Synarthrophyton papillatum sp. nov.: A new species of non-geniculate coralline algae (Rhodophyta, Corallinales, Hapalidiaceae) from South Africa and Namibia

G.W. Maneveldt [a,*], D.W. Keats [a], Y.M. Chamberlain [b]

[a] *Department of Biodiversity and Conservation Biology, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa*
[b] *Institute of Marine Sciences, University of Portsmouth, Ferry Road, Portsmouth PO4 9LY, United Kingdom*

Abstract

Polychaete worm tubes within the mid to lower intertidal zone along the South African west coast were frequently observed to be overgrown by a minutely papillate species of encrusting coralline algae. Analysis of the vegetative and reproductive morphology and anatomy of this alga shows that it is new to science and belongs to the subfamily Melobesioideae and, in particular, to the genus *Synarthrophyton*, which is for the most part restricted to the Southern Hemisphere. *Synarthrophyton papillatum* is the tenth species from this genus and the sixth recorded from southern Africa. The new species is described in detail and compared with recently documented species found to conform to the generic description of *Synarthrophyton*. *Synarthrophyton papillatum* differs from *S. patena* and *S. eckloniae* in being epilithic, not epiphytic; from *S. munimentum* and *S. robbenense* in lacking raised rims on the tetrasporangial conceptacles; and from *S. magellanicum* in bearing minutely warty to fruticose protuberances and generally lacking the leafy to layered, weakly attached thalli present in the latter species. A key to the southern African species of *Synarthrophyton* is provided.

© 2007 SAAB. Published by Elsevier B.V. All rights reserved.

Keywords: Corallinales; Hapalidiaceae; Non-geniculate coralline algae; South Africa; *Synarthrophyton*; *S. papillatum*; Taxonomy

1. Introduction

Non-geniculate coralline algae are widespread in all of the world's oceans, where they often cover close to 100% of rocky substrata (Lee, 1967; Adey, 1978; Littler, 1973; Adey and MacIntyre, 1973; Adey et al., 1982; Steneck, 1986; Keats and Maneveldt, 1994; Littler and Littler, 2000, 2003). Despite their ubiquity, they are a poorly known group of marine organisms (Keats and Chamberlain, 1993, 1994a,b). Much of this lack of knowledge stems from a legacy of poor quality taxonomic work (summarised by Woelkerling and Lamy, 1998) and it is not surprising that the non-geniculate coralline algae have been considered to constitute a 'difficult' taxonomic group (see Taylor, 1942, 1945, 1950, 1960; Woelkerling, 1988). This said,

a study is being made of the taxonomy of South African non-geniculate coralline algae and many are now known in a modern context. Priority is being given to study ecologically significant species [e.g. *Spongites yendoi* (Foslie) Y. Chamberlain (Chamberlain, 1993; Keats et al., 1993; Maneveldt et al., 2006)] and new or otherwise taxonomically interesting species [e.g. *Pneophyllum amplexifrons* (Harvey) Chamberlain et Norris Chamberlain and Norris (1994), *Clathromorphum tubiforme* Chamberlain, Norris, Keats et Maneveldt Chamberlain et al. (1995), *Synarthrophyton eckloniae* (Foslie) Chamberlain et Keats Keats and Chamberlain (1997), and *Lithothamnion superpositum* Foslie (Keats et al., 2000)]. The need to provide a taxonomic basis for ecological studies on non-geniculate coralline algae (e.g. Keats et al., 1994a,b; Keats and Maneveldt, 1994; Maneveldt et al., 2006) precludes the postponement of taxonomic publication until after the completion of monographic studies of particular genera. During these investigations, an encrusting coralline alga attributable to the

* Corresponding author.
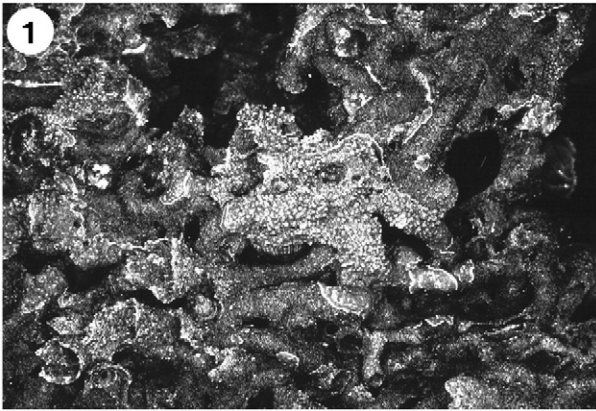*E-mail address:* gmaneveldt@uwc.ac.za (G.W. Maneveldt).

Fig. 1. Individuals of *Synarthrophyton papillatum* in their common habitat from Holbaaipunt, Western Cape Province, overgrowing polychaete worm tubes in the mid to lower intertidal zone.

Fig. 3. The isotype specimen consists of worm tube substrate from Groenriviermond, covered with individuals of *S. papillatum*.

genus *Synarthrophyton* was found to occur commonly in the mid to lower intertidal zone where it most often overgrew polychaete worm tubes (Fig. 1). This paper presents a formal description of the new species, compares it against recently documented species found to conform to the generic description of *Synarthrophyton*, and provides a key to the known species of this genus from Southern Africa.

2. Materials and methods

Field collections were made in the middle to low intertidal zone of the Northern Cape and Western Cape Provinces of South Africa. Specimens were removed by using a sledgehammer and cold chisel, and sorted as well as possible in the field using a hand lens. Thalli were examined as far as possible when fresh; otherwise they were air-dried or fixed in neutralized 10% commercial formalin seawater (4% formaldehyde) and stored in a 70% ethanol: 10% glycerol: 20% distilled water solution.

For scanning electron microscopy (SEM), air-dried material was fractured using either fingernails, forceps, diagonal cutters, or a s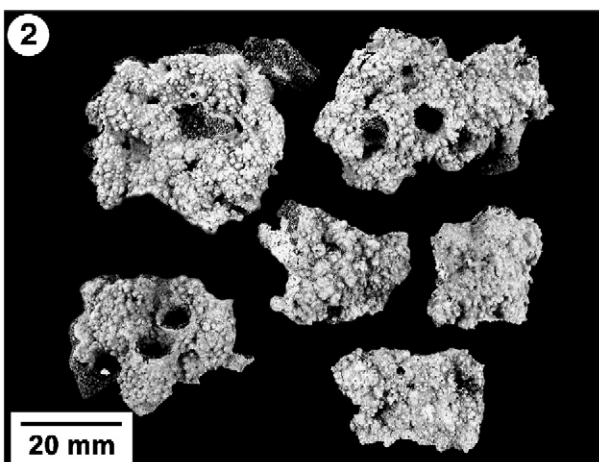mall hammer and cold chisel. Wherever possible a fracture perpendicular to a leading edge was used to determine internal anatomy. The fractured pieces were mounted on stubs, using adhesive tabs (Agar Scientific, 66a Cambridge Rd., Stanstead, Essex CM24 8DA, UK), stored in a desiccator for at least 24 h prior to examination, coated with gold for 4–6 min in an Edwards S150B sputter coater, and examined with a Hitachi X650 scanning electron microscope, equipped with a Mamiya 6X7 camera at an accelerating voltage of 20 or 25 kV.

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. Using a fine sable-hair brush, individual sections were transferred to a slide containing aniline blue in 40% 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 donates the distance between primary pit connections, and diameter the maximum width of the cell lumen at right angles to this. Conceptacle measurements follow Adey and Adey (1973). Thallus anatomical terminology follows Chamberlain (1990), while morphological terminology follows Woelkerling et al. (1993). Typification data follow Woelkerling (1993) unless otherwise stated.

