

First report of the melobesioid alga (Corallinales, Rhodophyta) *Mesophyllum incisum* (Foslie) Adey in South Africa

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Mesophyllum incisum is reported and studied for the first time in South Africa. It has a thallus surface (SEM) with *Leptophytum*-type epithallial cells. Tetra/bisporangial conceptacles are mound-like and lack a peripheral rim but have a flattened pore plate. The rosette cells surrounding the tetrasporangial pores are distinct from surrounding roof cells (SEM, surface view) in being narrower, and sunken below the level of the surrounding pore plate. The cells of filaments bordering the tetrasporangial conceptacle pore canal differ from the other roof cells within the pore plate in being more elongate, narrower, and often more densely staining. Pore canal filaments also generally contain fewer cells than the surrounding filaments of the pore plate and the pore canal is more-or-less parallel sided. Our material agrees closely with the species as reported in Australia.

Keywords: Algal taxonomy, coralline algae, *Mesophyllum incisum*, Melobesioideae, Rhodophyta, South Africa.

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Introduction

A study is being made of the taxonomy of South African non-geniculate coralline algae (Chamberlain 1993), which are beginning to become known in a modern context. Priority is being given to studying ecologically significant species on the one hand [e.g. *Spongites yendoi* (Foslie) Y. Chamberlain (1993); *Leptophytum acervatum* (Foslie) Chamberlain et Keats, *L. ferox* (Foslie) Chamberlain et Keats, and *L. foveatum* Chamberlain et Keats (Chamberlain & Keats 1994); *Hydrolithon onkodes* (Heydrich) Penrose et Woelkerling (Keats & Chamberlain 1994a)], and new or otherwise taxonomically interesting species on the other hand [e.g. *Pneophyllum amplexifrons* (Harvey) Chamberlain et Norris (1994a), *Hydrolithon pellire* Chamberlain et Norris (1994b), *Clathromorphum tubiforme* Chamberlain, Norris, Keats et Maneveldt (1995), *Heydrichia woelkerlingii* Townsend, Chamberlain et Keats (1994) and *H. groeneri* Keats et Chamberlain (1995)]. The need to provide a taxonomic basis for ecological studies (e.g. Keats, Matthews *et al.* 1994; Keats, Wilton *et al.* 1994; Keats & Maneveldt 1994) precludes delaying taxonomic publication until monographic studies of particular genera can be completed. Further details with respect to historical and geographical data on South African non-geniculate corallines are provided in Chamberlain (1993).

The taxonomy of non-geniculate coralline algae has undergone so many modifications in recent years that it is often impossible to determine to which genus a species belongs on the basis of older published descriptions. Presently however, on-going studies in many parts of the world are now correcting this situation [e.g. Campbell & Woelkerling (1990), Chamberlain (1990, 1991, 1992, 1993, 1994, 1996), Chamberlain & Keats (1994), Chamberlain & Norris (1994a,b), Harvey & Woelkerling (1986, 1995), Harvey *et al.* (1994), Keats (1995), Keats & Chamberlain (1993, 1994a,b), Keats *et al.* (1996), Irvine & Chamberlain (1994), May & Woelkerling (1988), Penrose (1991, 1992), Penrose & Chamberlain (1993), Penrose & Woelkerling (1988, 1991, 1992), Townsend (1979), Townsend, Chamberlain *et al.* (1994) Townsend, Woelkerling *et al.* (1995), Verheij (1993a,b, 1994), Wilks & Woelkerling (1994, 1995), Woelkerling (1983, 1988), Woelkerling & Campbell (1992), Woelkerling & Foster (1989), Woelkerling & Harvey (1992, 1993), Woelkerling & Irvine (1986)]. To make our studies useful in the long-term, in the light of on-going changes in non-geniculate coralline algal taxonomy, the approach has been adopted of describing all

aspects of South African non-geniculate coralline algae in sufficiently complete detail that future workers will be able to assess species without having to resort to an analysis of the type collections.

In this paper we report on *Mesophyllum incisum* (Foslie) Adey, a species previously reported only from Australia, New Zealand and the subantarctic islands in that region. Although the species has been characterised by Woelkerling and Harvey (1992, 1993) from Australia, we present a description of South African material here because we have additional information on the structure of the sporangial pore, and because it is important to include full descriptions of South African species towards the eventual development of a guide to the non-geniculate coralline algal flora.

Materials and Methods

South African material was collected using SCUBA diving. For scanning electron microscopy, air dried material was fractured using either finger nails, forceps, diagonal cutters, or a small hammer and cold chisel. Wherever possible a fracture perpendicular to a leading edge was used to determine internal anatomy. The fractured pieces were mounted on stubs, using adhesive tabs (Agar Scientific, 66a Cambridge Rd., Stanstead, Essex CM24 8DA, UK), stored in a desiccator for at least 24 h prior to examination, coated with gold for 4–6 min in an Edwards S150B sputter coater, and examined with a Hitachi $\times 650$ scanning electron microscope (SEM), equipped with a Mamiya 6×7 camera at an accelerating voltage of 25 KV.

For light microscopy, formalin preserved specimens were first decalcified in 10% nitric acid, and then sectioned at 10–30 μm thickness using a Leitz CO₂ freezing microtome. Each individual section was removed from the microtome blade using a fine sable hair brush, and transferred to a slide containing aniline blue in 50% Karo syrup. Drawings were made directly from prepared slides using a Zeiss microscope equipped with a drawing tube.

Conceptacle outside diameter 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 & Adey (1973). Thallus anatomical terminology follows Chamberlain (1990), while morphological terminology follows Woelkerling, *et al.* (1993). Typification data follow Woelkerling (1993).

Observations

Mesophyllum incisum (Foslie) Adey 1970: 24

Basionym: *Lithothamnion patena* f. *incisa* Foslie, 1906:6

Homotypic synonyms: *Lithothamnion incisum* (Foslie) Foslie;
Polyporolithon patena f. *incisa* (Foslie) Chapman et Parkinson;

Type specimen: TRH, Setchell No. 6354 (Bay of Islands, New Zealand). The type was not examined as it has been well characterized by Woelkerling and Harvey (1992).

Etymology: Foslie (1906) did not explain the origin of the specific epithet, but 'incisum' means cut deeply and sharply (Stearn 1992). How this applies to *M. incisum* is uncertain.

