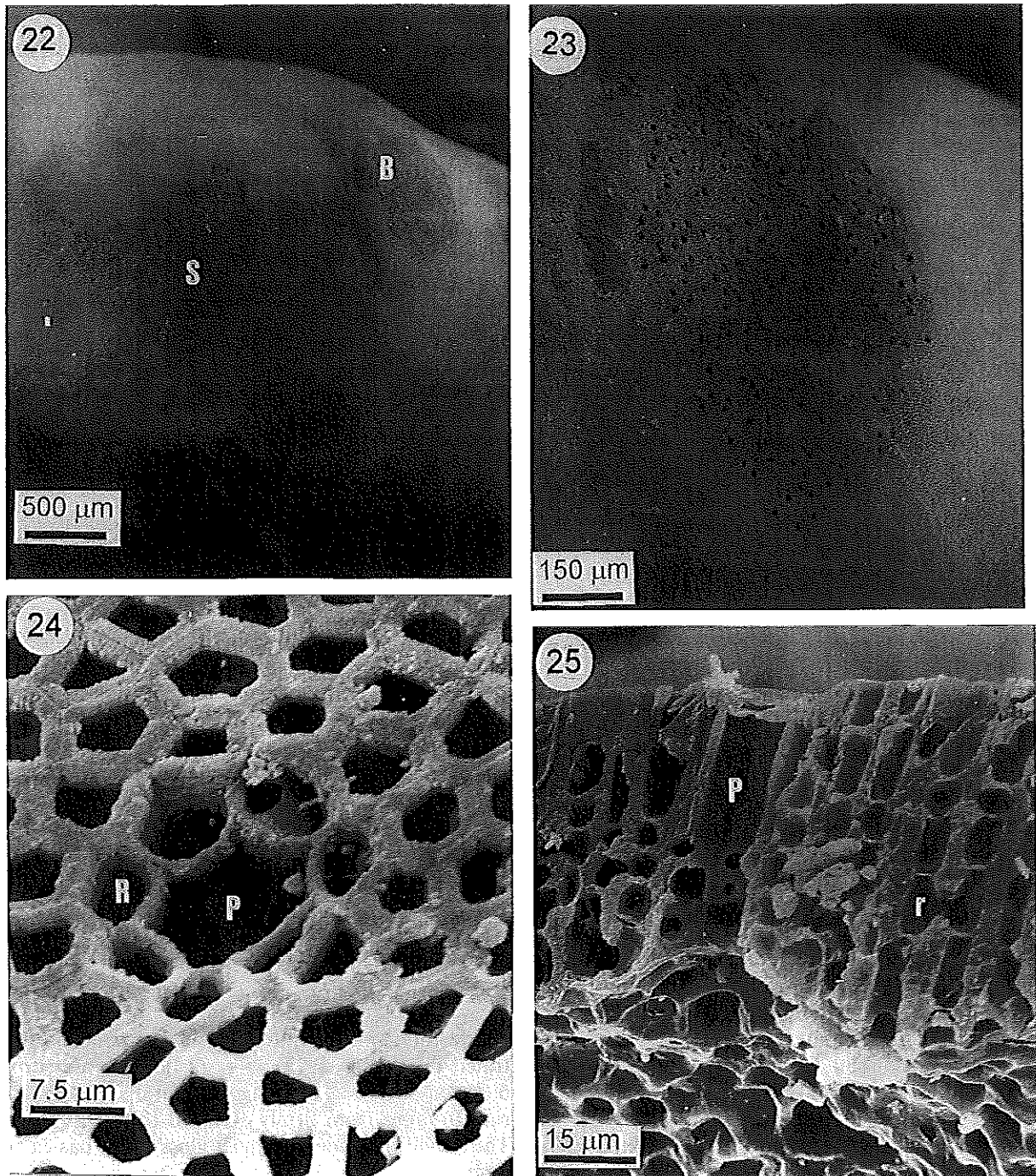
Structure of type material

Lithothamnion prolifer Foslie 1904: 18

The lectotype (L!) comprises a single specimen (illustrated by Verheij 1993 a, fig. 72, lower), measuring 6 \times 4 cm, that was growing over coral skeletal material. It varies from firmly attached to free in places. The surface is smooth, almost glossy, and has ca. 12 lumpy to almost fruticose protuberances. There are numerous ca. 100 μm diameter, crater-like depressions, particularly on protuberances and raised areas. Only a few multiporate conceptacles are present on the tips of the protuberances.