Fig. 2. The fragmented holotype specimen of *S. papillatum* (L0535938). The holotype consists largely of tetrasporangial individuals.
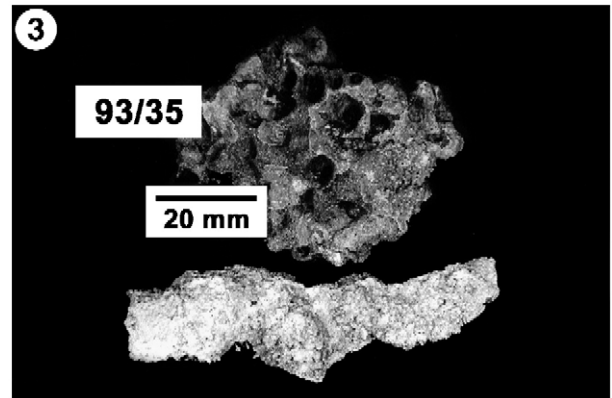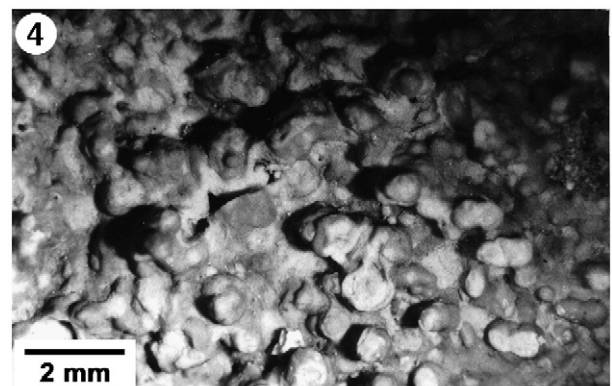

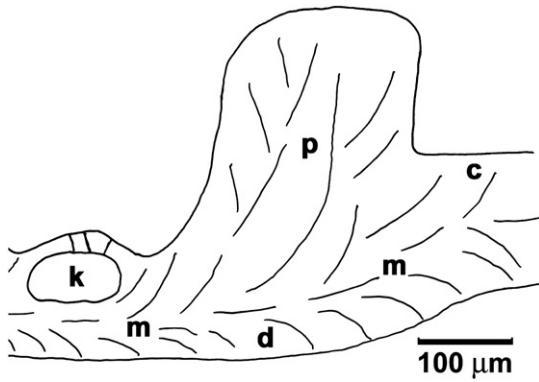Fig. 4. A warty surface with numerous minute papillate protuberances.

Fig. 5. Diagrammatic drawing of the thallus showing the cortex (c), medulla (m), downward curving filaments (d) and a tetrasporangial conceptacle (k) near the base of a protuberance (p).

2.1. Observations

Synarthrophyton papillatum G. Maneveldt, D. Keats & Y. Chamberlain sp. nov.

Holotype: L (Natinaal Herbarium Nederland, Universiteit Leiden branch, Leiden [previously known as the Rijksherbarium, Leiden, The Netherlands])! Groenriviermond, Northern Cape Province, South Africa; middle to low shore on worm tubes (*D.W. Keats* and *G.W. Maneveldt*, 8.v.1993, L0535938) (Fig. 2). An isotype specimen has been retained at UWC (UWC 93/95 – Fig. 3).

Etymology: *papillatum* refers to the minute protuberances, which give the appearance of numerous papillae.

2.2. Description of type

The following description is based on the isotype material housed at UWC (UWC 93/35 — Fig. 3).

Thalli praecipue affixi in vermium tubis polychaeticis in zona saxosa inter marinorum aestuum accessum et recessum emersa;
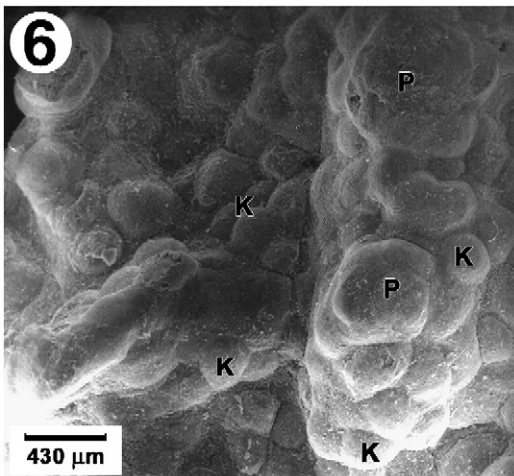

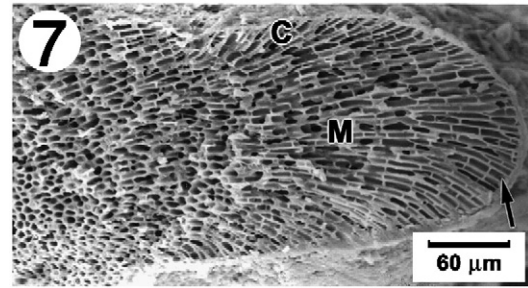Fig. 6. Surface view of thallus showing protuberances (P) and densely crowded multiporate conceptacles (K).

Fig. 7. Vertical fracture of the thallus margin showing cortex (C), medulla (M) and primary terminal initials (arrow).

thalli brunneole purpurei, aliquantum frondosi; superficies obtecta multis brevibus protuberationibus dense constipatis metientibusque minus quam 1 mm diametro; thalli monomeri; medulla plumosa; cellulae et medullae et corticis elongatae; tetrasporangialia conceptacula tholiformia, tectis perforatis 16–20 poris quorum unusquisque circumcinctus 6–8 cellulis rosulatis complanis cellulis tecti circumambientis; tetrasporangialis conceptaculi tectum latum 5–6 cellulis; cellulae filamentorum pori et conceptaculi orae non notabiliter dissimiles cellulis filamentorum quae scutellastram pororum componunt; vetera tetra/bisporangialia conceptacula senescentia se in thallo infodiunt.

Thalli mainly attached to polychaete worm tubes in the rocky intertidal zone; thalli brownish-purple, somewhat leafy; surface covered by numerous, densely crowded, short, protuberances that measure less than 1 mm in diameter; thalli monomerous; medulla plumose; cells of both medulla and cortex are elongate; tetrasporangial conceptacles domed, with the roofs perforated by 16–32 pores each of which is surrounded by 6–8 rosette cells that are flush with the cells of the surrounding roof; tetrasporangial conceptacle roof is 5–6 cells thick; cells of filaments lining the pore and those of the conceptacle rim not noticeably different from cells of filaments comprising the pore plate; old tetra/bisporangial conceptacles become buried in the thallus on senescence.

2.3. Diagnosis

Differing from southern African specimens of *S. patena* and *S. eckloniae* in being epilithic or epizoic, not epiphytic; from *S. munimentum* and *S. robbenense* in lacking raised rims on the
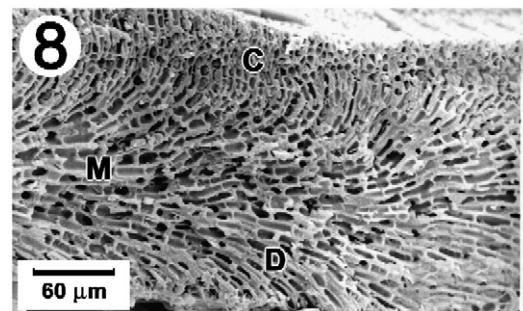

Fig. 8. Vertical fracture of the thallus away from the margin showing cortex (C), medulla (M) and downward curving filaments (D).
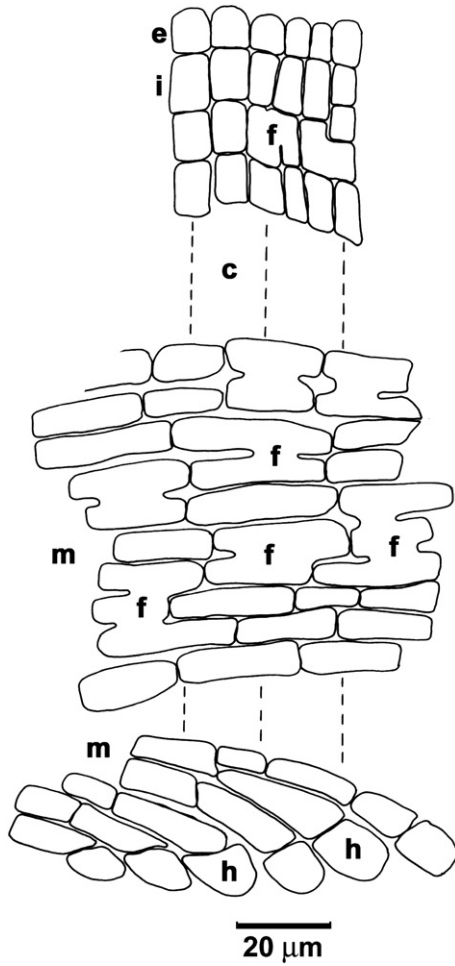
Fig. 9. VS of thallus showing epithallial cells (e), subepithallial initials (i), cells of cortical (c) and medullary (m) filaments with cell fusions (f) and downward curving filaments terminating in enlarged dome-shaped cells (h).

tetrasporangial conceptacles; and from *S. magellanicum* in bearing minutely warty to fruticose protuberances and lacking the generally leafy to layered, weakly attached thalli present in the latter species. Differing from the non-southern African specimens of *S. patena*, *S. chejuensis*, *S. pseudosorus*, *S. schmitzii* and *S. schielianum* in bearing minutely warty to fruticose protuberances and lacking the generally leafy to
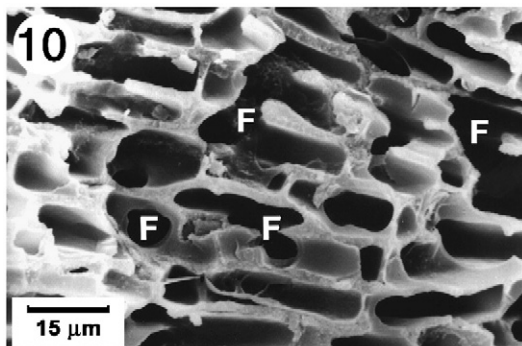