Representative specimens examined:

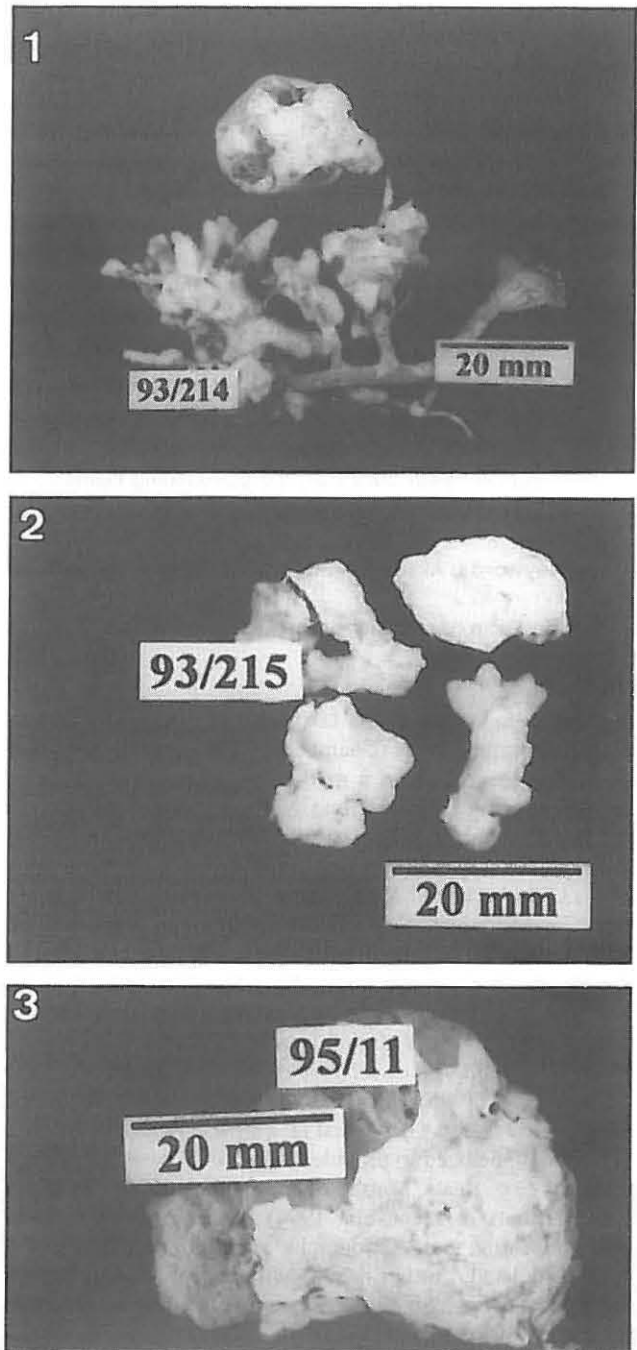
—**3418** (Simonstown): Partridge Point, Western Cape Province, 10–14m on dead horny coral, bryozoan skeletons, sponges (UWC: 93/214, UWC: 93/215, UWC: 95/11) (AD).

—**3318** (Cape Town): Robbeneiland, Western Cape Province, 9–12m on stony coral skeletons (UWC: 93/226) (CD).

Habitat and phenology: *Mesophyllum incisum* is an inconspicuous coralline that occurs in small patches on the dead parts of horny coral skeletons as well as on bryozoans, coral skeletons, and sponges. Only a few specimens were collected. All male, carposporangial and tetrasporangial conceptacles were found in March, August, and November but there are no collections at other times.

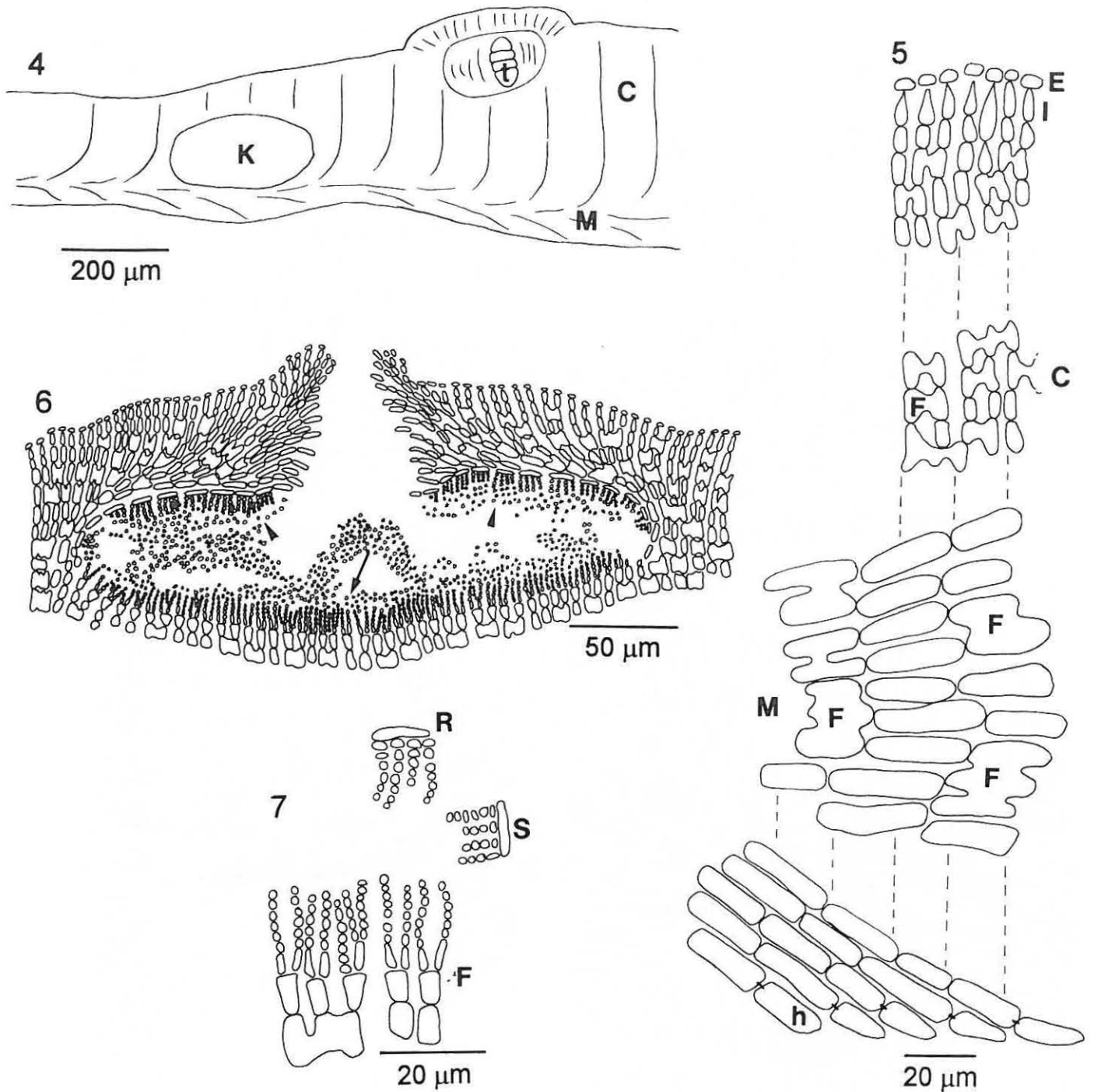
Distribution: Southern Africa: Cape Peninsula. World: Australia, New Zealand, South Africa, Chatham Islands, and sub-Antarctic islands south of New Zealand. Woelkerling and Harvey (1993) note that other than the type, records of this species outside of Australia have not been verified.