The isolectotype (L!) comprises a smaller specimen (illustrated by Verheij 1993 a, fig. 72, upper), measuring 4 \times 2 cm, that was growing over a coral pebble. It varies from firmly attached to free in places. The surface is smooth, rather more matte, and slightly warty. It is apparently sterile, and was not examined further.

The thallus of the lectotype is monomerous (Figs 27, 34). The medulla comprises up to 15% of the thallus thickness except at the margin (Fig. 34), and is composed of barrel-shaped to elongate cells (Figs 27,



Figs 22–25. Tetrasporangial conceptacles in *L. prolifer* (SEM, UWC: 94/1017).

Fig. 22. Low mound-like (B) and sorus-like (S) tetrasporangial conceptacles in *L. prolifer* at the end of a protuberance. Fig. 23. Magnification of conceptacle 'B' from Fig. 22, showing pore plate with numerous pores surrounded by clearly sunken rosette cells. Fig. 24. Tetrasporangial pore (P) with sunken rosette cells (R). Fig. 25. Vertical fracture of pore plate with pore canal (P) and roof filaments (r).

33) that measure 13.5–20 µm long × 4–12.5 µm in diameter. Broad cell fusions are common. The cortex (Figs 27, 32) is composed of tightly packed filaments of isodiametric, to barrel-shaped, to pear-shaped cells that measure 7.5–15 µm long × 6–9 µm in diameter, but groups of fairly clear, markedly elongate cells occur near the surface, and seem to be involved in the early stages of protuberance formation. Most cortical

filaments have cells with thick walls and relatively narrow lumens (Fig. 32). Broad cell fusions (Figs 27, 32) are common. Subepithallial initials are rectangular to more-or-less squarish to somewhat shorter than broad (Figs 27, 32), and measure 5–12 µm long × 6–9 µm in diameter (Fig. 27). Epithallial cells are flattened and flared (Fig. 27) and measure 4–6 µm long × 5–9 µm in diameter. In surface view (SEM)

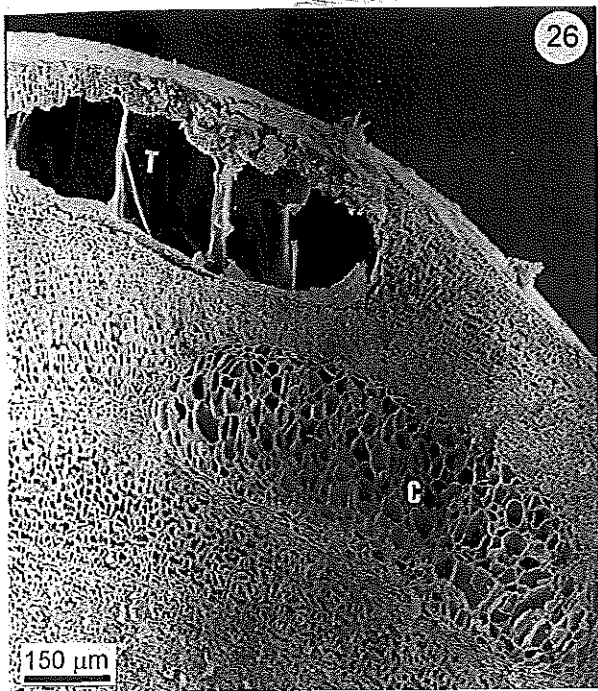


Fig. 26. Vertical fracture (SEM) showing mature tetrasporangial conceptacle with tetraporoidal (T) and old, buried conceptacle that has been infilled by calcified cells (C) (UWC: 94/1017).

they have broad concavities within which the remains of old primary pits are visible, and these are surrounded by relatively thin calcified walls (Fig. 31). Trichocytes were not seen.

Gametangial plants were not seen. Tetrasporangial conceptacles are raised very slightly, have flat tops, and are mainly found on the ends of protuberances (Fig. 35). Their chambers are elliptical (Fig. 28), and measure 550–750 μm in diameter \times 220–290 μm high, with the roofs 5–8 cells (49–72 μm) thick and composed of mostly isodiametric to oblong cells (Fig. 29). The pore canal is lined by filaments whose cells do not differ markedly from those of the surrounding roof. Epithallial cells of the pore-canal and surrounding filaments are often missing (Fig. 29). The tetrasporangial pore is surrounded by 7–8 rosette cells that are slightly sunken below the level of the surrounding pore plate (Fig. 36). Conceptacles are mostly empty, but a few senescent tetrasporangia were seen. Old conceptacles become buried in the thallus and are infilled by large, irregular, calcified cells (Fig. 30).

