Sporolithon ptychoides Heydrich and *S. episporum* (Howe) Dawson: two crustose coralline red algae (Corallinales, Sporolithaceae) in South Africa

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Received 16 June 1993; accepted 27 July 1993

The crustose coralline red alga, *Sporolithon ptychoides* Heydrich, is recorded from tide pools, subtidal surge channels, and on rock substrate on the southernmost coral reefs in the western Indian Ocean, at Sodwana Bay National Park, Natal Province, South Africa. *Sporolithon episporum* (Howe) Dawson is reported from large tide pools, surge channels, and shallow subtidal rocks subjected to sand scour and inundation in the same area, as well as from the south-western Cape Province. The material of *S. episporum* is compared with the type specimen, and the latter is described and illustrated. The two species are distinguished on the basis of cell connections and the burying of sporangia. *Sporolithon ptychoides* has both cell fusions and secondary pit connections, and sporangia buried in distinct rows. *Sporolithon episporum* has secondary pits but not cell fusions, and generally sheds old sporangia.

Die korsagtige koralloïde rooialg, *Sporolithon ptychoides* Heydrich, is aangeteken in getypoele, subgety-stukanale, en op rotssubstraat op die mees suidelike koraalriwwe in die westelike Indiese Oseaan by Sodwanabaai Nasionale Park, Natal, Suid-Afrika. *Sporolithon episporum* (Howe) Dawson kom in dieselfde gebied voor in groot getypoele, stukanale en vlak subgety-rotse wat deur sand weggevreet en oorspoel word, asook in die suid-westelike Kaapprovinsie. Die *S. episporum* materiaal word met die tipe-eksemplaar vergelyk, en laasgenoemde word beskryf en geïllustreer. Die twee spesies word onderskei op grond van selverbindings en die gesonke sporangiums. *Sporolithon ptychoides* het beide selversmelting en sekondêre stippelverbindings, en sporangiums wat in duidelike rye gesonke is. *Sporolithon episporum* het sekondêre stippels, maar geen selversmeltings nie, en werp ou sporangiums gewoonlik af.

Keywords: *Sporolithon ptychoides, Sporolithon episporum*, crustose coralline red alga, South Africa

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Introduction

Crustose coralline algae are important in the structure and ecology of coral reefs (Adey & MacIntyre 1973; Adey 1979; Adey *et al.* 1982). The southern-most coral reef system in the western Indian Ocean, at Sodwana Bay, Natal Province, South Africa, is conserved as part of the St. Lucia Marine Reserve. Except for the recent publication of Chamberlain (1993) giving details of three species which occur at Sodwana, the crustose coralline algae of this system are unknown, and further, there is no documentation of the flora for any of the related reefs in southern Mozambique. Indeed, no modern study of the coralline flora has been undertaken for any area of the western Indian Ocean.

The Sodwana Bay reefs are among the most southerly coral reefs in the world (Ramsay & Mason 1990). They occur as a series of patch reefs running parallel to the coast, and are composed of corals growing on sandstone rock of late Pleistocene dune and beach sequence (Ramsay & Mason 1990). Coralline algae are abundant in the reef system, and occur attached to sandstone rock, old coral, living coral, and as epiphytes, as well as in the adjacent rocky intertidal zone (Keats, pers. observ.).

We have therefore undertaken to study the crustose coralline algal flora of Sodwana Bay National Park, as part of a larger study of South African corallines (Chamberlain 1993), and to present detailed descriptions of all species to serve eventually as an identification guide for phycologists and ecologists. Each species which is common enough on the reef to be collected, will be described and illustrated in sufficient detail for it to be identified by non-specialist ecologists. General keys will be provided when descriptions of individual taxa have been reported. In this paper we report on the genus *Sporolithon*.

The taxonomy of the crustose coralline genus *Sporolithon* at the species level is confused, and it is very difficult to assign most collections to any recognized species (Woelkerling 1988), although recent studies are beginning to clarify species concepts within the genus (Verheij 1992, 1993). Dawson (1960) attempted to compose a worldwide key to the species, but this is based mainly on such external characters as habit and branching, characters which have since been shown to be unreliable (Verheij 1993). Dawson (1960) pointed out that vegetative and reproductive anatomical characteristics were poorly known. Despite a few better documented descriptions (e.g. Adey *et al.* 1982; Verheij 1992, 1993), the situation has improved only slightly since 1960 (Woelkerling 1988). In this paper we present observations, data and detailed descriptions of two species of *Sporolithon* from South Africa.

Materials and Methods

Material was collected from the subtidal zone and large tide pools 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 2 – 3 min in a 5000-V Edwards S150B sputter coater, and examined with a Hitachi X650 scanning electron microscope, equipped with a Mamiya 6×7 camera. Accelerating voltage was 20 kV initially, but was later increased to 25 kV for improved resolution.

For light microscopy, formalin-preserved specimens were first decalcified in 10% nitric acid, and then sectioned at 10 – 30 μm thickness using a Leitz CO_2 freezing microtome. Each individual section was removed from the microtome blade using a fine sable hair brush, and transferred to a slide containing either aniline blue or 4% potassium permanganate in 50% Karo syrup. In addition to South African material, the holotype specimen of *Archaeolithothamnion episporum* was obtained for study from US.

Sporangial pore diameter was measured directly from the SEM. All other measurements were made using a calibrated eyepiece micrometer. In cell measurements, length denotes the distance between primary pit connections, and diameter the maximum width of the cell lumen at right angles to this. Wherever possible, colour was determined by comparison with the *Methuen Handbook of Colour* (Kornerup & Wanscher 1978). Conceptacle measurements follow the system of Adey and Adey (1973). Thallus terminology follows that of Chamberlain (1983, 1990, 1993).

Observations

Sporolithon ptychoides Heydrich 1897: 67 – 69.

LECTOTYPE: TRH (not seen), El Tor, Red Sea, no number (as *Sporolithon ptychoides* f. *dura*) designated by Woelkerling and Townsend (Woelkerling 1988, p.204, Figure 239).

Habit and vegetative structure

Plants encrusting, thalli flat to lumpy (Figure 1), sometimes firmly adherent, but often weakly attached and undercut by burrowing organisms, up to 200 mm or more in diameter, up to 5 mm thick; margin ragged and flowing, sometimes entire, usually pale to whitish; surface flat, with flaky areas of sloughing epithallial cells, Methuen reddish brown in light to dark brown in shade, drying to greyish red, becoming pinkish in reproductive areas, surface smooth, glossy.

Sporangia in sori occurring in patches over the thallus surface (Figures 2, 9), circular to elongate, sori measuring 0.5 – 8 mm in longest dimension, patches slightly raised (*ca* 8 μm); each sporangial chamber with a single pore (Figures 5, 9, 10) measuring 10 – 14 μm in diameter and surrounded by 8 – 11 rosette cells (Figures 10, 45).