Habit and vegetative structure: Plants encrust mainly sponges (Figures 1–3), the horny parts of gorgonian coral, and other invertebrates, and are weakly adherent, with the margins often somewhat free. The surface is smooth and glossy and protuberances are lacking. The thallus is usually reddish purple to purplish pink, and sporangial conceptacles are sparsely distributed over the surface. They are mound-like with a flattened pore plate (Figure 18). The thallus is monomerous, measuring 250–550 μm in thickness. Medullary filaments form a plumose to coaxial ventral layer (Figures 4, 5, 9 and 10) that measures 40–150 μm in thickness. Cells of medullary filaments are elongate (Figures 5, 9 and 10), and measure 6–19 μm long \times 4–10 μm in diameter. Cell fusions are abundant, occupying most of the wall of adjoining cells (Figures 5 and 10). Medullary filaments terminate at the margin in primary meristematic cells which are usually flattened apically (Figure 9), and measure 9–22 μm in length \times 5–13 μm in diameter. Cortical filaments form a dorsal layer 100–500 μm thick (Figure 4). Cells of cortical filaments are elongate (Figures 5 and 11), and measure 6–19 μm in length \times 4–13 μm in diameter. Cell fusions are abundant and occupy most of the wall of adjoining cells (Figures 5 and 11). The subepithallial initial is as long as, or longer than, the cell subtending it (Figures 5 and 11), measuring 4–18 μm in length \times 2.5–6 μm in diameter. Epithallial cells occur singly, are more-or-less elliptical to dome-shaped or flat topped (Figures 5 and 11) and measure 2.5–4 μm long \times 2.5–6 μm in diameter. Surfaces of epithallial cells under the SEM show thin lateral walls, and the outer wall is usually cushion-like and not sunken into an epithallial concavity (Figure 8). This outer wall is thin with a minute central hole that is presumed to be a scar from the pit which connected the epithallial cell during its formation to the older epithallial cell dorsal to it (*Leptophytum*-type surface *sensu* Chamberlain 1990) (Figure 8).



Figures 1–3 Habit photographs of *M. incisum*.

Reproduction: Gametangial plants are dioecious. Carpogonial conceptacles were not seen, but male conceptacles and carposporangial conceptacles have not been seen on the same thallus. Male conceptacles are conical, with elliptical chambers (Figure 6) that measure 225–400 μm in diameter \times 31–62 μm in height, with the roof being 56–112 μm thick. The roof is formed from filaments that arise peripheral to the fertile area. These filaments have terminal initials, elongate more rapidly than surrounding cells, and curve inwards to form a pore. The terminal initials of roof filaments are papillate and project into the pore at maturity (Figure 6). A layer of epithallial cells is sloughed during conceptacle formation, but it may lie over the developing conceptacle until roof formation is complete. Unbranched spermatangial systems develop on the floor, walls and roof of the conceptacle (Figures 6 and 7). Carpogonial conceptacles have not been seen. Carposporangial conceptacles are conical (Figures 12 and 13),

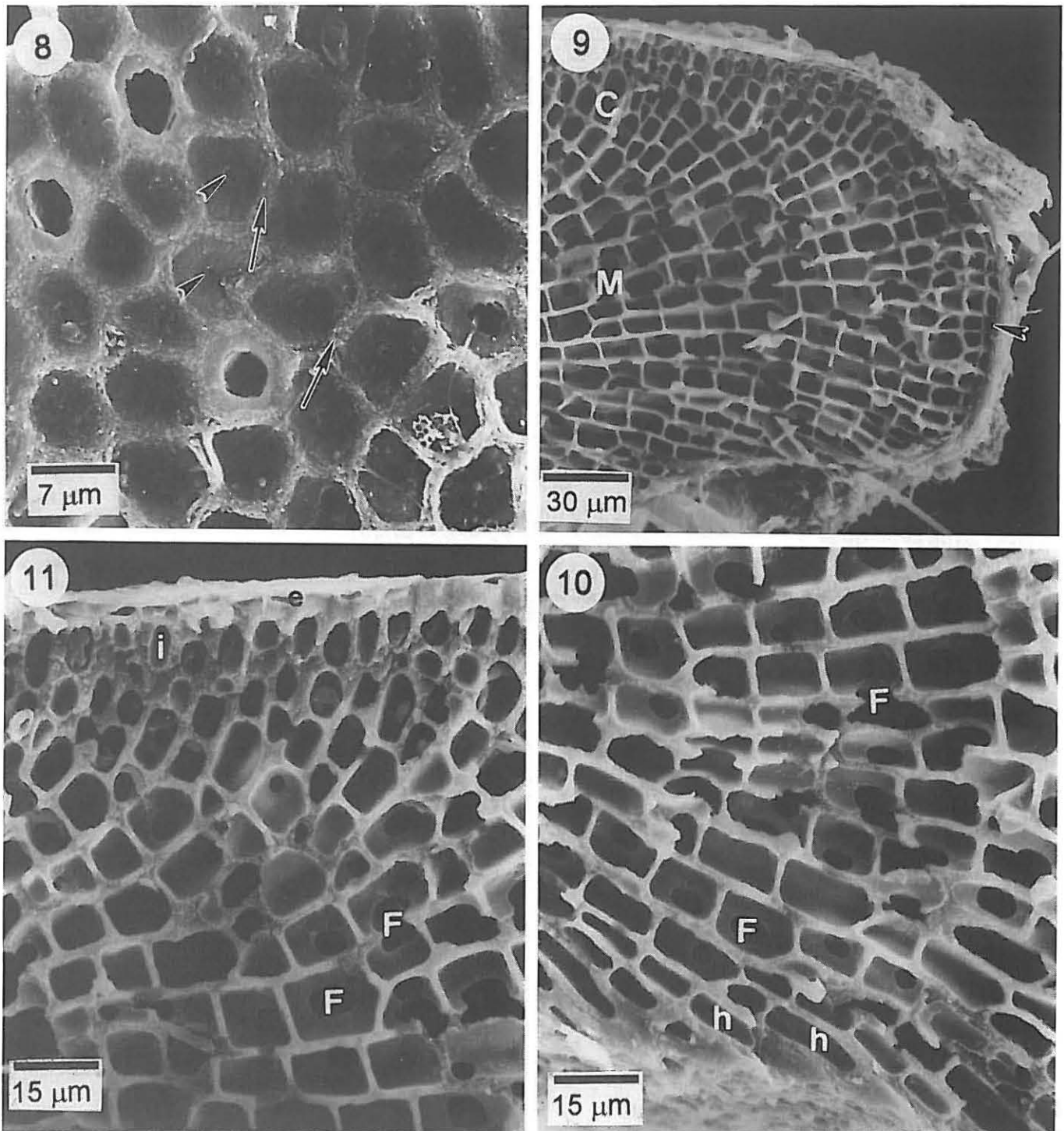


Figures 4–7 Vegetative and male anatomy of *M. incisum* (UWC). **4.** Diagrammatic drawing of VS of tetrasporangial thallus showing medullary filaments (M), cortical filaments (C), conceptacle with tetrasporangium (t), and old buried conceptacle (K). **5.** Thallus showing epithelial cells (E), subepithelial initial (I), lower cells of cortical (C) and medullary filaments (M), and cell fusions (F). Note that medullary filaments terminate at the base of the thallus in hyaline cells (h). **6.** Male conceptacle with simple spermatangial systems on the roof (arrowhead), walls and floor (arrow) of the chamber. **7.** Simple spermatangial branches from the floor (F), walls (S) and roof (R) of a male conceptacle.

with elliptical chambers that measure 315–380 μm in diameter × 135–165 μm in height with the roof being 80–140 μm thick. The fusion cell appears discontinuous in VS, with c. 5 celled gonimoblast filaments developing from the periphery (Figures 13 and 14) and terminating in a carposporangium, each bearing a carpospore measuring 14–20 μm in length × 18–24 μm in diameter (measurements from a single specimen).