Remarks

We consider the following combination of characters to distinguish this species (see also Table I):

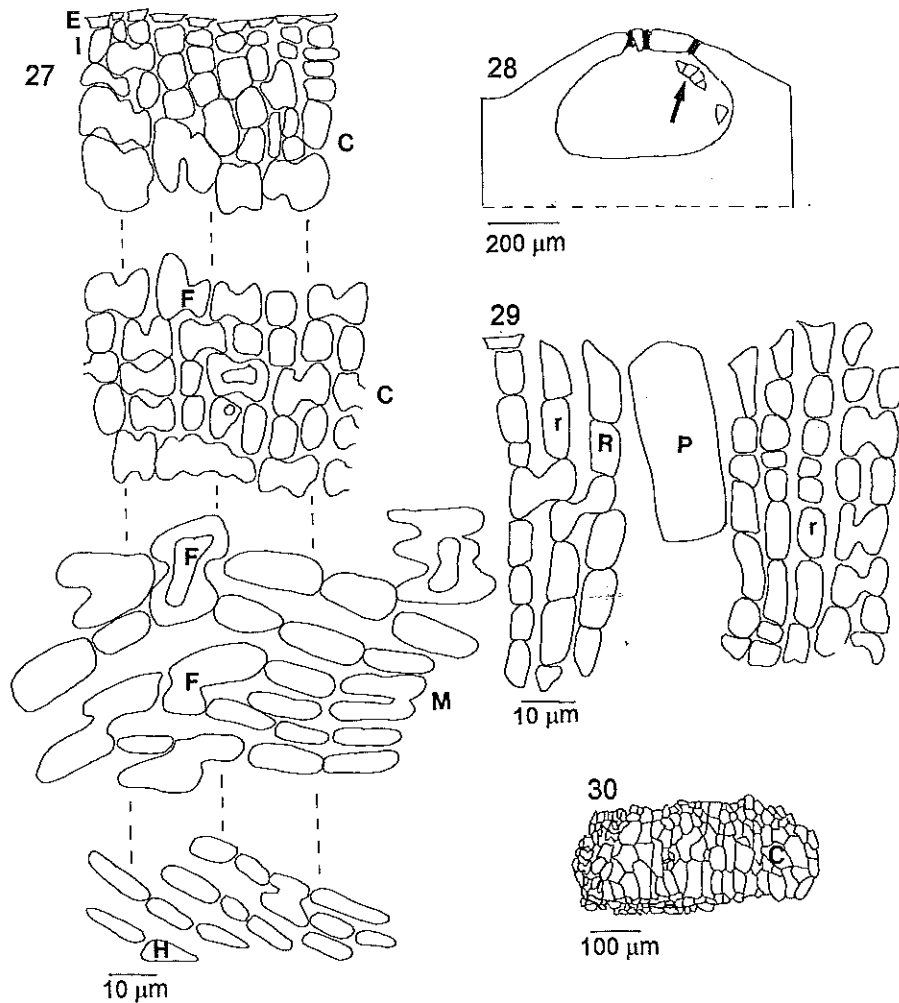
- thallus extremely glossy, smooth with a velvet texture, and rose-coloured;
- Thallus usually producing complanate protuberances, but protuberances may be terete when

- thalli grow on well-lit, horizontal substrata, when unattached, or when growing on loose substrata;
- conceptacles occurring mainly on the tips of protuberances;
- tetra/bisporangial conceptacles large (to 1300 μm external diameter, chambers to 1100 μm diameter);
- tetra/bisporangial conceptacles flush or only slightly raised, often extensive and irregularly shaped (resembling small sori);
- tetra/bisporangial conceptacles lacking a raised rim;
- tetra/bisporangial conceptacle pore plates flattened;
- rosette cells surrounding the tetra/bisporangial pore sunken below the surrounding roof cells in surface view (SEM);
- cells of filaments lining the pore canals and those forming the rims of tetra/bisporangial conceptacles not differing from the cells of filaments making up the rest of the roof;
- old tetra/bisporangial conceptacles persisting and becoming buried in the thallus;
- buried tetra/bisporangial conceptacles usually becoming completely filled in by relatively large, irregularly-arranged calcified cells.