The *medulla* is relatively shallow (Figure 2), rarely more than 200 μm thick, usually eroded away by undercutting, cells rectangular (Figure 3), 12 – 47 μm long × 4 – 8 μm diameter, more or less lacking contents, cell fusions abundant. The *cortex* is very thick and composes the major part of the thallus (Figure 2), cells squarish to elongate (Figures 3, 7, 8), 6 – 13 μm long × 4 – 8 μm in diameter, contiguous cells frequently fused (Figures 3, 8), somewhat papillate secondary pit connections also present but usually much less common than cell fusions (Figure 3), pronounced pit bodies present between successive cells; *subepithallial initials* squarish (Figures 3, 7), densely pigmented, measuring 5 – 17 μm long and 5 – 12 μm diameter; *epithallial cells* single, more or less elliptical with flared outer wall (Figures 3, 7), with thick walls and a tiny cell lumen, measuring 2 – 5 μm long × 6 – 11 μm diameter, showing pronounced epithallial concavities in surface view (Figure 6). Starch grains variably present or not in cells of lower cortex and medulla.

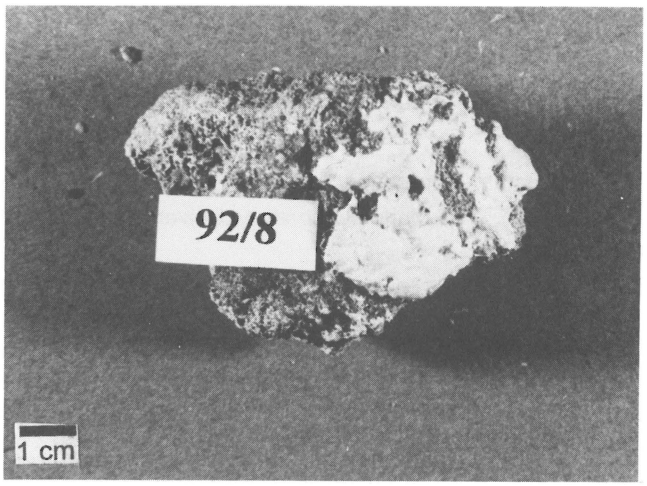
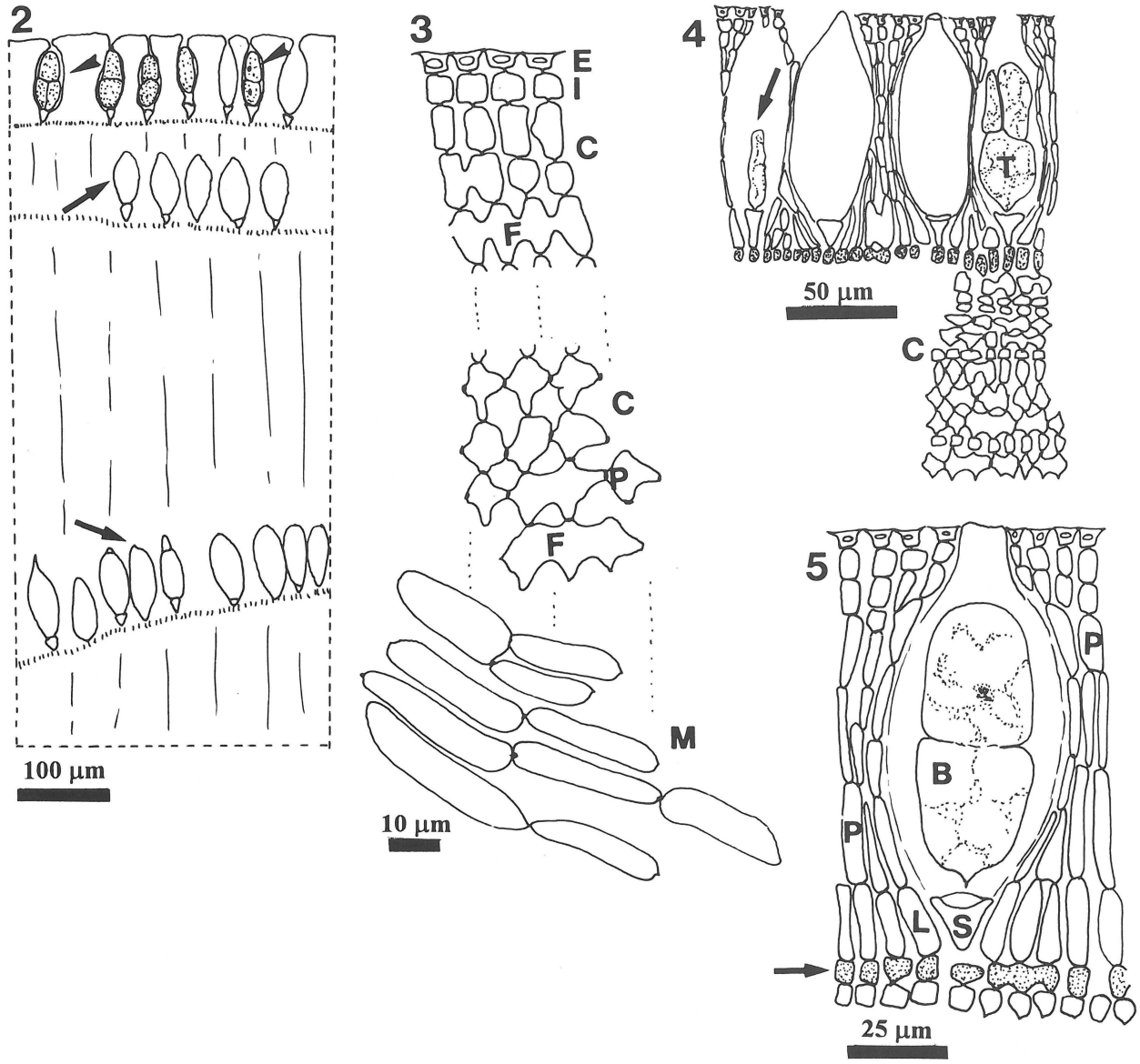


Figure 1 Habit photograph of specimens of *Sporolithon ptychoides* from Sodwana Bay, Natal Province (UWC: 92/8).

Reproduction

Gametangial plants: Unknown in South Africa. *Tetrasporangial plants*: Tetrasporangial chambers uniporate (Figures 5, 10), each containing a single tetrasporangium, each chamber lemon-shaped (Figures 5, 11, 12), measuring 77 – 108 μm long × 29 – 53 μm in diameter, pore 10 – 12 μm long. Sporangial primordia develop within the cortex when a group of cells elongates to form a distinct layer of elongate cells. Sporadic individual cells remain meristematic, dividing into a triangular stalk cell (Figure 5) plus sporangial initial. A calcified septum develops between the stalk cell and sporangium in mature sori (Figure 13). The surrounding cells elongate, and a chamber forms around the sporangium as it enlarges. One to several calcified paraphyses, consisting of 7 – 9 elongate cells, separate adjacent sporangial chambers (Figure 12). In the mature sporangial sorus, the layer of elongate cells is represented by the sporangial stalk cells, and the lowermost cell of each sporangial paraphysis (Figure 5). Below this layer of elongate cells is a layer of conspicuous squarish to rectangular, deeply pigmented cells (Figure 5). The sporangial initial divides simultaneously into a cruciately septate tetrasporangium with a plug leading to the surface pore (Figures 4, 5). Tetrasporangia measure 49 – 70 μm long × 37 – 50 μm diameter *in situ*; released ones measure 70 – 75 μm long × 40 – 50 μm in diameter. Some apparent bisporangia occurred (Figure 5). Unlike most sporangia with a single division in this plane, no other planes of division could be found by focussing up and down. Patches of sporangial sorus are