Tetrasporangial conceptacles are sparsely distributed over the dorsal surface of the thallus. They are mound-like with a flattened pore plate (Figures 18, 19 and 21), and measure 430–550 μm in

external diameter (Figure 19). Chambers of mature conceptacles are elliptical (Figures 15 and 21), and measure 225–400 μm in diameter × 115–190 μm in height with the roof being 40–62 μm thick. The roof is formed from filaments interspersed among the sporangia; the lower segments of these filaments degenerate, leaving a roof composed of 3–8 cells and perforated by 26–46 pores (Figure 19). Pore plugs are present, and stain densely with aniline blue (Figures 15 and 17). The pores measure 5–12 μm in diameter, and are surrounded by 6–7 rosette cells which are smaller than, and sunken below, the epithelial cells of the



Figures 8–11 SEM of vegetative anatomy of *M. incisum* (UWC: 93/214). **8.** Surface view of vegetative thallus; note centrally located pore in flat-topped cells (arrowhead) and thin lateral walls (arrow). **9.** Vertical fracture of thallus at margin, showing cortical filaments (C), medullary filaments (M), and short, flat-topped terminal marginal initial (arrowhead). **10.** Medullary cells showing cell fusions (F) and elongate hyaline cells at the lower surface (h). **11.** Vertical section of outer thallus away from the margin showing cortical filaments with cell fusions (F), subepithallial initial (i) and epithallial cells (e).

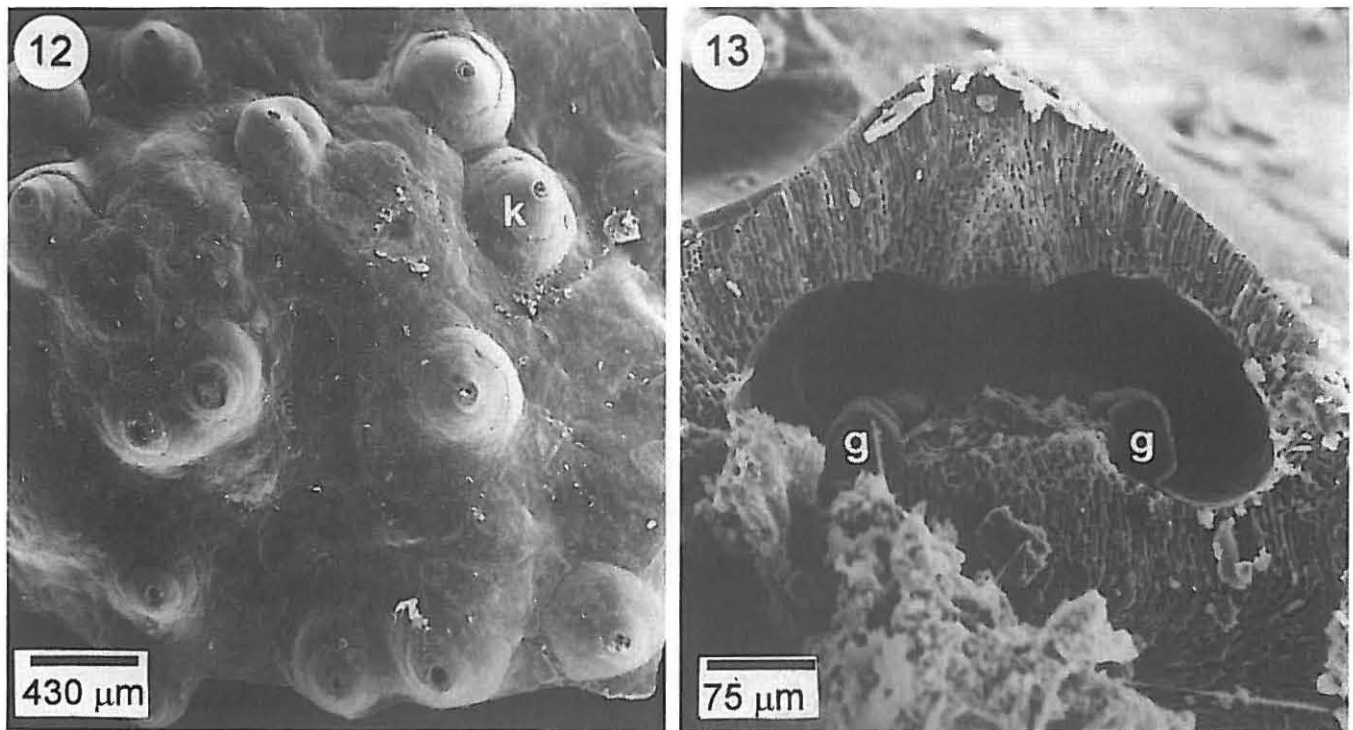
surrounding roof (Figures 19 and 20). Cells of the filaments lining the pore differ markedly from the cells which make up the rest of the roof in that they usually appear narrower, more elongate, and often more densely staining with aniline blue (Figure 17). The pore filaments are mostly 3–4 cells long compared with the filaments of the rest of the pore plate which are usually 5–8 cells long. The pore canal measures 37–50 μm in length \times 5–13 μm in diameter. Tetrasporangia measure 60–170 μm in length \times 20–100 μm in diameter (Figures 15 and 16). Old conceptacles persist and become buried in the thallus (Figure 4), where they are often filled

in by groups of elongate cells that are probably the sterile inter-sporangial filaments. Intact sporangia are sometimes contained within old buried conceptacles. Bisporangial conceptacles were not seen.

Remarks

This species is characterized as follows:

- thallus surface (SEM) with *Leptophytum*-type epithallial cells;
- tetrasporangial conceptacle mound-like, lacking a



Figures 12–13 Carposporangial conceptacles (UWC: 93/214). **12.** Carposporangial conceptacles (k) at the thallus surface. **13.** Vertical fracture of a carposporangial conceptacle showing gonimoblast filaments (g) arranged in a ring around the periphery of the conceptacle.

peripheral rim and having a flattened pore plate;
 – rosette cells distinct from surrounding roof cells (SEM, surface view) in being narrower, and sunken below the level of the surrounding pore plate;
 – cells of filaments bordering the tetrasporangial conceptacle pore canal differing in size and shape from the cells of the other filaments within the pore plate in being more elongate,