This species of *Lithothamnion* differs from any known species of the genus in a number of respects. It differs from the type species of *Lithothamnion*, *L. muelleri* Lenormand *ex* Rosanoff, in a number of characters particularly: protuberance shape, tetra/bisporangial pore characters, and conceptacle site (Table I). *Lithothamnion prolifer* is the only known species of this genus which usually has markedly flattened (complanate) protuberances, and conceptacles of all types mainly confined to the tips of the protuberances. It differs in those characters of the tetra/bisporangial conceptacles, listed as distinguishing characters above, from any recently treated species of the genus. However, there are over 700 taxa ascribed to *Lithothamnion* on a worldwide basis, and the value of the characters cited above will have to await further studies in a variety of geographical locations.

Adey *et al.* (1982: 61) reported '*Mesophyllum prolifer*' from Hawaii, but their description does not conform to the type of *L. prolifer*. In particular, the rounded epithallial cells, the absence of protuberances, the dome-shaped multiporate conceptacles, and the coaxial medulla (as 'hypothallium') which they described are inconsistent with either the type of *L. prolifer* or our recently collected material. Thus the species referred to as '*M. prolifer*' in Hawaii is not conspecific with the type of *L. prolifer*, and its true identity remains unknown.

Johnson *et al.* (1991 a, b) cited *Lithothamnion pseudosorum* in papers dealing with larval inducement substances from bacteria growing on the surface of the coralline. Identification of that species was based on an unpublished, but widely circulated



Figs 27–30. Vegetative and tetrasporangial conceptacle anatomy of the *L. prolifer* lectotype. Fig. 27. Section of thallus showing epithallial cells (E), subepithallial initial (I), cells of vortical (C) and medullary (M) filaments with cell fusions (F). Medullary filaments curve downward and terminate in a hyaline cell (H). Fig. 28. Diagrammatic drawing of section of thallus showing conceptacle with remains of tetrasporangium (arrow). Fig. 29. Vertical section of pore plate showing filaments (R) lining the pore canal, pore plug (P), and intervening roof filaments (r). Fig. 30. Diagrammatic drawing of buried tetrasporangial conceptacle that is infilled by calcified cells (C).

manuscript (Steneck *et al.*, unpublished), in which material now known to be *L. prolifer* was described as a new species. *Lithothamnion pseudosorum* is thus a *nomen nudum*, the only published references to which (Johnson *et al.* 1991 a, b) correspond to *L. prolifer*.

Discussion

Adey (1970: 25) transferred *Lithothamnion prolifer* into *Mesophyllum* on the basis of the type possessing a coaxial medulla. Neither Verheij (1993 a) nor ourselves found coaxial medulla in the type. *Mesophyllum* is currently delimited on the basis of the following combination of characters Woelkerling and Irvine (1986), Woelkerling and Harvey (1993):

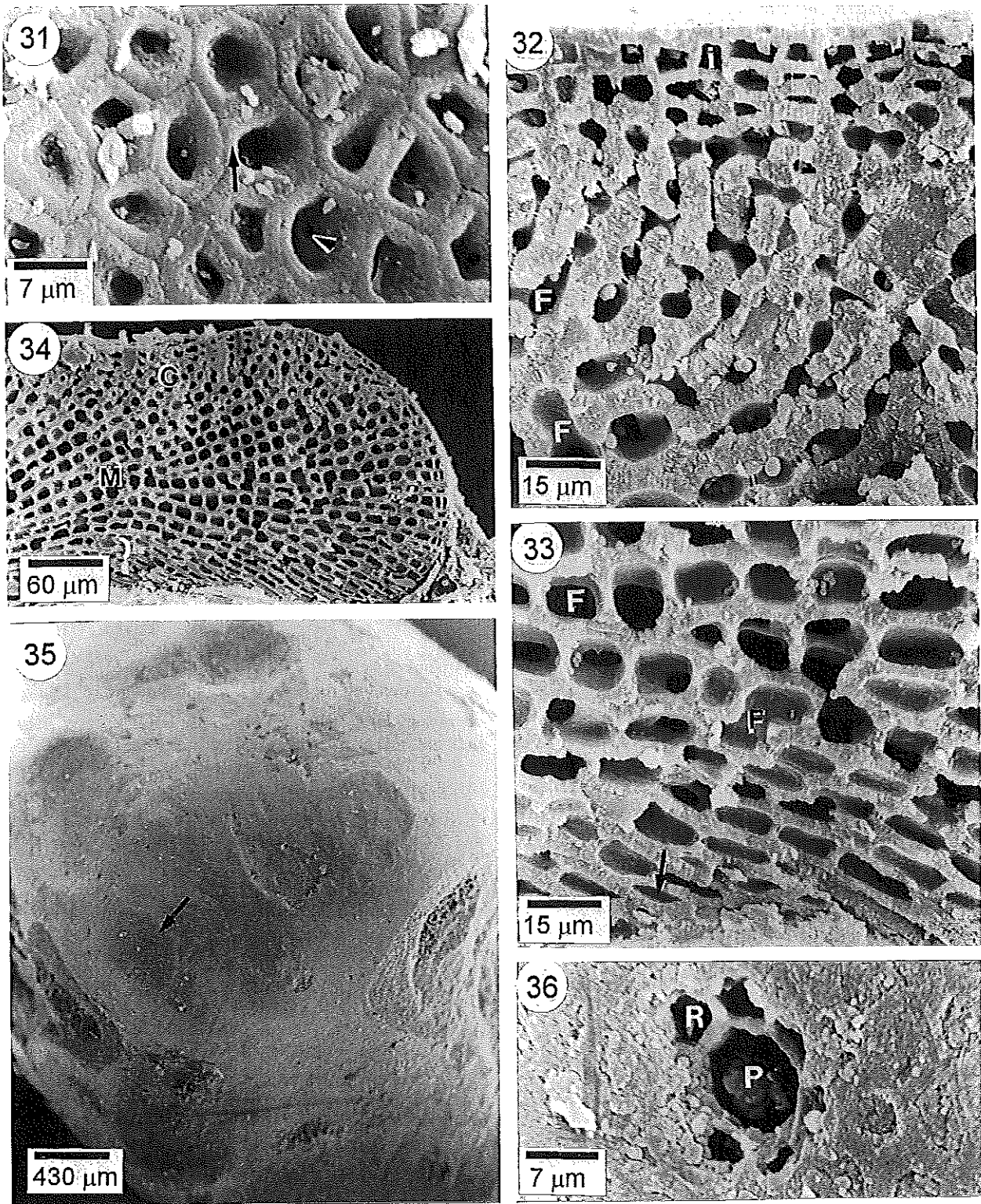
1. Internal construction monomerous;
2. haustoria absent;
3. outermost walls of terminal epithallial cells rounded or flattened but not flared;