Figures 2 – 5 Vertical sections of *Sporolithon ptychoides* from Sodwana Bay [UWC:COR/327A (= YMC 91/60)]. **2.** Thallus showing superficial (arrowheads) and buried (arrows) tetrasporangial sori. **3.** Thallus showing epithallial cells (E), subepithallial initial (I), upper and lower cortex (C) with cell fusions (F) and secondary pit connections (P), and medulla (M). **4.** Upper thallus with immature tetrasporangia (arrow), mature, cruciately dividing tetrasporangium (T), and cortex (C). **5.** Sporangial chamber with apparent bisporangium (B). Note stalk cell (S), a 7-celled paraphysis (P), layer of elongate cells (L), and layer of deeply pigmented cells (arrow).

slightly raised by 2 – 3 cell layers above the surrounding vegetative thallus near the margin of the sorus, but up to 8 cells among the sporangial chambers (this pattern is illustrated for *S. episporum* in Figures 40 – 42). Groups of senescent tetrasporangial chambers, some containing partially developed tetrasporangia and stalk cells, persist and become buried in distinct layers in the thallus (Figures 2, 11).

Habitat and phenology

Found in tide pools and surge channels, and on rock substrates on coral reefs, at Sodwana Bay and adjacent areas. Sporangia recorded in January, July and November. This species overgrows most other crustose algae.

Distribution

South Africa: Sodwana Bay area of Natal Province. *World:* Recorded from the Red Sea and many other Indo-Pacific tropical and subtropical areas.

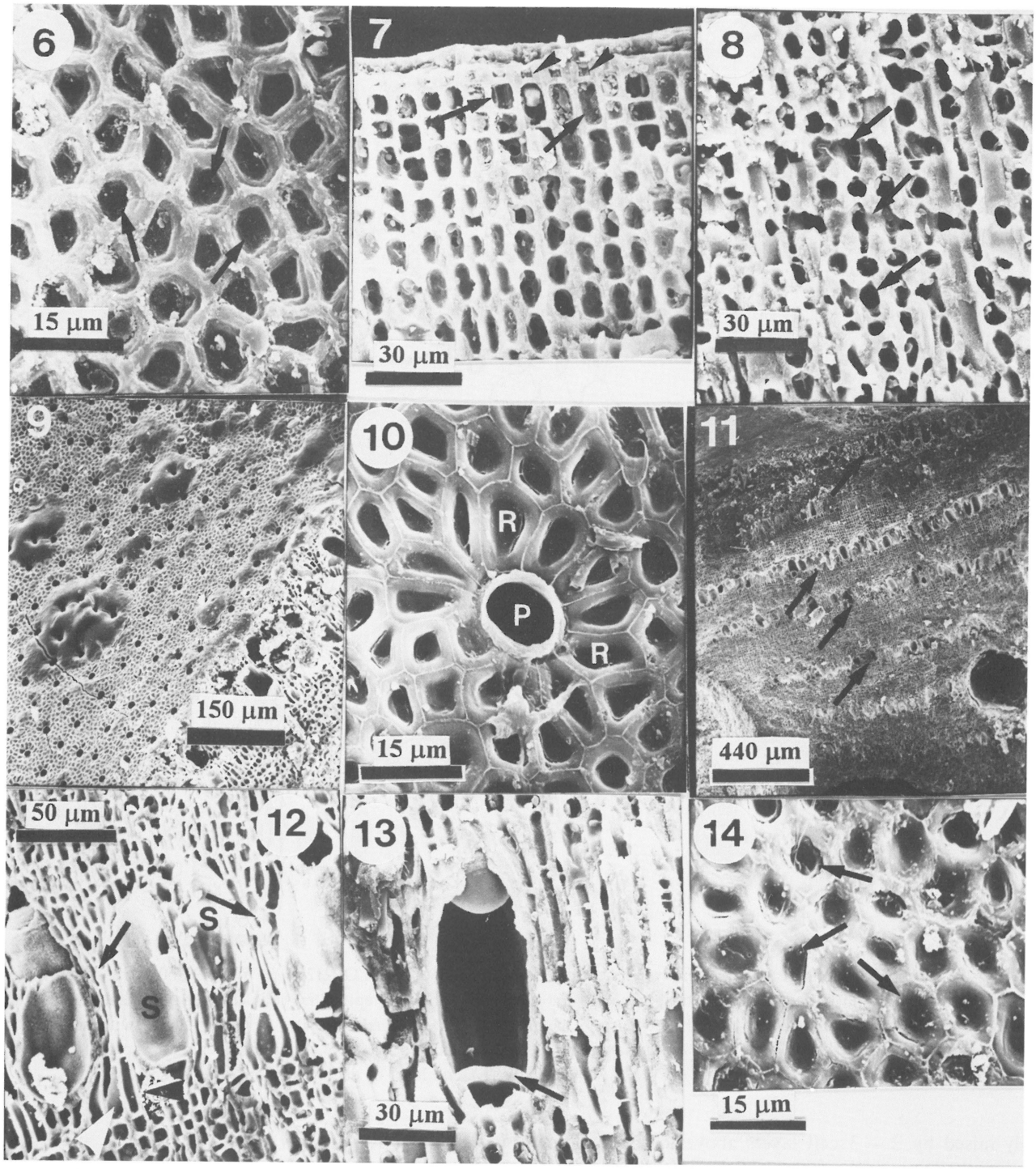
Specimens examined

—**2732** (Ubombo): Two-mile Reef, Sordwanabaai, 12 m depth on vertical rock in crevice, *D. Keats* (UWC: COR/327A); Mbibi, 1 – 2 m depth in very large tide pool, *D. Keats & Y. Chamberlain* (UWC: 91/153); Mbibi, on vertical walls and overhangs in big tide pool, *D. Keats & Y. Chamberlain* (UWC: 91/153); Seven Mile Reef, Sordwanabaai, on old coral and rock, *D. Keats & Y. Chamberlain* (UWC: 91/115); Mbibi, 1 – 2 m on rock in very large tide pool, *D. Keats*, 18.1.1992 (UWC: 92/8A); Lala Neck, Natal Province, *ca* 1 m depth on rock under overhanging walls in surge area, *D. Keats* (UWC: 92/58) (–DA).

Sporolithon episporum (Howe) Dawson 1960: 40

Basionym: *Archaeolithothamnion episporum* Howe 1918: 2, Pls 1 – 6

HOLOTYPE: NYBG!