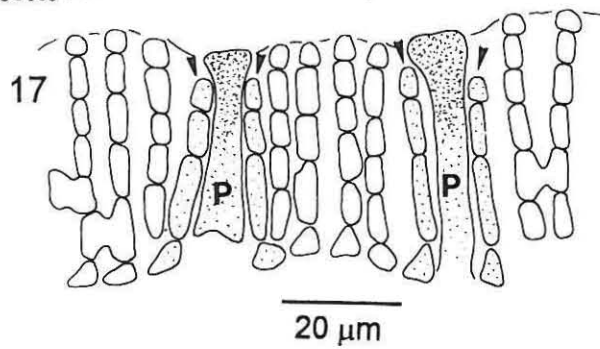
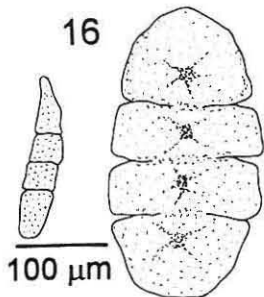
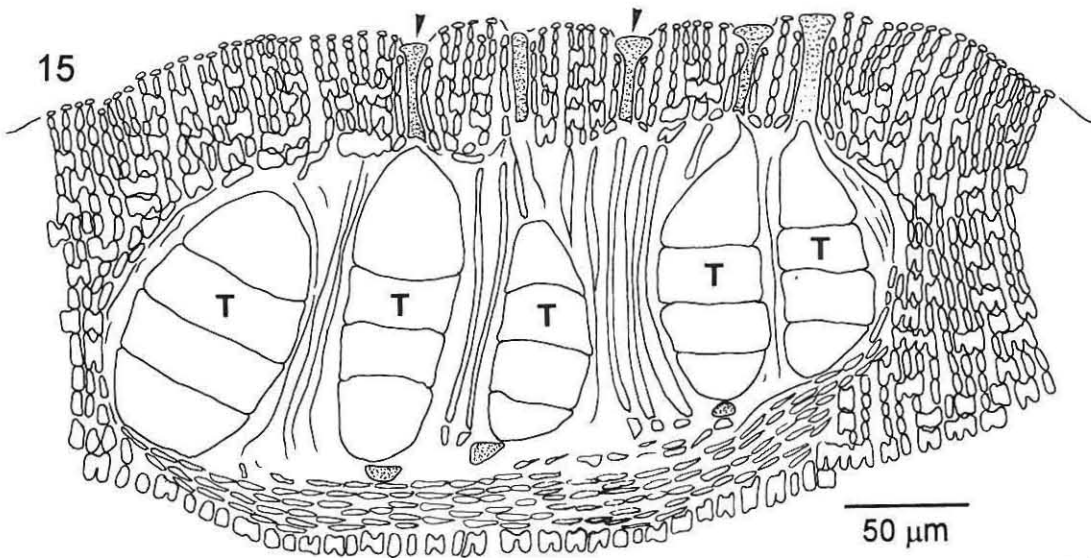
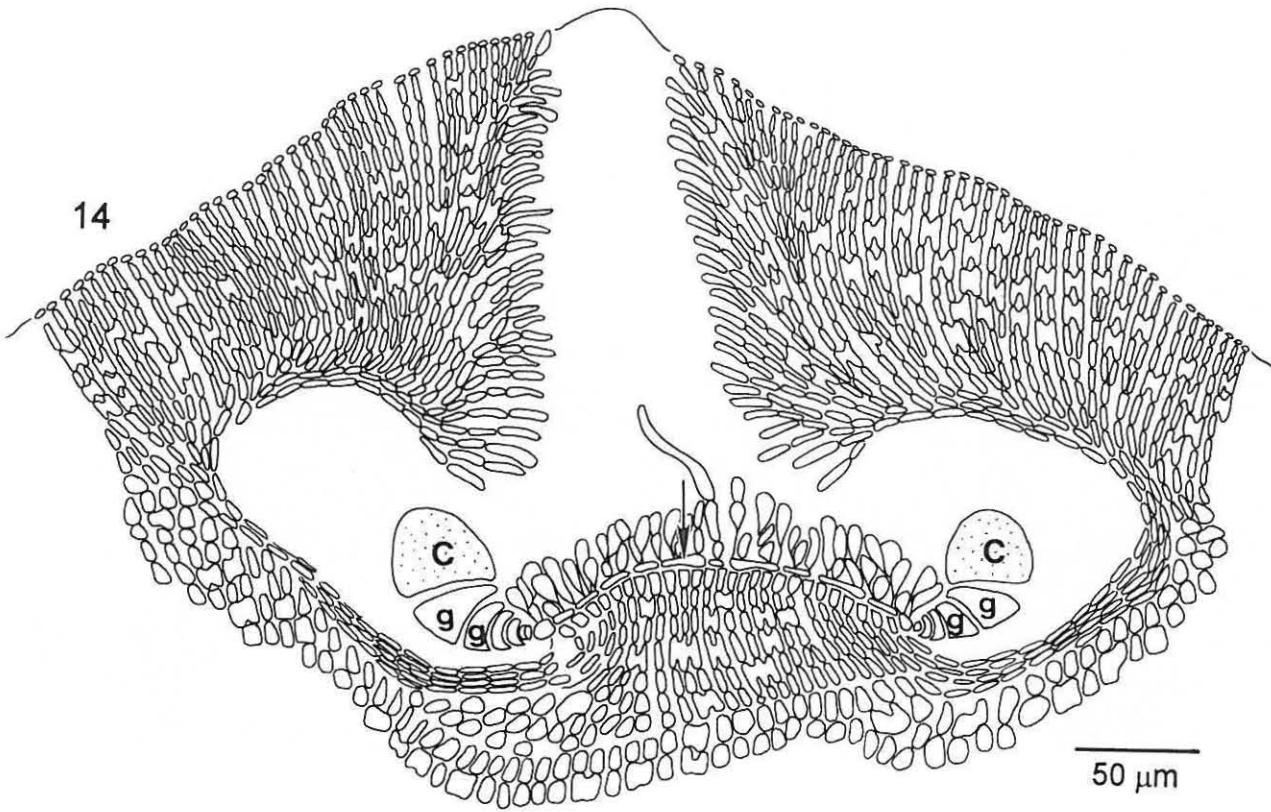
narrower, and often more densely staining;
 – pore canal filaments containing fewer cells than the surrounding filaments of the pore plate;
 – pore canal more-or-less parallel sided.

It is most commonly seen as a thin, delicate encrustation on sponges, horny corals, and bryozoans.