Fig. 10. Cells of medullary filaments with extensive cell fusions (F).
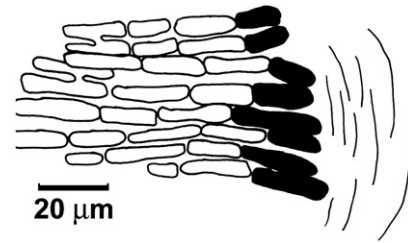

Fig. 11. VS of the thallus margin showing primary terminal initials (black). The curved lines to the right of the initials show the presence of a thick, protective cuticle.

layered thalli present in these species. In addition to this feature, *S. papillatum* differs from *S. patena* in being mostly epilithic, not epiphytic and bearing tetrasporangial conceptacles that have an external diameter of less than 500 μm; from *S. chejuensis* and *S. pseudosorus* in lacking the dense sorus-like clustering of the tetra/bisporangial conceptacles; and from *S. schielianum* in lacking ventral struts and volcano-like tetrasporangial conceptacles.

2.4. Representative specimens examined

In total, eleven (11) specimens (including the holotype and isotype) have been examined, these representing our entire collection for this taxon.

Holbaaipunt, Western Cape Province, South Africa, middle to low shore on worm tubes in wave exposed crevices (D.W. Keats, 16.ii.1991, UWC: COR/184); (D.W. Keats, 26.xi.1991, UWC: 91/250); (D.W. Keats, 05.v.1992, UWC: 92/87); (D.W. Keats, 18.v.1992, UWC: 92/101); (D.W. Keats & P. Wilton, 01. vi.1992, UWC: 92/149); (D.W. Keats & G. Maneveldt, 09. iii.1993, UWC: 93/3).

Groenriviermond, Northern Cape Province, South Africa; middle to low shore on worm tubes (D.W. Keats and G.W. Maneveldt, 8.v.1993, L0535938); (D.W. Keats and G.W. Maneveldt, 8.v.1993, UWC: 93/35).
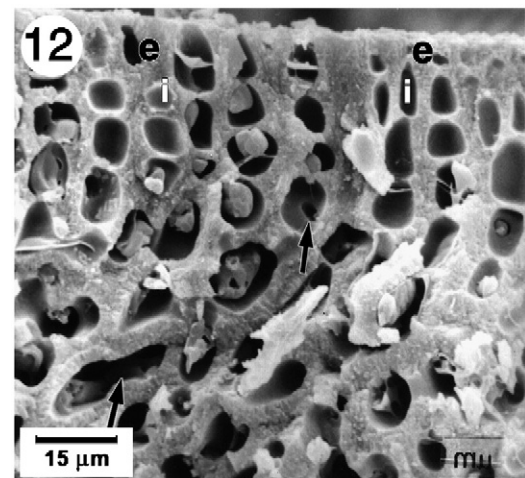

Fig. 12. Vertical fracture near the thallus surface showing epithallial cells (e), subepithallial initials (i) and cell fusions (arrows) in cells of cortical filaments.
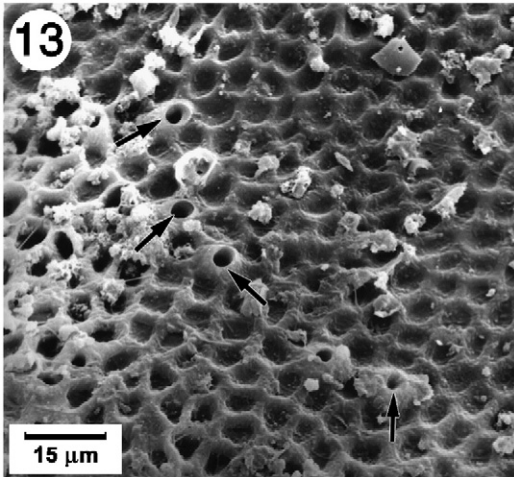
Fig. 13. Surface view of thallus showing probable trichocytes (arrows).

Fig. 15. Male conceptacles (K) at thallus surface.

Port Nolloth, Northern Cape Province, South Africa, middle to low shore on worm tubes (D.W. Keats, 16.vii.1992, UWC: 92/333); (D.W. Keats & G. Maneveldt, 26.ii.1994, UWC: 94/32).

Grossebucht, Lüderitz, Namibia, middle to low shore on worm tubes (D.W. Keats & A. Groener, 13.vii.1992, UWC: 92/310).

2.5. Habitat and phenology

Synarthrophyton papillatum is common on polychaete worm tubes and only occasionally on rock surfaces and mussels in the middle to low intertidal zone. It is most abundant along the sides of rock crevices and in shaded locations. Reproductive specimens occur throughout the year.

2.6. Distribution

Southern Africa: Lüderitz, Namibia to Cape Agulhas, South Africa.

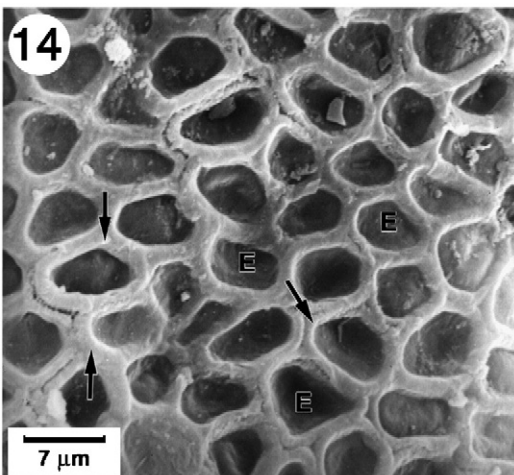World: Presently known only from southern Africa.

2.7. Habit and vegetative structure

The purplish brown, warty thalli are strongly adherent and have smooth surfaces with a somewhat matt (eggshell) texture. Thalli measure 200–700 µm thick in flat areas, but are covered with densely packed, pale-tipped, protuberances that measure 0.2–3 mm high and 0.2–0.7 mm in diameter (Figs. 4, 5). Protuberances are sometimes flattened laterally, are often fused, and commonly have tiny branches and dome-shaped sporangial conceptacles, which cause them to resemble tiny, bunches of grapes when viewed with a dissection microscope (Fig. 6). The thallus is monomerous and haustoria are absent (Figs. 7–9). The medulla is plumose (Figs. 9, 10), measuring 100–300 µm thick, and occupying *c*. 90% of the thallus thickness near the margins, but often less than 10% of the thallus thickness in older areas. Medullary filaments are often eroded away in old specimens. Cells of the medullary filaments are very elongate, often up to 7 times their diameter (Figs. 9–11), and measure 15–45 µm long by 6–9 µm in diameter. Cell fusions are abundant and

Fig. 14. Surface view of thallus showing epithallial cells (E) with central cavities and relatively thick lateral walls (arrows).

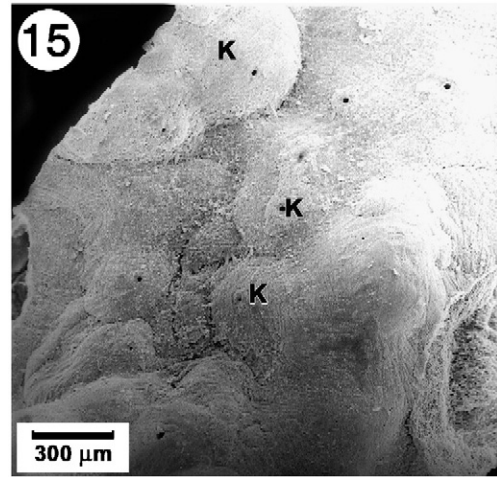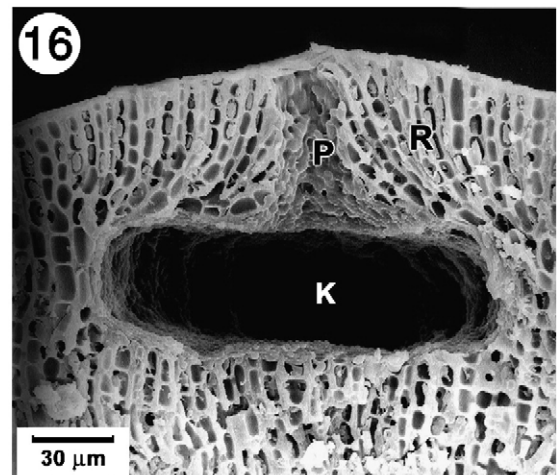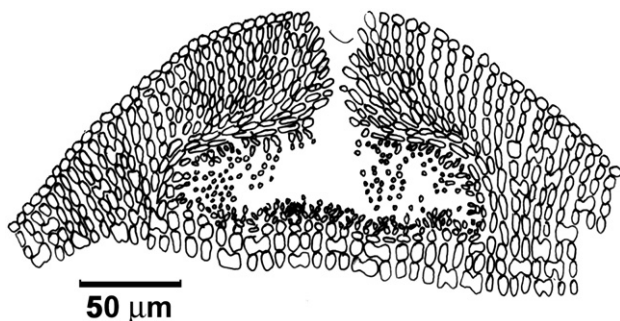Fig. 16. Vertical fracture of a male conceptacle showing the chamber shape (K), pore canal (P) and roof filaments (R).