Figures 6 – 14 Scanning electron micrographs of *Sporolithon ptychoides* and *S. episporum* from Sodwana Bay, Natal. [Figures 6 – 13, *S. erythraeum* (UWC: COR/327A); Figure 14, *S. episporum* (UWC: 92/3)]. **6.** Surface view of vegetative thallus; note epithallial concavities (arrow). **7.** Outer cortex showing epithallial cells (arrowheads) and subepithallial initials (arrows). **8.** Cortical cells showing cell fusions (arrows). **9.** Surface view of sorus with sporangial pores. **10.** Detail of sporangial pore (P) with 12 rosette cells (R). **11.** Layers of sporangia (arrows) buried in cortex. **12.** Old buried sporangia (S) with paraphyses (P), and layer of elongate cells (arrowhead). **13.** Detail of old sporangium showing remains of calcified septum (arrow). **14.** Surface view of vegetative thallus of *Sporolithon episporum* with epithallial concavities (arrow).

Habit and vegetative structure

Plants encrusting, thalli flat to lumpy (Figure 15), usually firmly adherent, but sometimes weakly attached and undercut by burrowing organisms, up to 500 mm or more in diameter, 0.2 – 4 mm thick, but building up to 4 cm thick by overgrowing in layers in some situations, margin entire, surface flat, with flaky areas of sloughing epithallus, usually pale purple-red (Methuen violet brown), becoming conspicuously white in reproductive patches, surface smooth, glossy.

Sporangia in small sori occurring in discrete patches over the thallus surface (Figure 27), sori measuring from 0.5 to 3 mm in longest dimension (usually <1 mm); each sporangial chamber with a single pore (Figures 20, 28, 29) measuring 16 – 20 µm in diameter and surrounded by 8 – 12 rosette cells (Figures 28, 44).

The *medulla* is relatively shallow (Figure 23), rarely more than 50 μm thick, usually eroded away due to undercutting of the thallus, cells rectangular (Figures 19, 26), 9 – 31 μm long × 5 – 12 μm in diameter, more or less lacking contents, papillate secondary pit connections abundant (Figures 19, 25, 26); *cortex* very thick and composing the major part of the thallus (Figures 16, 23), cells squarish to elongate, 5 – 21 μm long × 6 – 13 μm in diameter, contiguous cells joined by secondary pits (Figures 17, 18, 25), cell fusions not observed in our specimens, pronounced pit bodies present between successive cells; *subepithallial initials* squarish (Figures 17, 22), densely pigmented, measuring 6 – 10 μm long and 5 – 9 μm in diameter; *epithallial cells* single, more or less elliptical with slightly flared outer wall (Figure 17, 22), with thick walls and a tiny cell lumen, measuring 3.5 – 6 μm long × 8.5 – 11 μm in diameter, showing pronounced epithallial concavities in surface view (Figure 14), frequently sloughing (Figure 21). Starch grains variably present or not in cells of lower cortex and medulla (Figure 24).

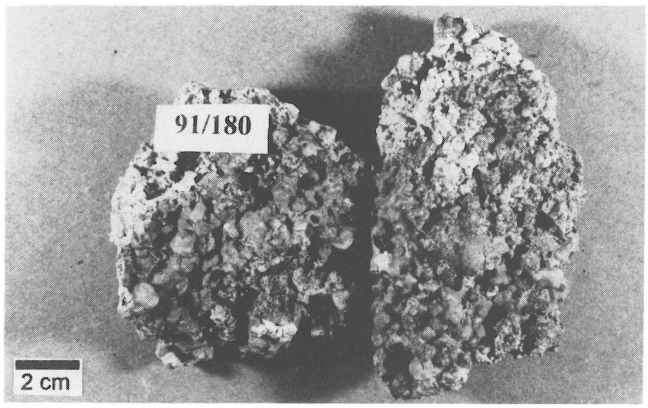
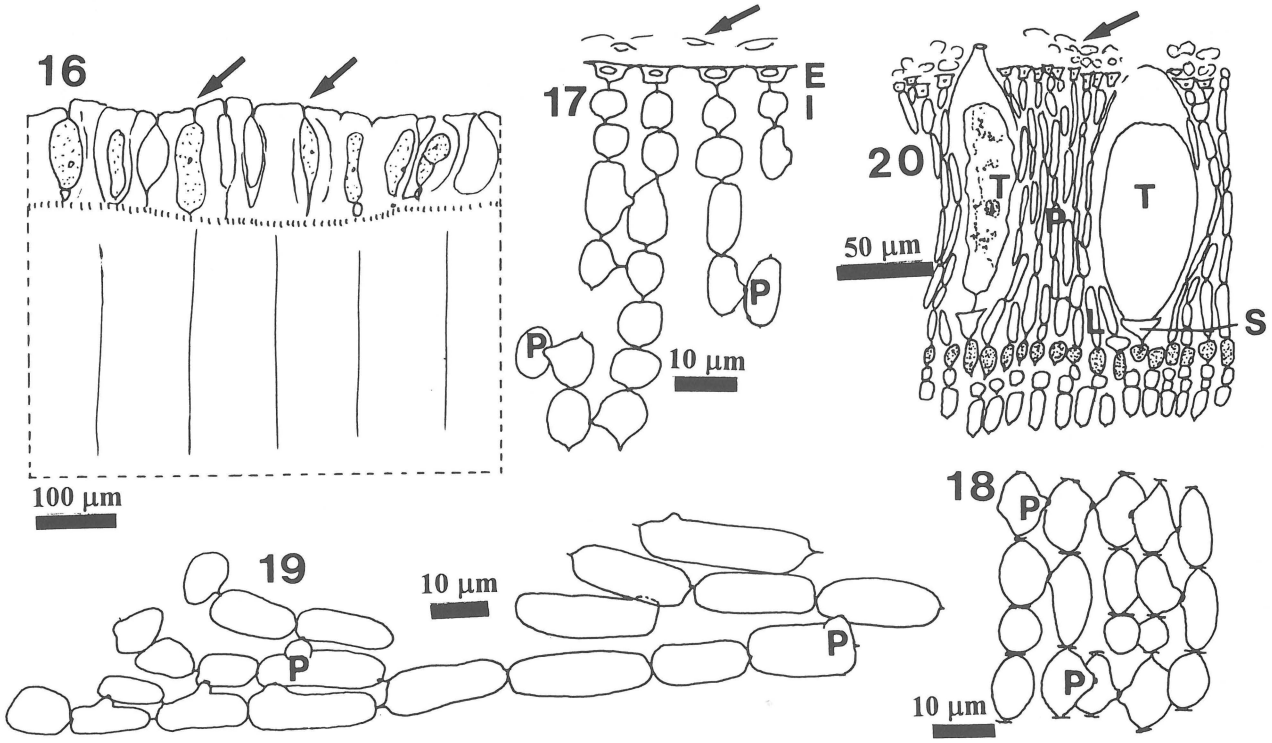