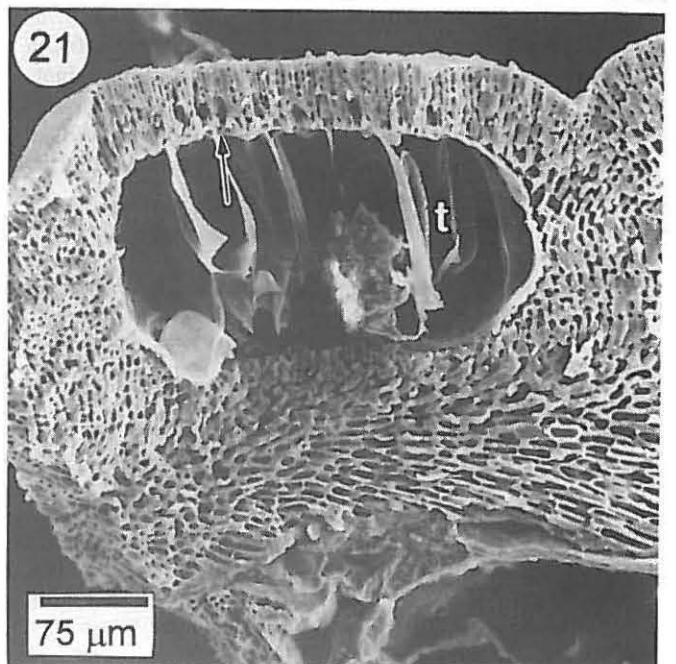
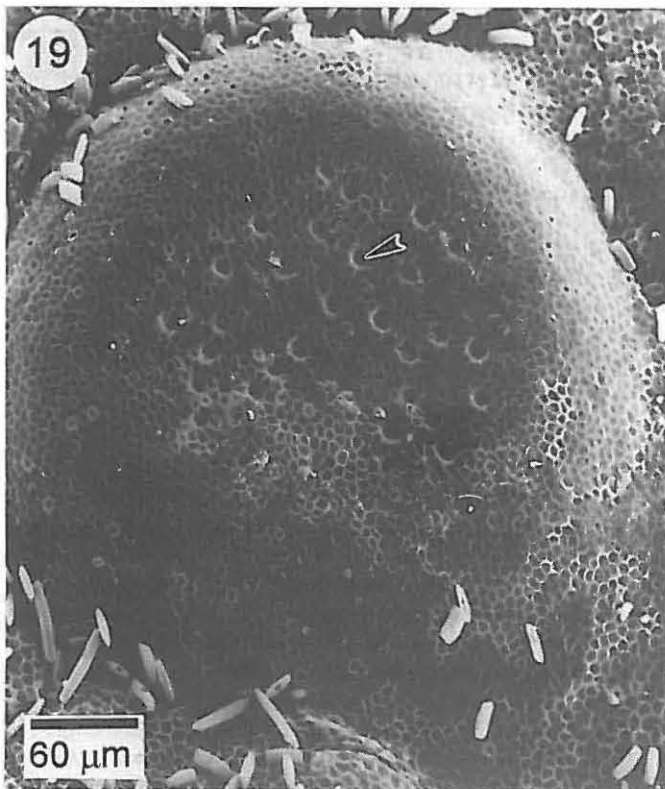
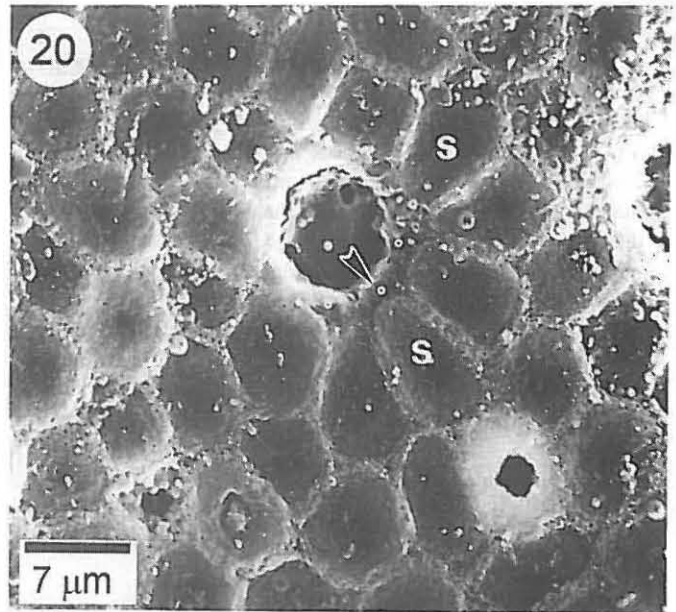
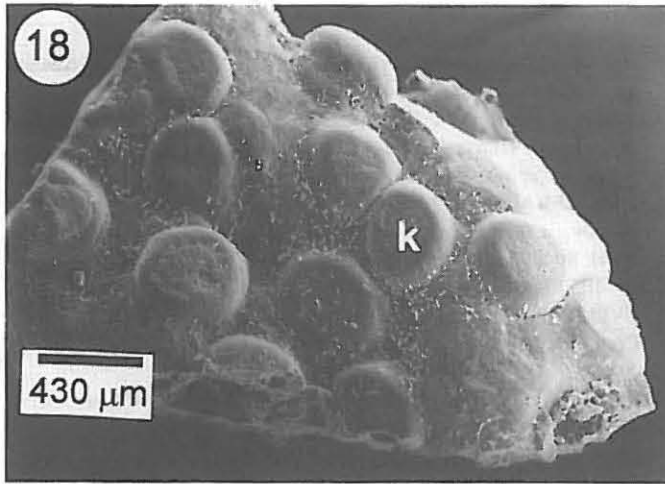
Table 1 Comparison of *Mesophyllum incisum* with the type of the genus, *M. lichenoides* (Ellis) Lemoine (not recorded in South Africa), and the other South African species of *Mesophyllum* according to selected characters considered to have diagnostic value

Character	<i>M. lichenoides</i> ¹	<i>M. incisum</i>	<i>M. erubescens</i> ⁵	<i>M. engelhartii</i>	<i>M. funatutiense</i> ⁵
Growth form	mainly leafy (lamellate)	encrusting to leafy	lumpy to fruticose	encrusting	encrusting to layered to foliose
Thallus surface (SEM)	<i>Phymatolithon</i> -type ²	<i>Leptophytum</i> -type	<i>Phymatolithon</i> -type	<i>Phymatolithon</i> -type	block-like
Tetra/bisporangial conceptacle type	mound-like, flattened to convex pore plate	mound-like, flattened pore plate	mound-like, convex pore plate	mound-like, flattened to convex pore plate	hemispherical, convex pore plate
Rosette cells of tetra/bisporangial conceptacle pore	same size as and flush with surrounding roof cells (possibly tilted somewhat into pore) ³	sunken, smaller than surrounding roof cells	sunken, smaller than surrounding roof cells	same size as and flush with surrounding roof cells	forming a ring, raised above surrounding roof cells
Filaments lining pore canal of tetra/bisporangial conceptacle	cells mainly more squat than surrounding cells	cells more elongate, narrower and denser than surrounding cells	cells more elongate and narrower than surrounding cells	cells same size as those in surrounding roof filaments	cells same size as those in surrounding roof filaments
Cell number in filaments lining pore canal	more cells than surrounding filaments ⁴	fewer cells than surrounding filaments	fewer cells than surrounding filaments	same number of cells as surrounding filaments	same number of cells as surrounding filaments
Pore canal shape	walls more-or-less parallel ⁴	walls more-or-less parallel	walls taper markedly towards the pore	walls more-or-less parallel	walls more-or-less parallel

¹data from Woelkerling & Harvey (1986) and Irvine & Chamberlain (1994); ²based on Woelkerling & Harvey (1986, Fig. 9); ³based on Woelkerling & Harvey (1986, Fig. 12); ⁴based on Woelkerling & Harvey (1986, Fig. 24) and Irvine & Chamberlain (1994, Fig. 99c); ⁵data from Keats & Chamberlain (1994b)



Figures 14–17 Carposporangial and tetrasporangial anatomy of *M. incisum* (UWC: 93/214). **14.** VS of carposporangial conceptacle showing discontinuous fusion cell (arrow), gonimoblast (g) and carposporangium (c). **15.** VS tetrasporangial conceptacle showing chamber with tetrasporangia (T) and pore plugs (arrowhead). **16.** Young (left) and mature (right) tetrasporangia. **17.** VS of tetrasporangial pore plate to show the cells of filaments lining the pore canal (arrowhead) and pore plugs (P). Note that the cells lining the pore canal are laterally compressed, and fact that they are narrower than the surrounding cells (right) of the pore plate is not always obvious (left) unless viewed in the correct plane. However, they always stain differently, as indicated by the stippling.