Fig. 17. VS of mature male conceptacle showing spermatangial systems on the floor, walls and roof of the conceptacle.

Fig. 19. VS of developing male conceptacle with protective cells (arrowhead) above spermatangial initials that are located on the floor (arrow).

frequently occupy most of the wall of adjoining cells (Figs. 9, 10). Downward curving filaments are well developed in younger specimens, each commonly terminating in an enlarged, dome-shaped cell (Fig. 9). Medullary filaments terminate at the margin in primary meristematic cells (Fig. 9) that are rectangular with rounded corners and measure 8–16 µm long by 5–7 µm in diameter. The cortex is 75–610 µm thick, comprising 10–90% of thallus thickness (Figs. 7, 8). Cells of cortical filaments elongate progressively down into the thallus, and measure 6–25 µm long by 3–9 µm diameter. Cell fusions are abundant, frequently occupying most of the wall of adjoining cells (Figs. 9, 12). Lower cells of cortical filaments and cells of medullary filaments often contain numerous starch bodies. Individual probable trichocytes are sometimes observed in scanning electron microscopy (Fig. 13), but have not been seen in sectioned material. It is likely that these probable trichocytes are very uncommon as well as scattered and that this is the reason they have not been observed in sections. This is only the second reporting (see Keats and Chamberlain, 1997 — S. magellanicum) of trichocytes for the genus Synarthrophyton. Subepithallial initials are elongate, measuring 7–13 µm long by 4–7 µm in diameter, with each being usually as long as, or longer than, the cell subtending it (Figs. 9, 12). Epithallial ce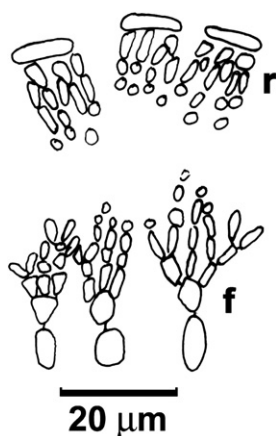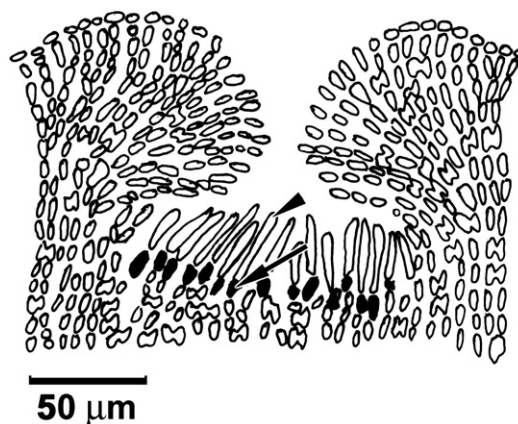lls occur in a single layer. They vary from a rounded to an elongately-domed shape (Figs. 9, 12) and measure 5–9 µm long by 6–9 µm in diameter. The surface of epithallial cells under the SEM shows thick lateral walls with the outer wall usually sunken into an epithallial concavity (Fig. 14).

2.8. Reproduction

Gametangial plants are dioecious. Male conceptacles project as domes or may be flush with the surrounding thallus (Fig. 15). Their chambers are elliptical, and measure 145–225 µm in diameter by 30–55 µm high, with the roof c. 60–65 µm thick (Figs. 16, 17). The roof is formed from filaments that arise peripheral to the fertile area and which have terminal initials that elongate more rapidly than surrounding cells. As they divide, the forming filaments curve inwards to form the roof and pore, with the terminal initials becoming papillae that project into the pore in fully developed conceptacles. Spermatangial systems develop on the floor, walls and roof of the conceptacle (Fig. 17). Those on the floor are branched, while those on the walls and roof vary from simple to slightly branched (Fig. 18). Protective cells occur above spermatangial initials in young conceptacles (Figs. 19, 20). Carpogonial conceptacles are dome-shaped to conical and measure 210–360 µm in external diameter. Their chambers vary from elliptical to flattened, and measure 118–

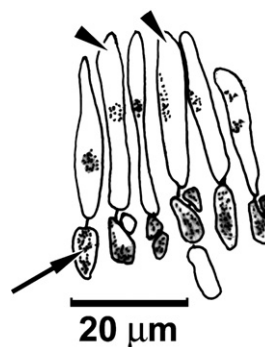Fig. 18. Spermatangial systems from the roof (r) and floor (f) of a mature male conceptacle.

Fig. 20. Detail of protective cells (arrowheads) above spermatangial initials (arrow) from Fig. 19.
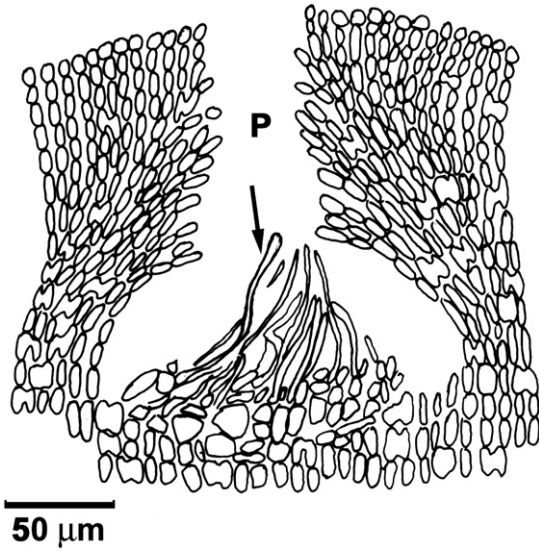
Fig. 21. VS of a carpogonial conceptacle showing roof and pore canal (P) structure and the distribution of the carpogonial branches (arrow) across the conceptacle floor.

Fig. 23. VS of a mature carposporangial conceptacle showing the more-or-less discoid fusion cell (f) with peripheral gonimoblast filaments (g) terminating in carposporangia (c).

200 µm in diameter by 45–80 µm high, with the roof 78–115 µm (7–10 cells) thick (Fig. 21). The roof is formed as described for male conceptacles, and the pore is lined by papillae. Carpogonial branches develop across the floor of the conceptacle, and may comprise one to several supporting cells and a hypogynous cell bearing a carpogonium extended into a trichogyne (Figs. 21, 22). Sometime, no supporting cells are visible (Fig. 21). A sterile cell may also be present on the hypogynous cell. After presumed karyogamy a few carpogonial remnants persist in the centre of the conceptacle floor. As carposporangia mature, the conceptacles become markedly conical, measuring 265–375 µm in external diameter and bear elliptical chambers that measure 200–265 µm in diameter by 100–170 µm high, with roofs 60–100 µm in thickness (Fig. 23).

The fusion cell appears flattened and discoid, and more-or-less continuous in vertical section, with 5–6 celled gonimoblast filaments (incl. a terminal carporangium) developing from the periphery, often clustered in groups of 2–3 in sections (Fig. 23). Gonimoblast filaments terminate in a carposporangium that measures 35–60 µm long by 30–50 µm in diameter at maturity.