4. vegetative initials usually as long as or longer than cells immediately subtending them;
5. spermatangial initials formed from meristematic cells;
6. spermatangial initials overlain by a layer of protective cells;
7. spermatangial conceptacle roofs formed centripetally from groups of peripheral filaments;
8. spermatangial branches simple;
9. spermatangial branches occur on the floor, walls and roof of male conceptacles.

The lectotype material of *L. prolifer* does not correspond to *Mesophyllum* on the basis of characters 3, 6 and 8. The status of character 5 remains uncertain.

The following features are presently considered to delimit *Lithothamnion* (Chamberlain and Keats 1994, Woelkerling 1988, Wilks and Woelkerling 1996):

1. Thallus non-geniculate;
2. thallus not arborescent in growth form;



Figs 31–36. Vegetative and tetrasporangial conceptacle anatomy of the *L. prolifer* lectotype (SEM).

Fig. 31. Surface view of thallus showing broad epithallial concavities with remains of primary pit connection (arrowhead) and relatively thin lateral walls (arrow). Fig. 32. Fracture near thallus surface showing cell fusions (F) in cells of cortical filaments, and subepithallial initials (I). Fig. 33. Medullary filaments near the ventral surface, showing their termination in cells with angular end walls (arrow) (F = cell fusions). Fig. 34. Thallus margin showing medulla (M) and cortex (C). Fig. 35. Tetrasporangial conceptacles (arrow) on the edge of a protuberance. Fig. 36. Tetrasporangial pore (P) with sunken rosette cells (R). Note the granular material covering most of the surface.

Table I. Comparison of *L. prolifer* with the type species of *Lithothamnion* (*L. muelleri* Lenormand *ex* Rosanoff) on the basis of selected characters considered to have value in distinguishing among species. *Lithothamnion muelleri* data from Woelkerling (1983) and Wilks and Woelkerling (1996).