Figures 18–21 SEM of tetrasporangial conceptacles of *M. incisum* (UWC: 93/214). 18. Mound-like conceptacles (k) with flattened pore plate. 19. Conceptacle showing pore plate with numerous pores (arrowhead). 20. Detail of pore showing pore plug, tiny sunken rosette cells (arrowhead and small white circle), and cells of the pore plate surface (s) surrounding the rosette cells. 21. VS of tetrasporangial conceptacle to show shape, pore canals (arrow) and tetrasporangia (t).

Discussion

Mesophyllum is currently considered to possess the following combination of characters (Chamberlain & Keats 1994, 1995, Woelkerling 1988, Woelkerling & Harvey 1992, 1993):

1. internal construction monomerous;
2. haustoria absent;
3. outermost walls of terminal epithallial cells rounded or flattened but not flared;
4. actively dividing vegetative initials usually as long as or longer than cells immediately subtending them;
5. spermatangial initials formed directly from meristematic cells;
6. spermatangial initials overlaid 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.

Although characters five and six were not observed in South African specimens, they have been observed in Australian material (Woelkerling & Harvey 1992). The species studied here thus conforms to *Mesophyllum* on the basis of its possession of all of the above generic characters. This is the fourth species of *Mesophyllum* reported from South Africa (Keats & Chamberlain 1994b, Chamberlain & Keats 1995). See Table 1.

Key to South African species of *Mesophyllum*

It is important to verify the occurrence of all characters used in the key to confirm identification.

1. Tetra/bisporangial conceptacle pores lined by filaments made up of cells which do not differ from those of the surrounding roof filaments 3
1. Tetra/bisporangial conceptacle pores lined by filaments made up of cells which are different from those of the surrounding roof filaments 2
2. Thallus mainly warty to lumpy to fruticose; conceptacles found mainly on the protuberances, pore canal lined by filaments that

differ from those of the surrounding roof in having an elongate cell at their base; walls of pore canal tapering towards the surface, rosette cells flush with surrounding roof

..... *M. erubescens*

2. Thallus mainly encrusting to warty; conceptacles found mainly on flat areas of thallus; pore canal lined by filaments that differ from those of the surrounding roof in being narrower and more elongate; walls of pore canal more-or-less parallel; rosette cells distinct from surrounding roof cells in being narrower, and sunken below the level of the surrounding pore plate (this may be difficult to see even in SEM)

M. incisum

3. Tetra/bisporangial conceptacles very large (up to 1.2 mm), rosette cells raised, forming a distinct ring surrounding the pore

..... *M. funafutiense*

3. Tetra/bisporangial conceptacles not huge (just visible with naked eye, rarely exceeding 600 µm in diameter), rosette cells flush with the surrounding roof