Tetrasporangial plants have conceptacles that are distributed over the entire dorsal surface of the thallus as well as on the protuberances. On protuberances, conceptacles occur in high densities and subsequently may often become partially fused (Fig. 6). They are low domed and measure 200–500 µm in external diameter (Fig. 24). Bisporangia were not seen. Conceptacle initiation occurs superficially in a layer of thallus cells immediately below the subepithallial initial (Fig. 25), and the layer containing the epithallial cells and subepithallial initials is shed early in development. Chambers are circular to somewhat elliptical (Figs. 26, 27), and measure 130–215 µm in diameter by 110–150 µm high with the roof 37–43 µm thick.
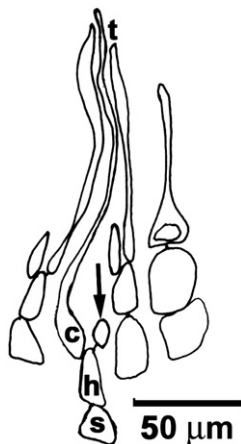

Fig. 22. Individual carpogonial branches showing carpogonia (c) extended into trichogynes (t), hypogynous cells (h), supporting cells (s) and sterile cells (arrow).
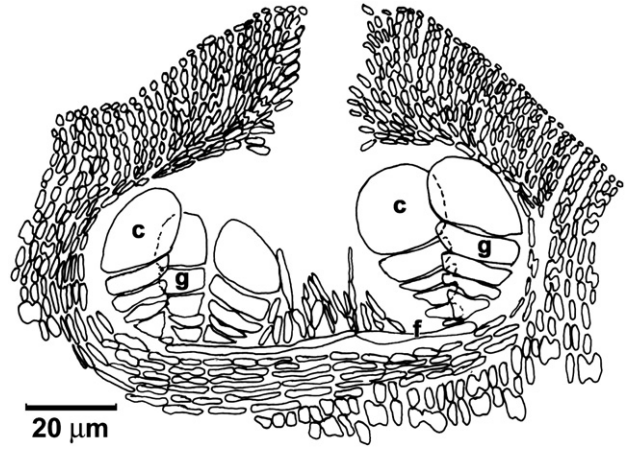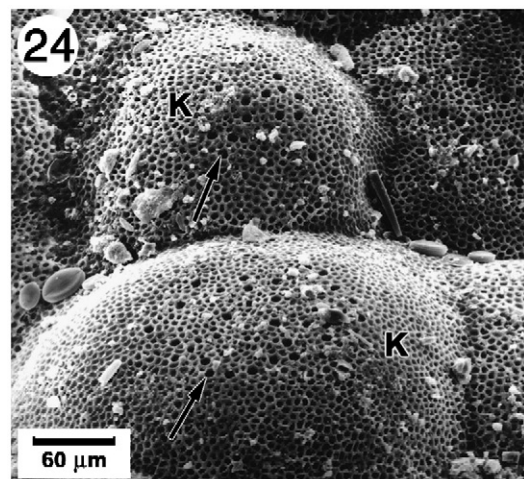

Fig. 24. Surface of two multiporate (arrows) tetrasporangial conceptacles (K).
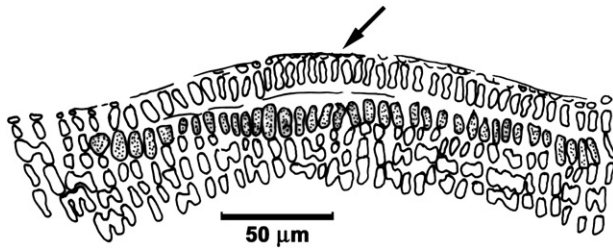
Fig. 25. Conceptacle primordium showing tetrasporangial initials (stippled) and a shedding layer (arrow) of subepithallial initials and epithallial cells.

Fig. 27. Mature tetrasporangial conceptacle showing zonately divided tetrasporangia (t) and roof structure consisting of a more-or-less flat pore plate with pores and pore plugs (P).

The roof is formed from filaments interspersed among the sporangia (Fig. 28). The lower segments of these filaments degenerate, leaving a roof composed of 4–6 cells including an epithallial cell that is sometimes missing (Figs. 26, 27). Roofs are perforated by 16–32 pores (Fig. 24) that measure 7–8 μm in diameter, and that contain pore plugs (Fig. 29). Pores are surrounded by 6–8 rosette cells that are flush with the epithallial cells of the surrounding roof (Fig. 30). The cells of the filaments lining the pore canal are rectangular to elongate (i.e. when the long axis of the cell is notably more than twice the length of the short axis) and not markedly different from the cells that make up the rest of the roof, each terminating in a rounded epithallial cell (Figs. 29, 31). Pore canals measure 37–40 μm long by 5–9 μm in diameter. Tetrasporangia measure 80–115 μm long by 25–60 μm in diameter (Fig. 27). Old conceptacles persist and become buried in the thallus on senescence, but are not in-filled, and often contain a full complement of intact sporangia. Tetrasporangial and gametangial conceptacles are often found on what is apparently the same thallus, and may appear next to one another in sections.

3. Discussion

The genus *Synarthrophyton* was erected by Townsend (1979) and has been reassessed a number of times since (see May and Woelkerling, 1988; Woelkerling, 1988; Woelkerling and Foster, 1989; Harvey et al., 1994). At present, the following seven characters collectively delimit *Synarthrophyton* from all

other genera belonging to the Melobesioideae (Harvey et al., 1994): 1) thallus not arborescent in growth form; 2) haustoria absent; 3) outermost walls of epithallial cells rounded or flattened but not flared; 4) actively dividing subepithallial initials as long or longer than their immediate inward derivatives; 5) tetrasporangia bearing apical plugs and borne within multiporate conceptacles; 6) spermatangial initials overlain by a layer of protective cells; and 7) dendroid, or both dendroid and simple spermatangial systems present. All the above characters are present in the taxon described here and clearly it fits within the generic delimitation of the genus *Synarthrophyton*.

Two studies (Keats and Chamberlain, 1997; Keats and Maneveldt, 1997) have highlighted the variable nature of the branched spermatangial systems in the southern African species ascribed to the genus *Synarthrophyton*. These authors suggested that there appears to be a gradation between the simple spermatangial systems seen in the type of the genus *Mesophyllum* [*M. lichenoides* (Ellis) Lemoine (Woelkerling and Irvine, 1986;
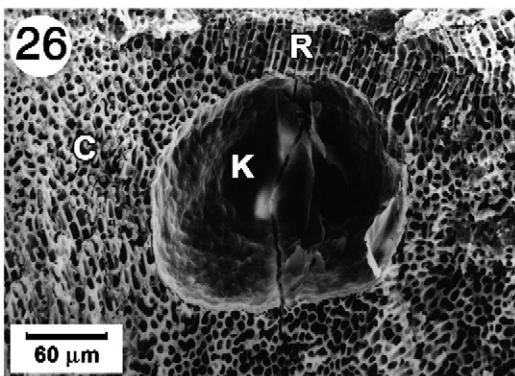

Fig. 26. Vertical fracture of the outer cortex (C) through the chamber (K) of a tetrasporangial conceptacle showing a more-or-less flat roof (R), lacking raised rims.
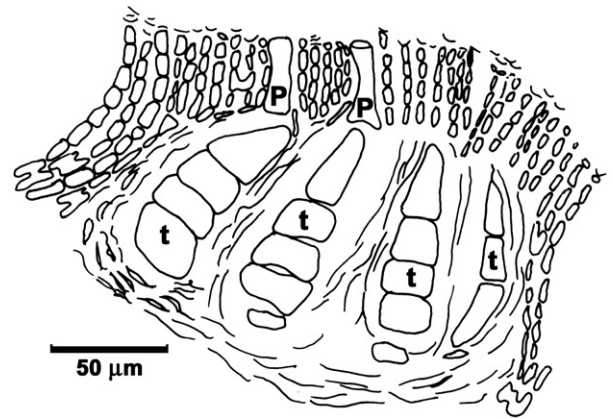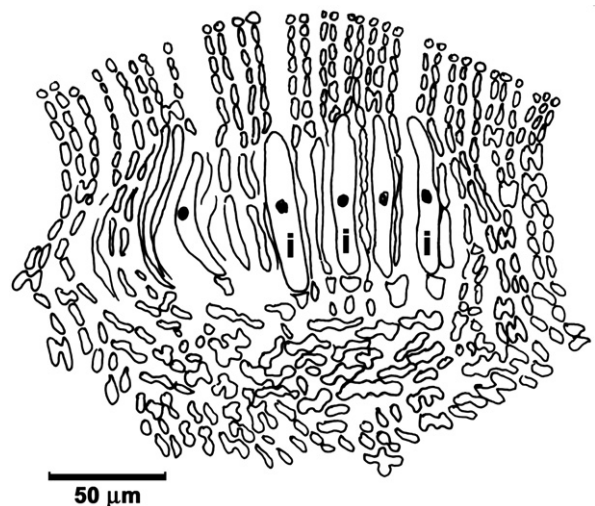

Fig. 28. Young tetrasporangial conceptacle with sporangial initials (i) clearly visible.
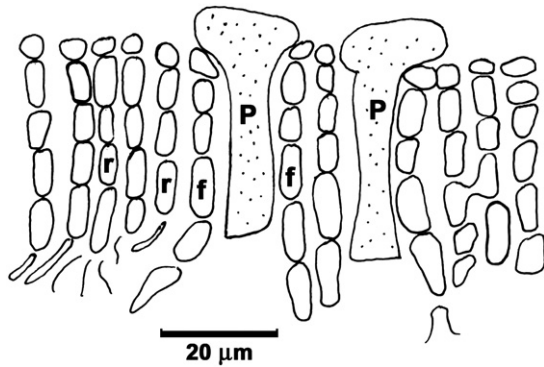
Fig. 29. VS of pore plate showing intact pore plugs (P), roof filaments (r) and filaments lining the pore canal (f).
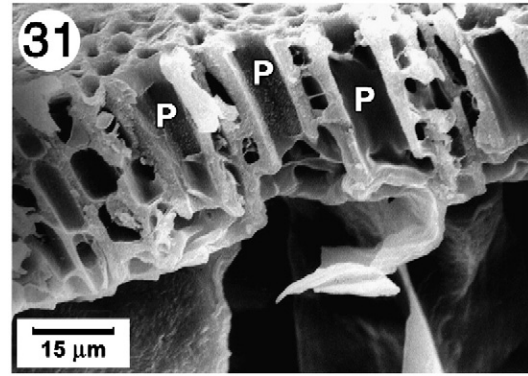

Fig. 31. Vertical fracture through a tetrasporangial conceptacle pore plate showing a number of pore canals (P).