Character	<i>L. prolifer</i> (recent collections)	<i>L. prolifer</i> Lectotype	<i>L. muelleri</i>
Thallus thickness	150–5000 µm	500–1000 µm	up to 4000 µm
Thallus form	warty to lumpy to fruticose	warty	encrusting to warty
Thallus texture	extremely glossy smooth, porcelain-like	extremely glossy smooth	not known
Protuberance shape	complanate to terete	terete, but scarce on lectotype	terete
Tetra/bisporangial conceptacle distribution	mainly on the tips of protuberances	apparently mainly on protuberances and raised areas	across thallus surface
Tetra/bisporangial conceptacle shape	mainly flush, flat, lacking raised rim, often grouped to resemble a sorus	mainly flush, flat, lacking raised rim	flush to raised, with or without a raised rim
Tetra/bisporangial conceptacle chamber diameter	320–1100 µm	550–750 µm	280–750 µm
Tetra/bisporangial conceptacle pores-position of rosette cells	sunken below surrounding roof	sunken below surrounding roof	flush with surrounding roof
Cells of pore canal filaments in tetra/bisporangial conceptacles distinct from other roof cells	no	no	no
Cells of filaments in rims of tetra/bisporangial conceptacles distinct from other roof cells	no	no	no
Number of cells in pore canal filaments	5–9 cells (mainly 5–7)	5–8 cells	5–9 cells
Tetra/bisporangial conceptacle buried	yes, infilled with irregular calcified cells	yes, infilled with irregular calcified cells	yes, whether they are infilled is unknown

3. internal construction monomerous;
4. haustoria absent;
5. cell fusions present;
6. secondary pit connections absent;
7. outermost walls of terminal epithallial cells flared;
8. actively dividing vegetative initials as long as or longer than their immediate inward derivatives;
9. tetrasporangia bearing apical plugs and borne within multiporate conceptacles;
10. male conceptacle roofs formed centripetally from groups of peripheral filaments;

11. spermatangial initials not overlain by a layer of protective cells;
12. spermatangia on the floor, walls, and roof of male conceptacles;
13. spermatangial systems on the conceptacle floor dendroid, on roof simple (but see below).

The species studied here conforms to *Lithothamnion* on the basis of its possession of all of the above generic characters, thus confirming the earlier conclusion of Verheij (1993 a).

It has been suggested, but not confirmed, that in the genus *Lithothamnion* the spermatangial systems

are distributed all around the chambers of male conceptacles, and that those on the floors are mainly dendroid, while those on the roof are mainly simple (Lebednik 1978). It has also been suggested that protective cells are lacking in young male conceptacles. However, Woelkerling (1983, 1988) did not describe spermatangial conceptacles from the type species, so whether these characters hold for the type species remains uncertain. However, all species of *Lithothamnion* for which male conceptacles have been described recently in detail have shown mainly dendroid spermatangial systems on the floor of the male conceptacle, and more-or-less simple ones on the roof (e.g. Chamberlain and Irvine 1994, Verheij 1993a). The presence of this character, and the absence of protective cells are also confirmed for the present species.