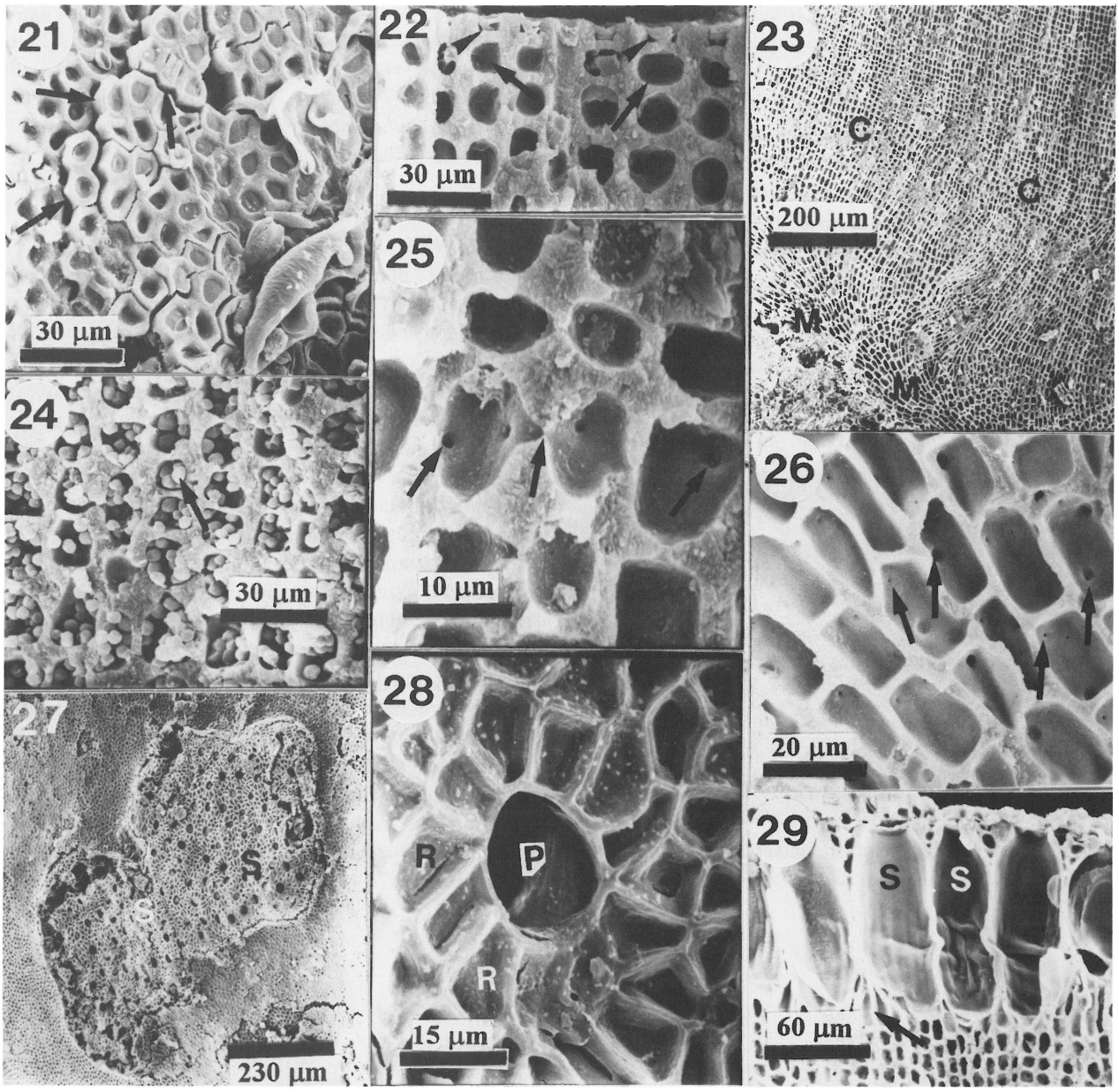
Figure 15 Habit photograph of specimens of *Sporolithon episporum* from Sodwana Bay, Natal (UWC: 91/180).

Reproduction

Gametangial plants: Unknown in South Africa. *Tetrasporangial plants*: Tetrasporangial chambers uniporate (Figures 20, 28), each containing a single tetrasporangium, each chamber lemon-shaped (Figures 20, 29), measuring 95 – 112 μm long × 33 – 50 μm in diameter, pore *ca* 6 μm long. Sporangial primordia develop within the cortex when a group of cells elongates to form a distinct layer of elongate cells. Sporadic individual cells remain meristematic, dividing into a triangular stalk cell (Figure 20) plus sporangial initials. The surrounding cells elongate, and a chamber forms around the sporangium as it enlarges. One to several calcified paraphyses, consisting of 7 – 8 elongate cells, separates adjacent sporangial chambers (Figure 20). In the mature sporangial sorus, the layer of elongate cells is represented by the sporangial stalk cells, and the lowermost cell of each sporangial paraphysis (Figure 20). Below this layer of elongate cells is a layer of very obvious squarish to rectangular, deeply pigmented cells (Figure 20). The sporangial initial divides into a cruciately septate tetrasporangium with a plug leading to the surface pore (Figure 20). Sporangial sori are slightly raised, 3 – 4 cell layers above the surrounding vegetative thalus (Figures 40 – 42). Tetrasporangia measure 74 – 96 μm long × 30 – 43 μm in diameter



Figures 16 – 20 Vertical sections of *Sporolithon episporum* from Sodwana Bay, Natal (UWC: COR/348). **16.** Thallus showing superficial, immature tetrasporangial sorus (arrow). **17.** Upper thallus showing epithallial cells (E), shedding epithallial cells (arrow), subepithallial initial (I), and cortex with papillate secondary pit connections (P). **18.** Lower filaments of cortex with papillate secondary pit connections (P). **19.** Medulla with papillate secondary pit connections (P). **20.** Upper thallus with immature sporangia (T) borne on stalk cells (S), paraphyses (P), and epithallial shedding (arrow).



Figures 21 – 29 Scanning electron micrographs of *Sporolithon episporum* from Sodwana Bay, Natal (UWC: 91/180, 92/3). **21**. Surface view of sloughing epithallial cells (arrows). **22**. Upper thallus showing epithallial cells (arrowheads) and subepithallial initials (arrows). **23**. Vertical fracture through thallus, showing medulla (M) and lower filaments of cortex (C). **24**. Cells of lower cortex packed with starch (arrow). **25**. Secondary pit connections (arrows) in cortical cells. **26**. Medullary cells with secondary pits (arrows). **27**. Tetrasporangial sorus (S) at thallus surface. **28**. Detail of sporangial pore (P), with 12 rosette cells (R). **29**. Vertical fracture through sporangial chambers (S) at thallus surface. Note layer of elongate cells (arrow).

in situ. Patches of sporangial sorus are shed, and sporangial chambers do not become buried in the thallus.

Habitat and phenology

Found in large tide pools, surge channels, and shallow subtidal rocks subjected to sand scour and inundation. Sporangia recorded in January, May and November. This species overgrows most other crustose species.

Disbribution

South Africa: Sodwana Bay area of Natal Province and Holbaaipunt, south-western Cape Province. *World*: Recorded from Caribbean Panama, Indonesian archaepelago.