Fig. 31)], to the more complex, branched system of the type of *Synarthrophyton* [*S. patena* (Hooker et Harvey) Townsend (May and Woelkerling, 1988; Figs. 35–38)] and a diagram depicting the degree of elaboration of spermatangial systems was produced (see Keats and Maneveldt, 1997). Keats and Chamberlain (1997) continued by stating that the demarcation between these genera may have to be reassessed when data from further species are available. While this study documents a new species of *Synarthrophyton* from southern Africa, we have not shed any light on this debate as *S. papillatum* possesses a spermatangial system within the range of those already described from southern Africa, being very similar to that of *S. magellanicum* (see Keats and Chamberlain, 1997).

Of 10 species now ascribed to the genus *Synarthrophyton* (Table 1), a genus with a predominantly Southern Hemisphere distribution (one record from the northern hemisphere — see Kim et al., 2004), six are now known from southern Africa: *S. eckloniae* (Foslie) Keats et Chamberlain (Keats and Chamberlain, 1997), *S. magellanicum* (Foslie) Keats et Chamberlain (Keats and Chamberlain, 1997), *S. munimentum* Keats et Maneveldt (Keats and Maneveldt, 1997), *S. robbe-*

Fig. 30. Detail of a tetrasporangial conceptacle pore plate showing pores (P) surrounded by rosette cells (r). Note that the rosette cells are flush with the surrounding roof surface.

nense Keats et Maneveldt (Keats and Maneveldt, 1997), *S. papillatum* and *S. patena* (Hooker et Harvey) Townsend (Townsend, 1979). *Synarthrophyton eckloniae* and *S. patena* have only been found as epiphytes in South Africa, although Harvey et al. (1994) have found *S. patena* growing both epiphytically and epilithically in southern Australia. The remaining taxa are predominantly epilithic. *Synarthrophyton papillatum* differs from *S. munimentum* and *S. robbenense* in lacking raised rims and bearing sunken pore plates on the tetrasporangial conceptacles, and from *S. magellanicum* in bearing minutely warty to fruticose protuberances and generally lacking the layered to leafy, weakly attached smooth thalli present in the latter species.

Of the remaining three species with a Southern Hemisphere affinity, *S. schielianum* Woelkerling et Foster (Woelkerling and Foster, 1989; see also Harvey et al., 2005) has only been recorded from the Chatham Islands off New Zealand. Woelkerling and Foster (1989, Table 2) tabulated the differences between *S. patena* and *S. schielianum* and data from their table have been incorporated to show the differences between the currently known species of *Synarthrophyton* (Table 1). Another reported Southern Hemisphere species, *S. schmitzii* (Hariot) Mendoza, Molina et Ventura (Mendoza et al., 1996) has been recorded from various Argentinean territories. Mendoza et al. (1996; 56) lists *Lithothamnion magellanicum* Foslie (Foslie, 1895; 8, basionym of *S. magellanicum*) as a heterotypic synonym of *S. schmitzii*. As *S. schmitzii* was described first, this should render *S. magellanicum* (Foslie) Keats et Chamberlain (Keats and Chamberlain, 1997) superfluous and thus illegiti-mate. However, Mendoza et al. (1996) failed to provide a full description of the type of *S. schmitzii*, or even a comparative analysis of those taxa (incl *L. magellanicum*) they considered to be heterotypic synonyms. Their conclusions must therefore be considered with a degree of skepticism. Furthermore, Mendoza et al. (1996) have not provided sufficient data for even a comparative analysis of the Argentinean material with the rest of those taxa ascribed to the genus *Synarthrophyton* (see Table 1). In their descriptions, Keats and Chamberlain (1997) indicated that the final generic placement of *L. schmitzii* (Hariot, 1895: 98, basionym of *S. schmitzii*) cannot be ascertained until the TRH (syntype, Woelkerling, 1993; 198:
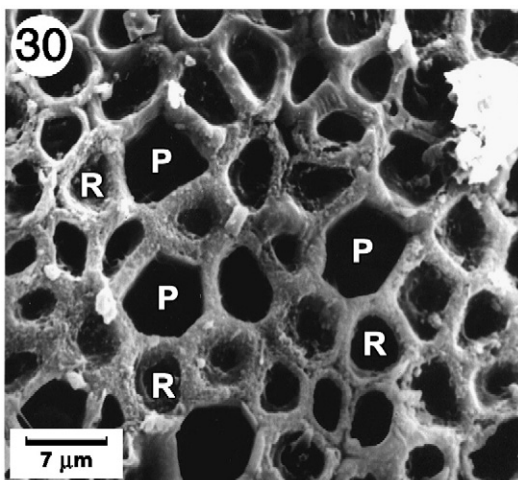
Table 1
A comparison of recently documented species of *Synarthrophyton* based on selected characters (after Keats and Maneveldt, 1997)

Character	S. papillatum (this study)	S. chejuensis [a]	S. eckloniae [b]	S. magellanicum [b]	S. munimentum [c]	S. patena [d, e]	S. pseudosorus [e]	S. robbenense [c]	S. schmitzii [f]	S. schielianum [g]
Growth form	Encrusting, warty to fruticose	Discoid, encrusting, to layered (leafy)	Encrusting	Encrusting to layered (leafy)	Encrusting to warty	Encrusting, discoid, warty, fruticose to layered (leafy)	Encrusting to layered (leafy)	Encrusting, warty	Encrusting to layered (leafy)	Encrusting to layered (leafy)
Protuberances	Present, minutely papillate	Absent	Absent	Absent	Rare, narrow when present	Present or absent	Largely absent	Low, narrow, fused into scrolled patterns	Absent	Absent
Struts	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Present
Substrata	Mostly epilithic, but also epizoic	Sometimes epilithic, mainly epiphytic	Epiphytic on stipes of *Ecklonia maxima*	Epilithic and epizoic	Epilithic and epizoic & epiphytic on kelp holdfasts	Sometimes epilithic, mainly epiphytic	Epiphytic and epizoic	Epilithic and epizoic	Epilithic and epizoic	Mainly epizoic, also epilithic and epiphytic
Trichocytes	Rare	Absent	Absent	Common	Absent	Absent	Absent	Absent	ND	ND
Form of tetra/bisporangial conceptacle	Mound-like with a domed pore plate	Flush or mound-like with a more-or-less flattened pore plate	Flush or sunken below surface with flattened pore plate	Mound-like with a flattened pore plate	Volcano-like with a peripheral rim and central, depressed pore plate	Mound-like with a domed to flattened pore plate	Mound-like with a domed to flattened pore plate	Mound-like with a peripheral rim and central, depressed pore plate	ND	Volcano-like with a peripheral rim and central, depressed pore plate
Tetra/bisporangial conceptacle roof filaments	Uniform in structure	Uniform in structure	Uniform in structure	Uniform in structure	More or less uniform in structure	Uniform in structure	Uniform in structure	Of two distinct types	ND	Of two distinct types
Cell shape in tetra/bisporangial conceptacle roof	Rectangular to elongate in all filaments	Rectangular to elongate in all filaments	Elongate in all filaments	Elongate in all filaments	Rectangular to elongate in all filaments	More or less square or broader than long in all filaments	More or less square or broader than long in all filaments	Elongate in all filaments, but also square in pore plate filaments	ND	Elongate in all filaments, but also square in pore plate filaments
Tetra/bisporangial conceptacle external diameter	200–500	up to 780	up to 600	270–620	475–900	750–1300	ND	185–300	ND	ND
Tetra/bisporangial conceptacle chamber diameter	130–215	210–340	c. 300	200–325	350–450	160–560	140–195 (up to 2000 when fused)	140–220	370–550	420–815
Thickness of tetra/bisporangial conceptacle roof	37–43	25–40	40–78	20–50	41–55	18–45(68)	25–52?	12–25	ND	ND
Number of cells in tetra/bisporangial conceptacle roof filaments	4–6	4–6	5–7	4–6	5–7	3–8	4–5	3–4	ND	4–7
Rosette cell position with respect to surrounding roof	Flush	Flush	Flush	Flush	Sunken	Flush	Flush	Tilted inwards, but not sunken	ND	Flush