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References

- Adey, W. H. 1970. A revision of the Foslie crustose coralline herbarium. *K. norske Vidensk. Selsk. Skr.* 1970(1): 1–46.
- Adey, W. H. and P. J. Adey. 1973. Studies on the biosystematics and ecology of the epilithic crustose Corallinales of the British Isles. *Brit. phycol. J.* 8: 343–407.
- Adey, W. H., R. A. Townsend and W. T. Boykins. 1982. The crustose coralline algae (Rhodophyta: Corallinales) of the Hawaiian Island. *Smithson. Contr. mar. Sci.* 15: 1–74.
- Chamberlain, Y. M. 1990. The genus *Leptophytum* (Rhodophyta, Corallinales) in the British Isles with descriptions of *Leptophytum bornetii*, *L. elatum* sp. nov., and *L. laevae*. *Brit. phycol. J.* 25: 179–199.
- Chamberlain, Y. M. 1993. Observations on the crustose coralline red alga *Spongites yendoi* (Foslie) comb. nov. in South Africa and its relationship to *S. decipiens* (Foslie) comb. nov. and *Lithophyllum natalense* Foslie. *Phycologia* 32: 100–115.
- Chamberlain, Y. M. 1994. *Pneophyllum coronatum* (Rosanoff) D. Penrose comb. nov., *P. keatsii* sp. nov., *Spongites discoideus* (Foslie) D. Penrose and Woelkerling and *S. impar* (Foslie) Y. Chamberlain comb. nov. (Rhodophyta, Corallinales) from South Africa. *Phycologia* 33: 141–157.
- Chamberlain, Y. M. and L. M. Irvine. 1994. Melobesioideae. In: (Irvine, L. M. and Y. M. Chamberlain) *Seaweeds of the British Isles Volume 1 Rhodophyta Part 2B Corallinales, Hildenbrandiales*. The Natural History Museum, Lond. pp. 159–234.
- Chamberlain, Y. M. and D. W. Keats. 1994. Three melobesoid crustose coralline red algae from South Africa: *Leptophytum acervatum* (Foslie) comb. nov., *L. foventum* sp. nov. and *L. ferox* (Foslie) comb. nov. *Phycologia* 33: 111–133.
- Chamberlain, Y. M. and R. E. Norris. 1994a. *Pneophyllum amplexifrons* (Harvey) comb. nov., a mastophoroid crustose coralline red algal epiphyte from Natal, South Africa. *Phycologia* 33: 8–18.
- Chamberlain, Y. M. and R. E. Norris. 1994b. *Hydrolithon pellire* sp. nov., a mastophoroid, crustose coralline red alga epiphyte from Natal, South Africa. *Phycologia* 33: 291–297.
- Chapman, V. J. 1971. The marine algae of Fiji. *Rev. algol.* 2: 164–172.
- Chapman, V. J. 1977. Marine algae of Norfolk Islands and Cook Islands. *Bot. Mar.* 20: 161–165.
- Foslie, M. 1904. I. Lithothamnionae, Melobesiaeae, Mastophoreae. Pages 10–77. In: 'The coralline algae of the Siboga-expedition' (Weber-van Bosse, A. and M. Foslie, eds). *Siboga Expeditie, Monographie LXI*, Leiden, 110 pp, 16 plates.
- Gordon, G. D., T. Masaki and H. Akioka. 1976. Floristic and distributional account of the common crustose coralline algae on Guam. *Micronesica* 12: 247–277.
- Holmgren, P., N. H. Holmgren and L. C. Bartlett. 1990. *Index Herbariorum, Pt. 1. The Herbaria of the World*. 8th edition. *Regnum Vegetabile 120* (Koeltz Scientific Books, Königstein).
- Johnson, C. R., D. C. Sutton, R. R. Olson and R. Giddins. 1991a. Settlement of crown-of-thorns starfish: role of bacteria on surfaces of coralline algae and a hypothesis for deepwater recruitment. *Mar. Ecol. Prog. Ser.* 71: 143–162.
- Johnson, C. R., D. G. Muir and A. L. Reysenbach. 1991b. Characteristic bacteria associated with surfaces of coralline algae: a hypothesis for bacterial induction of marine invertebrate larvae. *Mar. Ecol. Prog. Ser.* 74: 281–294.
- Keats, D. W. and Y. M. Chamberlain. 1993. *Sporolithon ptychoides* Heydrich and *S. episporum* (Howe) Dawson:

- two crustose coralline red algae (Corallinales, Sporolithaceae) in South Africa. *S. A. J. Bot.* 59: 541–550.
- Keats, D. W. and Y. M. Chamberlain. 1994 a. Three species of *Hydrolithon* (Rhodophyta, Corallinaceae): *Hydrolithon onkodes* (Heydrich) Penrose and Woelkerling, *Hydrolithon superficiale* sp. nov., and *H. samoëense* (Foslie) comb. nov. from South Africa. *S. A. J. Bot.* 60: 8–21.
- Keats, D. W. and Y. M. Chamberlain. 1994 b. Two melobesoid coralline algae (Rhodophyta, Corallinales), *Mesophyllum rubescens* (Foslie) Lemoine and *Mesophyllum funafutiense* (Foslie) Verheij from Sodwana Bay, South Africa. *S. A. J. Bot.* 60: 175–190.
- Keats, D. W. and Y. M. Chamberlain. 1995. *Heydrichia groeneri* sp. nov.: a new species of crustose coralline alga (Rhodophyta, Sporolithaceae) from South Africa and Namibia. *Phycologia* 34: 51–57.
- Lebednik, P. A. 1978. Development of male conceptacles in *Mesophyllum* Lemoine and other genera of the Corallinaceae (Rhodophyta). *Phycologia* 17: 388–395.
- May, D. I. and W. J. Woelkerling. 1988. Studies in the genus *Synarthrophyton* (Corallinaceae, Rhodophyta) and its type species *S. patena* (J. D. Hooker et W. H. Harvey) Townsend. *Phycologia* 27: 50–71.
- O'Brien, T. P. and M. E. McCully. 1978. *The Study of Plant Structure. Principles and Selected Methods*. Termarcarphi, Melbourne. x + 271 pp.
- Penrose, D. 1991. *Spongites fruticulosus* (Corallinaceae, Rhodophyta), the type species of *Spongites*, in southern Australia. *Phycologia* 30: 438–448.
- Penrose, D. 1992. *Neogoniolithon fosliei* (Corallinaceae, Rhodophyta), the type species of *Neogoniolithon* in southern Australia. *Phycologia* 31: 338–350.
- Penrose, D. and Y. M. Chamberlain. 1993. *Hydrolithon farinosum* (Lamouroux) comb. nov.: implications for generic concepts in the Mastophoroideae (Corallinaceae, Rhodophyta). *Phycologia* 32: 295–303.
- Penrose, D. and W. J. Woelkerling. 1988. A taxonomic reassessment of *Hydrolithon* Foslie, *Porolithon* Foslie and *Pseudolithophyllum* Lemoine emend. Adey (Corallinaceae, Rhodophyta) and their relationships to *Spongites* Kützinger. *Phycologia* 27: 159–176.
- Penrose, D. and W. J. Woelkerling. 1991. *Pneophyllum fragile* in southern Australia: implications for generic concepts in the Mastophoroideae (Corallinaceae, Rhodophyta). *Phycologia* 30: 495–506.
- Penrose, D. and W. J. Woelkerling. 1992. A reappraisal of *Hydrolithon* (Corallinaceae, Rhodophyta) and its relationship to *Spongites*. *Phycologia* 31: 81–88.
- Printz, H. 1929. *M. Foslie. Contribution to a Monograph of the Lithothamnia*. Det Kongelige Norske Videnskabers Selskabs Museet, Trondheim, Norway. 60 pp.
- South, G. R. and H. Kasahara. 1992. A preliminary checklist of the benthic marine algae of the Fiji Islands, South Pacific. *Micronesica* 25: 41–70.
- Stearn, W. T. 1983. *Botanical Latin*. David and Charles, London. p. 566.
- Townsend, R. A., Y. M. Chamberlain and D. W. Keats. 1994. *Heydrichia woelkerlingii* gen. et sp. nov.: a newly discovered nongeniculate red alga (Corallinales, Rhodophyta) from Cape Province, South Africa. *Phycologia* 33: 177–186.
- Townsend, R. A., W. J. Woelkerling, A. S. Harvey and M. Borowitzka. 1995. An account of the red algal genus *Sporolithon* (Sporolithaceae, Corallinales) in Southern Australia. *Aust. Syst. Bot.* 8: 85–121.
- Verheij, E. 1993 a. *Marine Plants of the Reefs of the Spermonde Archipelago, SW Sulawesi, Indonesia: Aspects of Taxonomy, Floristics, and Ecology*. Rijsherbarium/Hortus Botanicus, Leiden. 320 pp.
- Verheij, E. 1993 a. The genus *Sporolithon* (Sporolithaceae fam. nov., Corallinales, Rhodophyta) from the Spermonde Archipelago, Indonesia. *Phycologia* 32: 184–196.
- Verheij, E. 1994. Nongeniculate Corallinaceae (Corallinales, Rhodophyta) from the Spermonde Archipelago, SW Sulawesi, Indonesia. *Blumea* 39: 95–137.
- Verheij, E. and W. J. Woelkerling. 1992. The typification of non-geniculate Corallinales (Rhodophyta) involving Siboga Expedition collections. *Blumea* 36: 273–291.
- Wilks, K. M. and W. J. Woelkerling. 1996. An account of Southern Australian species of *Lithothamnion* (Corallinaceae, Rhodophyta). *Aust. syst. Bot.*: In press.
- Woelkerling, W. J. 1983. A taxonomic reassessment of *Lithothamnion* Philippi (Corallinaceae, Rhodophyta) based on studies of R. A. Philippi's original collections. *Brit. phycol. J.* 18: 165–197.
- Woelkerling, W. J. 1988. *The Coralline Red Algae: An Analysis of the Genera and Subfamilies of Nongeniculate Corallinaceae*. British Museum (Natural History) and Oxford University Press. 268 pp.
- Woelkerling, W. J. 1993. Type collections of Corallinales (Rhodophyta) in the Foslie Herbarium (TRH). *Gunneria* 67: 1–289.
- Woelkerling, W. J. and M. S. Foster. 1989. A systematic and ecographic account of *Synarthrophyton schielianum* sp. nov. (Corallinaceae, Rhodophyta) from the Chatham Islands. *Phycologia* 29: 39–60.
- Woelkerling, W. J. and A. S. Harvey. 1993. An account of southern Australian species of *Mesophyllum* (Corallinaceae, Rhodophyta). *Aust. syst. Bot.* 6: 571–637.
- Woelkerling, W. J. and L. M. Irvine. 1986. The neotypification and status of *Mesophyllum* (Corallinaceae, Rhodophyta). *Phycologia* 25: 379–396.
- Woelkerling, W. J., L. M. Irvine and A. S. Harvey. 1993. Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). *Aust. syst. Bot.* 6: 277–293.