Specimens examined

—**2732** (Ubombo): Anton's Reef, Sordwanabaai, 10 m depth on walls, covering old coral and rock substrates, *D. Keats* (UWC: COR/148); Jesser Point, Sordwanabaai, forming thick layer, up to 4 cm thick around base of sand-influenced boulders at *ca* 1 – 2 m depth, *D. Keats & Y. Chamberlain* (UWC: 91/180); Mbibi, Natal Province, *ca* 1 m depth at bottom and sides of large surge bowl, *D. Keats* (UWC: 92/3) (–DA).

—**3419** (Caledon): Holbaaipunt, southwestern Cape Province, *ca* 1 m depth on rock, *D. Keats* (UWC: 93/61) (–BD).

Holotype

Archaeolithothamnion episporum Howe 1918: 2

US No. 68672. *M.A. Howe* No. 6832, Panama Canal Zone,

Point Toro, near Colon, 7 January 1910.

The holotype (Figure 30) comprises a lumpy thallus measuring 35 mm × 20 mm, plus a smaller fragment. It is composed of a small core of coral, overgrown by superimposing layers of thallus up to 2 mm thick, only the outermost thallus layer seems to have been alive at the time of collection. Irregularly shaped tetrasporangial sori, measuring up to *ca* 7 mm diameter, are present and are slightly raised 3 – 4 cells above the vegetative thallus surface; in surface view the pores measure up to 30 μm diameter and are surrounded by 12 – 16 rosette cells (Figures 38, 39, 43).

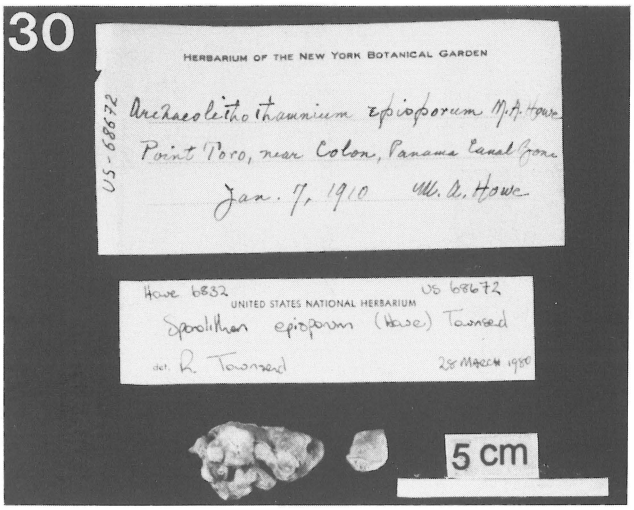
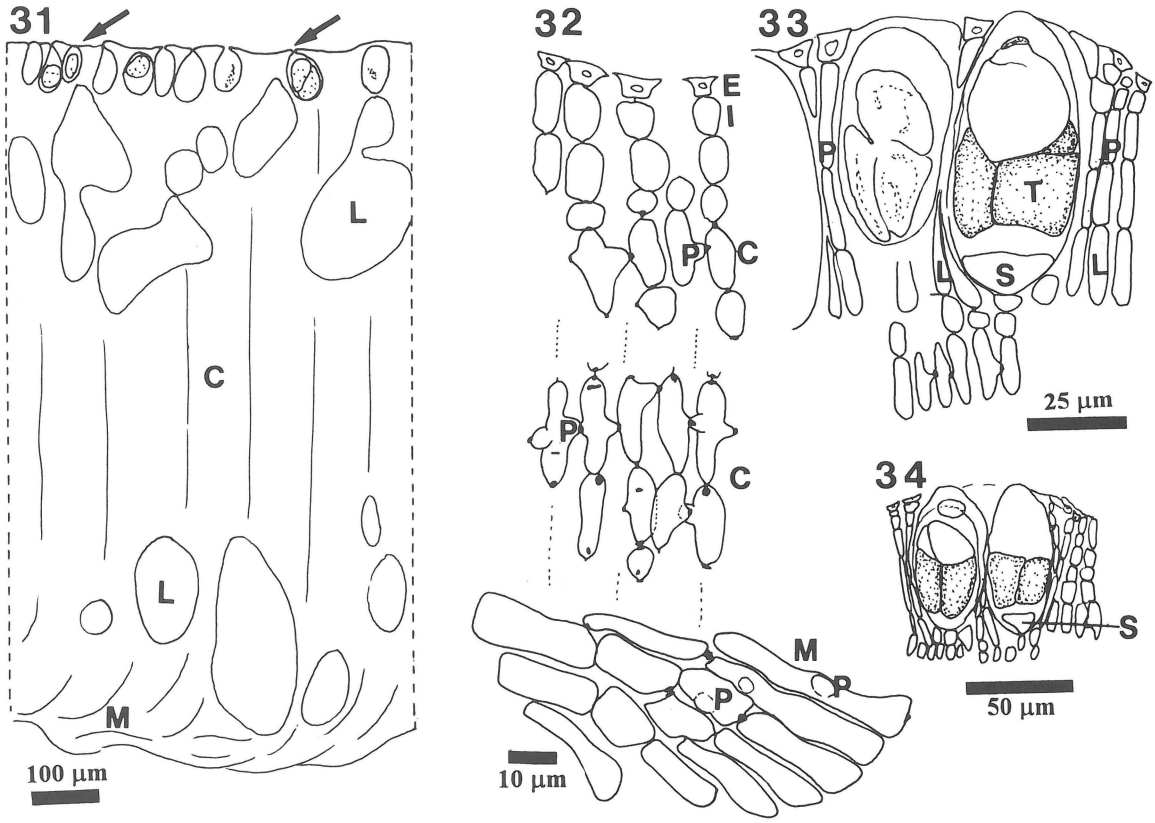


Figure 30 Holotype specimen of *Archaeolithothamnion episporum* Howe.