Table 1 (*continued*)

Character	*S. papillatum* (this study)	*S. chejuensis* [a]	*S. eckloniae* [b]	*S. magellanicum* [b]	*S. munimentum* [c]	*S. patena* [d, e]	*S. pseudosorus* [e]	*S. robbenense* [c]	*S. schmitzii* [f]	*S. schielianum* [g]
Epithallial cells on tetra/bisporangial conceptacle pore plate filaments	Present	Present	Present	Present	Present	Present	Present	Present	ND	Absent
Initials of tetra/bisporangial conceptacle roof filaments	Longer than broad	Longer than broad	Longer than broad	Longer than broad	Variable, but not enlarged	Square or broader than long	Square or broader than long	Commonly enlarged somewhat	ND	Longer than broad
Tetra/bisporangial conceptacle fusion	Common	Abundant	Common	Common	Common	Occasional	Very abundant	Not observed	ND	Rare
Occurrence of tetra/bisporangia and dimensions (L=length; D=diameter)	Only tetrasporangia (L=80–115; D=25–60) seen	Tetra- and bisporangia (L=50–110; D=ND) seen	Only bisporangia (L=78–130; D=52–104) seen	Only tetrasporangia (L=80–117; D=27–56) seen	Tetra- and bisporangia (L=120–185 (275); D=40–110) seen	Only tetrasporangia (L=70–250; D=30–110) seen	Only tetrasporangia (L=55–95; D=30–70) seen	Tetra- and bisporangia (L=35–120; D=15–60) seen	ND	Only tetrasporangia (L=160–200; D=50–90) seen
Gametangial thalli	Dioecious	Monoecious or dioecious	Monoecious	Monoecious or dioecious	Monoecious	Dioecious	Dioecious	Dioecious	ND	Dioecious?
Shape of hypogynous cells of carpogonial filaments	Rectangular to elongate	Squarish	Elongate	Elongate	Squarish to rectangular	More or less globular or ovoid; not markedly elongate	ND	Rectangular to elongate	ND	Cylindrical and more or less elongate
Shape of fusion cell	Discoid and continuous	Discoid and discontinuous	Absent/discontinuous?	Discoid and discontinuous	More or less discoid and discontinuous	More or less discoid and discontinuous	More or less discoid and discontinuous	Discoid and discontinuous	ND	'Arachnoid' [h] to discontinuous
No. of cells in gonimoblast filament (incl. terminal carposporangium)	5–6	4–5	3–7	4–5	4–8	4–7?	7–11?	3–6	5?	4?
Cell shape in roof filaments of male conceptacles	Elongate	Square to elongate	Narrow and elongate	Narrow and elongate	Commonly narrow and elongate	Mostly more or less square	Square to elongate	Commonly narrow and elongate	ND	Commonly narrow and elongate
Occurrence of inflated cells among spermatangial systems	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	ND	Present

All measurements are in micrometres; ND = no data available; ? = data is combined with that observed in figures from the relevant publications.

[a] Kim et al. (2004).
[b] Keats and Chamberlain (1997).
[c] Keats and Maneveldt (1997).
[d] Townsend (1979), May and Woelkerling (1988), Harvey et al. (1994).
[e] Harvey et al. (2003).
[f] Mendoza et al. (1996).
[g] Woelkerling and Foster (1989) and Harvey et al. (2005).
[h] Described as spidery by Woelkerling and Foster (1989).

isolectotype, Keats and Chamberlain, 1997; 68) specimen is examined, but they had concluded that the two species are distinct. Until such time that the TRH material is examined, or new material is collected from the type locality, the disposition of *S. schmitzii* may remain unresolved (see also Woelkerling et al., 2005; 472).

The most recently described Southern Hemisphere species of *Synarthrophyton*, *S. pseudosorus* Harvey (Harvey et al., 2003) was recorded from New South Wales, Australia. This species is unlike any recorded thus far, and although being superficially similar to *S. magellanicum* and *S. patena* (Harvey et al., 2003; see also Table 1), this species differs from all taxa ascribed to the genus *Synarthrophyton* by possessing both discrete and, in particular, numerous scrolls of fused, sorus-like groups of sporangial conceptacles.

Until recently, it was thought that the genus *Synarthrophyton* was restricted to the Southern Hemisphere. One taxon, *S. chejuensis* Kim, Chung, Choi et Lee (Kim et al., 2004) has, however, been recorded from the Northern Hemisphere (Cheju Island, Korea). Based on the description of this new species (Kim et al., 2004) it appears that it is an epiphytic form of *S. magellanicum* (see Table 1). The only real differences between the two taxa are the substrata on which they occur, and the proposed unique fusion between adjacent sporangial conceptacles. While *S. chejuensis* is described as being predominantly epiphytic, Kim et al. (2004) have recorded epilithic individuals. Similarly, Keats and Chamberlain (1997; 62) have recorded the free margins of lamellae of *S. magellanicum* overgrowing other non-geniculate corallines and even foliose algae, suggesting a possible epiphytic habit. While Kim et al. (2004) include conceptacle fusion prominence as another characterizing feature of *S. chejuensis*, this feature is by no means unique to this species, as densely crowded conceptacles often become fused. Such fusion has been observed in a number of species (see Table 1) including *S. magellanicum* (pers. obs.) and even more so in the sorus-like clusters of fused tetrasporangial conceptacles observed in *S. pseudosorus* (Harvey et al., 2003). What is perhaps less common, is the degree to which entire pore plates may become fused in *S. chejuensis*. But, this too could simply be a consequence of overcrowding by sporangial conceptacles.

Based on the information contained in Table 1, *S. papillatum* most closely resembles *S. magellanicum*, followed by *S. chejuensis* and *S. munimentum*. These taxa share by far the most number of sporangial and gametangial characters with *S. papillatum*. Also, *S. papillatum* and *S. magellanicum* are the only known species of *Synarthrophyton* in which trichocytes have been recorded. *Synarthrophyton papillatum* differs from *S. magellanicum* in bearing minutely warty to fruticose protuberances and lacking the layered to leafy, smooth thalli; from *S. chejuensis* in being predominantly epilithic, not epiphytic, and in lacking discoid to layered to leafy thalli and; from *S. munimentum* in possessing mound-like sporangial conceptacles with domed pore plates as opposed to volcano-like sporangial conceptacles with peripheral rims and centrally depressed pore plates.

Southern African specimens of *Synarthrophyton* can be identified by the following key. This key is designed for southern

African specimen identification only and the ecological characters used in the key are not necessarily diagnostic of the species to which they pertain.

1. Thalli known only as epiphytes……………………………..……... **2**
   Thalli predominantly epilithic or epizoic……………………..….… **3**
2. Only known as epiphytes on *Ecklonia*; sporangial conceptacles almost flush with the surrounding thallus surface, with slightly raised rims and slightly sunken mature pore plates. ……………..……………………………………..……………………….. *S. eckloniae*
   Epiphytic mainly on *Gelidium*, not known to occur on *Ecklonia*; sporangial conceptacles raised above surrounding thallus surface, with domed roofs …..……………..………… *S. patena*
3. Thalli commonly leafy, frequently forming many thin, weakly adherent overlapping lamellae that often build up in layers; sporangial conceptacles raised with flattened roofs …………………………………………………………………. *S. magellanicum*
   Thalli smooth to warty to minutely papillate, strongly adherent; sporangial conceptacles raised with domed or sunken pore plates …………………………………………………………..……… **4**
4. Thalli smooth to warty; sporangial conceptacles with sunken pore plates …………..……….………….…...…....…….……....... **5**
   Thalli warty to minutely papillate; sporangial conceptacles with domed pore plates; plants usually occurring on intertidal polychaete tubes…………..…………………....………...... *S. papillatum*
5. Thalli smooth to occasionally warty, not forming scrolled structures; sporangial conceptacles large (475–900 μm external diam.), volcano-like with high rims and deeply depressed pore plates…………………………………..…….………….....… *S. munimentum*
   Thalli warty, protuberances forming scrolled structures; sporangial conceptacles small (185–300 μm external diam.), with shallowly depressed pore plates ……..……..... *S. robbenense.*

Acknowledgements

References

Adey, W.H., 1978. Algal ridges of the Caribbean Sea and West Indies. Phycologia 17, 361–367.