..... *M. engelhartii*

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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., & ADEY P.J. 1973. Studies on the biosystematics and ecology of the epilithic crustose Corallinaceae of the British Isles. *Brit. Phycol. J.* 8: 343–407.
- CAMPBELL S.J. & WOELKERLING W.J. 1990. Are *Titanoderma* and *Lithophyllum* (Corallinaceae, Rhodophyta) distinct genera? *Phycologia* 29: 114–125.
- 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*. *Br. phycol. J.* 25: 179–199.
- CHAMBERLAIN Y.M. 1991. Historical and taxonomic studies in the genus *Titanoderma* (Rhodophyta, Corallinales) in the British Isles. *Bull. Br. Mus. Nat. Hist. (Bot.)* 21: 1–80.
- CHAMBERLAIN, Y.M. 1992. Observations on two melobesioid crustose coralline red algal species from the British Isles: *Exilicrusta parva*, a new genus and species, and *Lithothamnion sonderi* Hauck. *Br. phycol. J.* 27: 185–201.
- CHAMBERLAIN, Y.M. 1993. Observations on the crustose coralline red alga *Spongites yendoii* (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* D. Penrose et Woelkerling and *S. impar* (Foslie) Chamberlain comb. nov. (Rhodophyta, Corallinaceae) from South Africa. *Phycologia* 33: 141–157.
- CHAMBERLAIN, Y.M. 1996. Lithophylloid Corallinaceae (Rhodophyta) of the genera *Lithophyllum* and *Titanoderma* from southern Africa. *Phycologia* 35: 204–221.
- CHAMBERLAIN, Y.M. & IRVINE, L.M. 1994. Lithophylloideae. In: Seaweeds of the British Isles. Volume 1. Rhodophyta. Part 2B. Corallinales, Hildenbrandiales. Eds. Irvine, L.M. & Chamberlain, Y.M. p. 58–112. HMSO, London.
- CHAMBERLAIN, Y.M. & KEATS, D.W. 1994. Three melobesioid crustose coralline red algae from South Africa: *Leptophytum acervatum* (Foslie) comb. nov., *L. foveatum* sp. nov. and *L. ferox* (Foslie) comb. nov. *Phycologia* 33: 111–133.
- CHAMBERLAIN, Y.M. & KEATS, D.W. 1995. The melobesioid red alga *Mesophyllum engelhartii* (Rhodophyta, Corallinaceae) in South Africa. *S.Afr. J. Botany* 61: 134–146.
- CHAMBERLAIN, Y.M. & NORRIS, R.E. 1994a. *Pneophyllum amplexifrons* (Harvey) comb. nov., a mastophoroid crustose coralline red algal epiphyte from Natal, South Africa. *Phycologia* 33: 8–18.
- CHAMBERLAIN, Y.M. & NORRIS, R.E. 1994b. *Hydrolithon pellire* sp. nov., a mastophoroid, crustose coralline red alga epiphyte from Natal, South Africa. *Phycologia* 33: 291–297.
- CHAMBERLAIN, Y.M., NORRIS R.E., KEATS, D.W. & MANEVELDT, G. 1995. *Clathromorphum tubiforme* sp. nov. (Rhodophyta, Corallinaceae) in South Africa with comments on generic characters. *Bot. Mar.* 38: 443–453.
- FOSLIE, M. 1906. Algologiske notiser II. *K. norske Vidensk. Selsk. Skr.* 1906(2): 1–28.
- HARVEY, A.S. & WOELKERLING, W.M. 1995. An account of *Austrolithon intumescens* gen. et sp. nov. and *Boreolithon van-heurkii* (Heydrich) gen et comb. nov. (Austrolithoideae subfam. nov., Corallinaceae, Rhodophyta). *Phycologia* 34: 362–382.
- HARVEY, A.S. & WOELKERLING, W.M. 1986. The neotypification and status of *Mesophyllum* (Corallinaceae, Rhodophyta). *Phycologia* 25: 379–396.
- HARVEY, A.S., WOELKERLING, W.M. & WILKS, K.M. 1994. The genus *Synarthrophyton* (Corallinaceae, Rhodophyta) in southern Australia. *Phycologia* 33: 331–342.
- IRVINE, L.M. & CHAMBERLAIN, Y.M. 1994. Seaweeds of the British Isles, Volume 1, Rhodophyta Part 2B, Corallinales, Hildenbrandiales. pp. 58–112. The Natural History Museum, London.
- KEATS, D.W. 1995. *Lithophyllum cuneatum* sp. nov. (Corallinaceae, Rhodophyta), a new species of non-geniculate coralline alga semi-endophytic in *Hydrolithon onkodes* (Heydrich) Penrose et Woelkerling and *Neogoniolithon* sp. from Fiji, South Pacific *Phycol. Res.* 1: 151–160.
- KEATS, D.W. & CHAMBERLAIN, Y.M. 1993. *Sporolithon ptychoides* Heydrich and *S. episorum* (Howe) Dawson: two crustose coralline red algae (Corallinales, Sporolithaceae) in South Africa. *S.A. J. Bot.* 59: 541–550.
- KEATS, D.W. & CHAMBERLAIN, Y.M. 1994a. Three species of *Hydrolithon* (Rhodophyta, Corallinaceae): *Hydrolithon onkodes* (Heydrich) Penrose and Woelkerling, *Hydrolithon superficiale* sp. nov., and *H. samoense* (Foslie) comb. nov. from South Africa. *S.A. J. Bot.* 60: 8–21.
- KEATS, D.W. & CHAMBERLAIN, Y.M. 1994b. Two melobesioid coralline algae (Rhodophyta, Corallinales), *Mesophyllum erubescens* (Foslie) Lemoine & *Mesophyllum funafutiense* (Foslie) Verheij from Sodwana Bay, South Africa. *S.A. J. Bot.* 60: 175–190.
- KEATS, D.W. & CHAMBERLAIN, Y.M. 1995. *Heydrichia groeneri* sp. nov.: a new species of crustose coralline alga (Rhodophyta, Sporolithaceae) from South Africa and Namibia. *Phycologia* 34: 51–57.
- KEATS, D.W. AND MANEVELDT G. 1994. *Leptophytum foveatum* Chamberlain & Keats (Rhodophyta, Corallinales) retaliates against competitive overgrowth by other encrusting algae. *J. Exp. Mar. Biol. Ecol.* 175: 243–251.
- KEATS, D.W., MATTHEWS, I. & MANEVELDT G. 1994. Competitive relationships and coexistence in a guild of crustose algae in the eulittoral zone, Cape Province, South Africa. *S. Afr. J. Bot.* 60: 108–113.
- KEATS, D.W., WILTON, P. & MANEVELDT, G. 1994. Ecological significance of deep-layer sloughing in the eulittoral zone coralline alga, *Spongites yendoii* (Foslie) Chamberlain (Corallinaceae, Rhodophyta) in South Africa. *J. Exp. Mar. Biol. Ecol.* 175: 145–154.
- KEATS, D.W., STENECK, R.S., TOWNSEND, R.A. & BOROWITZKA, M.A. 1996. *Lithothamnion prolifer* Foslie: a common non-geniculate coralline alga (Rhodophyta: Corallinaceae) from the tropical and subtropical Indo-Pacific. *Botanica Marina* 39: 187–200.
- MAY, D.I. & WOELKERLING, W.J. 1988. Studies on the genus *Synarthrophyton* (Corallinaceae, Rhodophyta) and its type species, *S. patena* (J.D. Hooker et W.H. Harvey) Townsend. *Phycologia*, 27: 50–71.
- PENROSE, D. 1991. *Spongites fruticosus* (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. & CHAMBERLAIN, Y.M. 1993. *Hydrolithon farinosum* (Lamouroux) comb. nov.: implications for generic concepts in the Mastophoroideae (Corallinaceae, Rhodophyta). *Phycologia* 32: 295–303.
- PENROSE, D. & WOELKERLING, W.J. 1988. A taxonomic reassessment of *Hydrolithon* Folsie, *Porolithon* Foslie and *Pseudolithophyllum* Lemoine emend. Adey (Corallinaceae, Rhodophyta) and their relationships to *Spongites* Kützing. *Phycologia* 27: 159–176.
- PENROSE, D. & WOELKERLING, W.J. 1991. *Pneophyllum fragile* in southern Australia: implications for generic concepts in the Mastophoroideae (Corallinaceae, Rhodophyta). *Phycologia* 30: 495–506.
- PENROSE, D. & WOELKERLING, W.J. 1992. A reappraisal of *Hydrolithon* (Corallinaceae, Rhodophyta) and its relationship to *Spongites*. *Phycologia* 31: 81–88.
- STEARN, W.T. 1992. *Botanical Latin*. David and Charles, London, 546 pp.
- TOWNSEND, R.A. 1979. *Synarthrophyton*, a new genus of Corallinaceae (Cryptonemiales, Rhodophyta) from the southern Hemisphere. *J. Phycol.* 15: 251–259.
- TOWNSEND, R.A., CHAMBERLAIN, Y.M. & KEATS D.W. 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., WOELKERLING, W.M. J., HARVEY, A.S. & BOROWITZKA, M.S. 1995. An account of the red algal genus *Sporolithon* (Sporolithaceae, Corallinales) in southern Australia. *Aust. Syst. Bot.* 8: 85–121.
- VERHEIJ, E. 1993a. Marine Plants on the Reefs of the Spermonde Archipelago, SW Sulawesi, Indonesia: Aspects of Taxonomy, Floristics, and Ecology. Rijksherbarium/Hortus Botanicus, Leiden, 320 pp.
- VERHEIJ, E. 1993b. 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.
- WILKS, K.M. & WOELKERLING, W.J. 1994. An account of the southern Australian species of *Phymatolithon* (Corallinaceae, Rhodophyta) with comments on *Leptophyllum*. *Aust. Syst. Bot.* 7: 183–223.
- WILKS, K.M. and WOELKERLING, W.J. 1995. An account of Southern Australian species of *Lithothamnion* (Corallinaceae, Rhodophyta). *Aust. Syst. Bot.* 8: 549–583.
- 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) & 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. & CAMPBELL, S.J. 1992. An account of southern Australian species of *Lithophyllum* (Corallinales, Rhodophyta). *Bull. Br. Mus. nat. Hist. (Bot.)* 22 (1): 1–107.
- WOELKERLING, W.J. & FOSTER, M.S. 1989. A systematic and ecological account of *Synarthrophyton schielianum* sp. nov. (Corallinaceae, Rhodophyta) from the Chatham Islands. *Phycologia*, 28: 39–60.
- WOELKERLING, W.J. & HARVEY, A. 1992. *Mesophyllum incisum* (Corallinaceae, Rhodophyta) in southern Australia: implications for generic and specific delimitation in the Melobesioideae. *Br. Phycol. J.* 27: 381–399.
- WOELKERLING, W.J. & HARVEY, A. 1993. An account of southern Australian species of *Mesophyllum* (Corallinaceae, Rhodophyta). *Aust. J. Syst. Bot.* 6: 571–637.
- WOELKERLING, W.J. & IRVINE, L.M. 1986. The neotypification and status of *Mesophyllum* (Corallinaceae, Rhodophyta). *Phycologia* 25: 379–396.
- WOELKERLING, W.J., IRVINE, L.M. & HARVEY, A.S. 1993. Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). *Aust. Syst. Bot.* 6: 277–293.