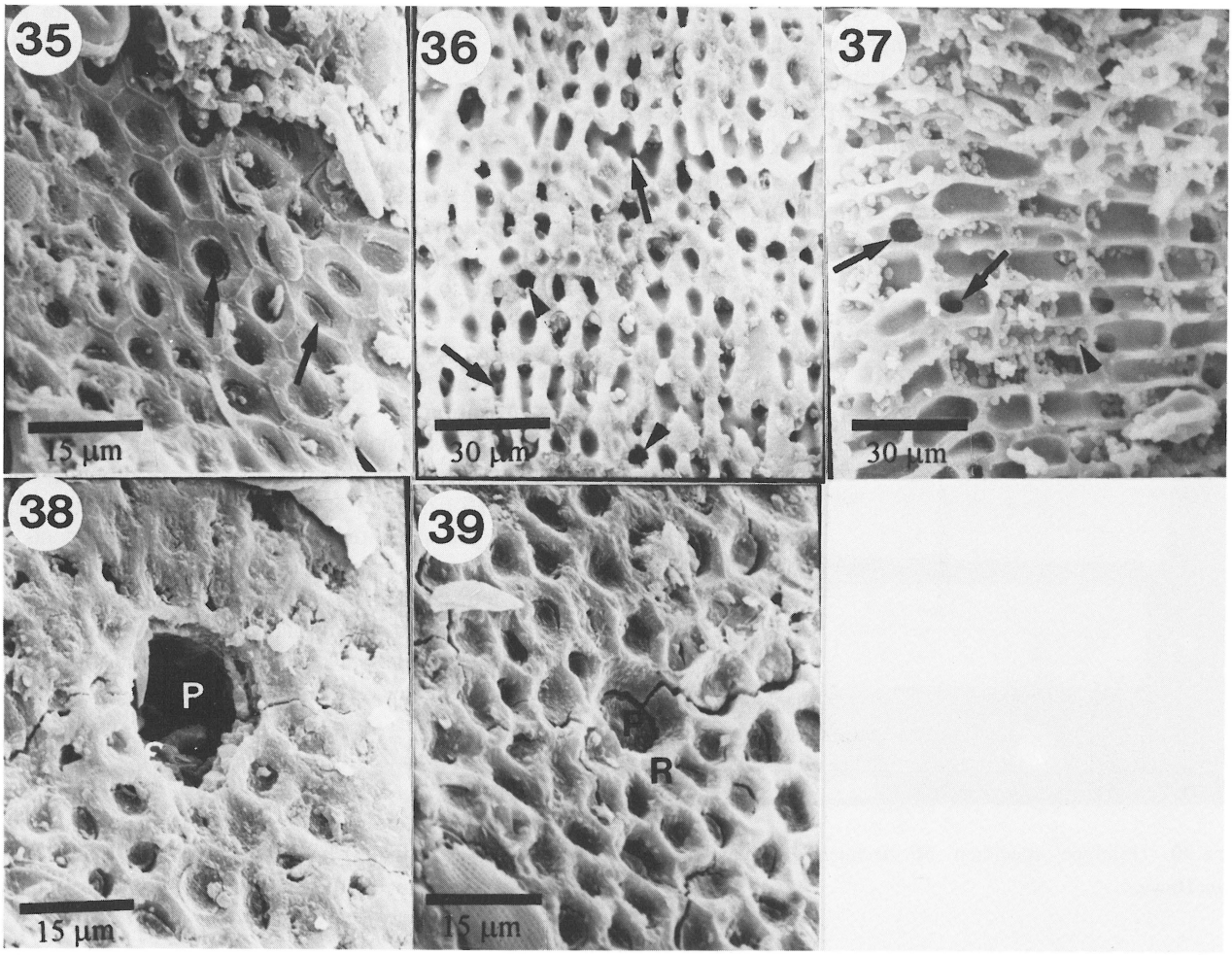
In vertical section (Figure 31), the thallus is composed mainly of cortex, with a very thin layer of medullary filaments, and tetrasporangial sori occur at the thallus surface but no buried ones were seen. Flared epithallial cells (Figure 32) occur at the thallus surface, measuring 4 – 5 μm long × 5 – 10 μm in diameter; cortical cells (Figure 32) are squarish to elongate measuring 5 – 20 μm long × 5 – 9 μm in diameter, and papillate secondary pit connections (Figure 32) occur frequently between adjacent cortical cells; medullary filaments (Figures 32, 37) are composed of elongate cells measuring 12 – 47 μm long × 4 – 10 μm diameter, and papillate secondary pit connections are present. Tetrasporangial chambers (Figures 33, 34) are elliptical measuring 50 – 70 μm high × 25 – 40 μm in diameter, adjacent chambers are separated by one to several filaments up to five cells long, composed of long, thin cells; cruciately divided tetrasporangia (Figures 33, 34) measure up to 50 μm long × *ca* 30 μm in diameter, they are attached to the base by a triangular stalk cell which appears to arise within a layer of elongate cells (Figures 33, 34).

Discussion

Until recently, *S. ptychoides* Heydrich, the type species of the genus, has been considered a heterotypic synonym of *S. erythraeum* (Rothpletz) Kylin, the type of which is a fossil. However, a recent study by Verheij (1993) has suggested



Figures 31 – 34 Vertical sections of type specimen of *Archaeolithothamnion episporum* (US). **31.** Thallus showing superficial sporangial sorus (arrow), cortex (C), and medulla (M). The thallus has many lacunae (L). **32.** Thallus showing epithallial cells (E), subepithallial initial (I), upper and lower cortex (C) with papillate secondary pit connections (P), and medulla with papillate secondary pit connections (P). **33.** Tetrasporangia (T) with stalk cell (S), 4- to 5-celled paraphyses, and layer of elongate cells (L). **34.** Tetrasporangia. Note stalk cell (S).



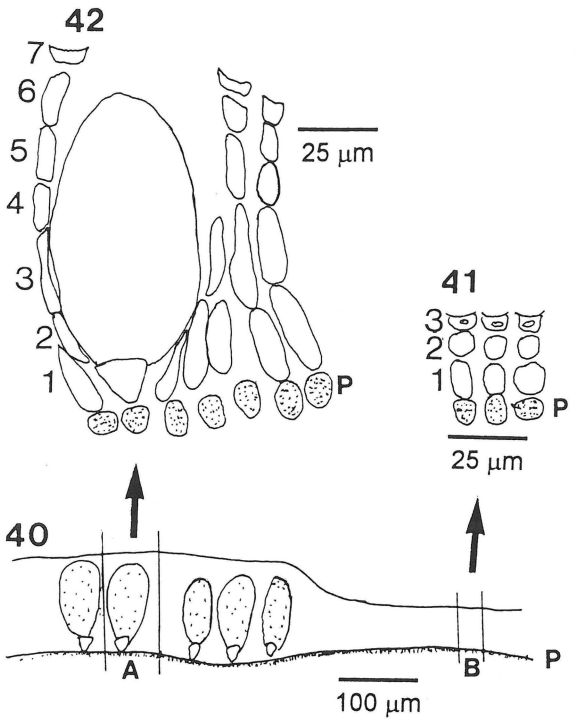
Figures 35 – 39 Scanning electron micrographs of holotype specimen of *Sporolithon episporum*. **35.** Surface view of epithallial cells with epithallial concavities (arrows). **36.** Vertical fracture through cortex, showing papillate secondary pit connections (arrow), and possible cell fusions (arrowhead). **37.** Vertical fracture through thallus, showing medulla with cell fusions (arrow). Note cells packed with starch granules (arrowhead). **38.** Detail of old, senescent sporangial pore (P). **39.** Detail of young pore with rosette cells (R). Note the intact pore plug blocking the pore (P).

that several differences exist between the types of *S. ptychoides* and *S. erythraeum* (Table 1). The type of *S. ptychoides* has a layer of elongate cells, within which sporangia are initiated, and sori are raised 1 – 2 cells above the surrounding thallus near the margin of the sorus (Figures 40 – 42), but up to 8 cells among the sporangial chambers [termed 'additional cell layers between the sporangia' by Verheij (1993)]. Sporangia are not initiated within a layer of elongate cells in the type of *S. erythraeum*, nor is the sporangial sorus raised (Verheij 1993). Verheij (1993) concluded that most recent specimens that have been identified as *S. erythraeum* (or *Archaeolithothamnion erythraeum*) will probably be referred to *S. ptychoides*, but further studies are required to determine if this suggestion is correct. As our specimens conform to Verheij's (1993) description of *S. ptychoides*, we have applied this epithet to our material.