Adey, W.H., Adey, P.J., 1973. Studies on the biosystematics and ecology of the epilithic crustose Corallinaceae of the British Isles. British Phycological Journal 8, 343–407.

Adey, W.H., MacIntyre, I.G., 1973. Crustose coralline algae: a re-evaluation in the geological sciences. Bulletin of the Geological Society of America 84, 883–904.

Adey, W.H., Townsend, R.A., Boykins, W.T., 1982. The crustose coralline algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands. Smithsonian Contributions to the Marine Sciences 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*. British Phycological Journal 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., Norris, R., 1994. *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., Keats, D.W., Maneveldt, G., 1995. *Clathromorphum tubiforme* sp. nov. (Rhodophyta, Corallinaceae) in South Africa with comments on generic characters. Botanica Marina 38, 443–454.

Foslie, M., 1895. New or critical lithothamnia. Det Kongelige Norske Videnskabers Selskabs Skrifter 1–10.

Hariot, P., 1895. Nouvelle contribution a l'étude des algues de la région magellanique. Journal de Botanique 9, 95–99.

Harvey, A.S., Woelkerling, Wm.J., Wilks, K.M., 1994. The genus *Synarthrophyton* (Corallinaceae Rhodophyta) in southern Australia. Phycologia 33, 331–342.

Harvey, A.S., Woelkerling, Wm.J., Miller, A.J.K., 2003. An account of the Hapalidiaceae (Corallinales, Rhodophyta) in south-eastern Australia. Australian Systematic Botany 16, 647–698.

Harvey, A., Woelkerling, W., Farr, T., Neill, K., Nelson, W., 2005. Coralline algae of central New Zealand: an identification guide to common 'crustose' species. NIWA Information Series, vol. 57. NIWA, Wellington, p. 145.

Keats, D.W., Chamberlain, Y.M., 1993. *Sporolithon ptychoides* Heydrich and *S. episporum* (Howe) Dawson: two crustose coralline red algae (Corallinales, Sporolithaceae) in southern Africa. South African Journal of Botany 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. South African Journal of Botany 60, 8–21.

Keats, D.W., Chamberlain, Y.M., 1994b. Two melobesioid coralline algae (Rhodophyta, Corallinales), *Mesophyllum erubescens* (Foslie) Lemoine and *Mesophyllum funafutiense* (Foslie) Verheij from Sodwana Bay, South Africa. South African Journal of Botany 60, 175–190.

Keats, D.W., Chamberlain, Y.M., 1997. The non-geniculate coralline algae *Synarthrophyton eckloniae* (Foslie) comb. nov. and *S. magellanicum* (Foslie) comb. nov. (Rhodophyta) in South Africa including comparison with relevant types. European Journal of Phycology 32, 55–79.

Keats, D.W., Maneveldt, G., 1994. *Leptophytum foveatum* Chamberlain & Keats (Rhodophyta, Corallinales) retaliates against competitive overgrowth by other encrusting algae. Journal of Experimental Marine Biology and Ecology 175, 243–251.

Keats, D.W., Maneveldt, G., 1997. Two new melobesioid algae (Corallinales, Rhodophyta), *Synarthrophyton robbenense* sp. nov. and *S. munimentum* sp. nov., in South Africa and Namibia. Phycologia 36, 447–467.

Keats, D.W., Groener, A., Chamberlain, Y.M., 1993. Cell sloughing in the littoral zone coralline alga, *Spongites yendoi* (Foslie) Chamberlain (Corallinales, Rhodophyta). Phycologia 32, 143–150.

Keats, D.W., Matthews, I., Maneveldt, G., 1994a. Competitive relationships and coexistence in a guild of crustose algae in the eulittoral zone, Cape Province, South Africa. South African Journal of Botany 60, 108–113.

Keats, D.W., Wilton, P., Maneveldt, G., 1994b. Ecological significance of deep-layer sloughing in the eulittoral zone coralline alga, *Spongites yendoi* (Foslie) Chamberlain (Corallinaceae, Rhodophyta) in South Africa. Journal of Experimental Marine Biology and Ecology 175, 145–154.

Keats, D.W., Maneveldt, G., Chamberlain, Y.M., 2000. *Lithothamnion superpositum* Foslie: a common crustose red alga (Corallinaceae) in South Africa. Cryptogamie. Algologie 21, 381–400.

Kim, J.H, Chung, H., Choi, D.S., Lee, I.K., 2004. A new Melobesioid alga *Synarthrophyton chejuensis* sp. nov. (Corallinales, Rhodophyta), including comparison with *Mesophyllum cystocarpideum*. Phycologia 43, 501–520.

Lee, R.K.S., 1967. Taxonomy and distribution of the Melobesioid algae on Rongelap Atoll, Marshall Islands. Canadian Journal of Botany 45, 985–1001.

Littler, M.M., 1973. The productivity of Hawaiian fringing-reef crustose Corallinaceae and an experimental evaluation of production methodology. Limnology and Oceanography 18, 946–952.

Littler, D.S., Littler, M.M., 2000. Caribbean Reef Plants. OffShore Graphics, Washington, p. 542.

Littler, D.S., Littler, M.M., 2003. South Pacific Reef Plants. OffShore Graphics, Washington, p. 331.

Maneveldt, G.W., Wilby, D., Potgieter, M., Hendricks, M.G.J., 2006. The role of encrusting coralline algae in the diets of selected intertidal herbivores. Journal of Applied Phycology 18, 619–627.

May, D.I., Woelkerling, Wm.J., 1988. Studies on the genus *Synarthrophyton* (Corallinaceae, Rhodophyta) and its type species, *S. patena* (J.D. Hooker et W.H. harvey) Townsend. Phycologia 26, 50–71.

Mendoza, M.L., Molina, S., Venura, P., 1996. Flora Cryptogamica de Tierra del Fuego. Corallinales (Rhodophyta), vol. 8 (3). Sigma, Buenos Aires, p. 77.

Steneck, R.S., 1986. The ecology of coralline algal crusts: convergent patterns and adaptive strategies. Annual Review of Ecology and Systematics 17, 273–303.

Taylor, W.R., 1942. Caribbean marine algae of the Allan Hancock Expedition,1939. Allan Hancock Atlantic Expedition Report, vol. 2, pp. 1–193.

Taylor, W.R., 1945. Pacific marine algae of the Allan Hancock expeditions to the Galapagos Islands. Allan Hancock Pacific Expeditions, vol. 12, pp. 1–528.

Taylor, W.R., 1950. Plants of Bikini and other Northern Marshall Islands. University of Michigan Press, Ann Arbor, Michigan, p. 218.

Taylor, W.R., 1960. Marine algae of the eastern tropical and subtropical coasts of the Americas. University of Michigan Press, Ann Arbor, Michigan, p. 860.

Townsend, R.A., 1979. Synarthrophyton, a new genus of Corallinaceae (Cryptonemiales, Rhododphyta) from the Southern Hemisphere. Journal of Phycology 15, 251–259.

Woelkerling, Wm. J.,1988. The Coralline Red Algae: An Analysis of the Genera and Subfamilies of Nongeniculate Corallinaceae. British Museum (Natural History) and Oxford University Press, Oxford, pp. 268.

Woelkerling, Wm.J., 1993. Type collections of Corallinales (Rhodophyta) in the Foslie Herbarium (TRH). Gunneria 67, 1–289.

Woelkerling, Wm.J., Foster, M.S., 1989. A systematic and ecographic account of *Synarthrophyton schielianum* sp. nov. (Corallinaceae, Rhodophyta) from the Chatham Islands. Phycologia 28, 39–60.

Woelkerling, Wm.J., Irvine, L.M., 1986. The neotypification and status of *Mesophyllym* (Corallinaceae, Rhodophyta). Phycologia 25, 379–396.

Woelkerling, Wm.J., Lamy, D., 1998. Non-geniculate coralline red algae and the Paris museum: Systematics and scientific history. Publications Scientifiques du Muséum/ADAC, Paris, p. 767.

Woelkerling, Wm.J., Irvine, L.M., Harvey, A.S., 1993. Growth-forms in Non-geniculate Coralline Red Algae (Corallinales, Rhodophyta). Australian Systematic Botany 6, 277–293.

Woelkerling, Wm.J., Gustavsen, G., Myklebost, H.E., Prestø, T., Såstad, S.M., 2005. The coralline red algal herbarium of Mikael Foslie: revised catalogue with analysis. Gunneria 77, 1–627.