Table 1 Comparison of specimens according to the characters used by Verheij (1993) and in the present study to distinguish among species of *Sporolithon*

	S. episporum (Verheij 1993)	*S. episporum* type (this study)	*S. episporum* (this study)	*S. ptychoides* (Verheij 1993)	*S. erythraeum* (Verheij 1993)	*S. ptychoides* (this study)
Arrangement of tetraspores	Cruciate	Cruciate	Cruciate	Cruciate	Unknown	Cruciate
Number of cells to which sporangial sorus is raised above vegetative thallus	1 – 2	3 – 4	3 – 4	1 – 2	None	2 – 8
Number of cells in sporangial paraphyses	3 – 5	4 – 8	7 – 8	3 – 5	3 – 5	7 – 9
Sporangial development from elongate cell layer	Present	Present	Present	Present	Absent	Present
Fate of old sporangia	Sloughed off	Sloughed off	Sloughed off	Buried	Buried	Buried
Sporangial pore diameter (µm)	No data	16 – 30	16 – 20	No data	No data	10 – 14

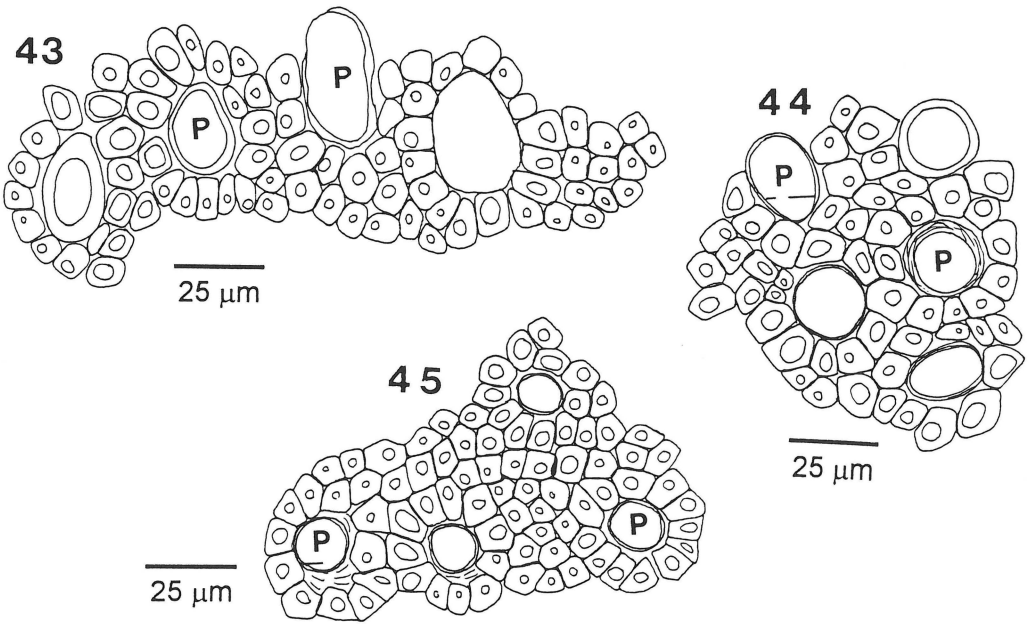
Recent material ascribed to *S. erythraeum* has been recorded very widely and described in some detail (Woelkerling 1988). It is regarded as a flat to lumpy plant, with a smooth surface and discrete tetrasporangial sori that become buried in the thallus when old. The thallus form and the structure of the specimens collected in Natal conform to the concept of *Sporolithon erythraeum* as published, for example, by Lemoine (1911, as *Archaeolithothamnion*), Adey *et al.* (1982, as *Archaeolithothamnion*) from Hawaii, Segonzac (1982, as *Archaeolithothamnion*) from the Indian Ocean, and Krishnamurthy and Jayagopal (1985) from India. One notable difference from the above records is the statement by Adey *et al.* (1982) that tetrasporangia were zonately divided in Hawaiian plants. However, they did not illustrate tetrasporangia, so we are unable to assess how they compare with the cruciately divided tetrasporangia from Natal plants. R. Townsend (pers. commun.) examined the Hawaiian material, and confirmed the presence of *cruciate* sporangia.



Figures 40 – 42 Drawings to illustrate the concept of the sorus being raised above the surrounding vegetative thallus, using *S. episporum* as an example (UWC: COR/348). **40.** Vertical section of sorus, showing layer of deeply pigmented cells (P) below sorus. **41.** Vertical section through upper part of vegetative thallus in region B of Figure 40. Note that there are three cells above the pigmented layer (P). **42.** Vertical section through sorus in region A of Figure 40. Note that the paraphyses contain seven cells above the pigmented layer (P). Thus the sorus in this region is raised four cells above the vegetative region of the thallus.

Species characteristics that we consider significant in delineating *S. ptychoides* are: a flat to lumpy external morphology; a thallus composed mainly of aligned cortical cells, with a thin medulla; the presence of cell fusions as well as secondary pit connections; discrete tetrasporangial sori that are raised at least 1 – 3 cells above the surface of the vegetative thallus; cruciately divided tetrasporangia borne on a single stalk cell from which they are separated by a calcified septum; stalk cell formed within a layer of elongate cells, elongate cells formed above a layer of deeply pigmented squarish to rectangular cells; and sori becoming buried in distinct layers within the thallus when old.

Sporolithon episporum differs from *S. ptychoides* in having larger sporangial pores, having secondary pit connections but rarely cell fusions, and in not burying conceptacles in distinct rows but rather sloughing them in sheets. In his description of the type of *S. episporum*, Howe (1918, p.3) noted that sporangia are 'imperfectly and irregularly embedded in the thallus'. None of the material which we examined contained buried sporangia, nor were buried sporangia seen in the type specimen. The combination of mainly papillate



Figures 43 – 45 Surface views of cell patterns in *Sporolithon* (*Archaeolithothamnion*) sori (P, pore). **43.** Type specimen of *Archaeolithothamnion episporum* Howe. **44.** *Sporolithon episporum* from Sodwana Bay, Natal (YMC 91/180). **45.** *Sporolithon ptychoides* from Sodwana Bay, Natal (UWC: COR/327A, YMC: 91/60).

secondary pits rather than cell fusions, and non-burying sporangia, together with sporangial initiation within a layer of elongate cells, and a raised sporangial sorus are probably diagnostic of this species. Our material is in agreement with Indonesian plants described by Verheij (1993).

Dawson (1960, pp. 38 – 40) described *Sporolithon pacificum* Dawson from Costa Rica, and noted its similarity to *S. episporum*. *Sporolithon pacificum* was said to differ from *S. episporum* in having smaller protuberances, smaller cells, and in the shape of sori. From our studies we do not believe that these characters are reliable, and indeed the illustration of the type of *S. pacificum* (Dawson 1960, Figure 4A) looks very similar to some of our plants from Natal. This suggests that *Sporolithon pacificum* Dawson should be subsumed into *Sporolithon episporum* (Howe) Dawson, but an examination of the type specimen of *S. pacificum* will be necessary to confirm this suggestion.

Acknowledgements

We thank the University of the Western Cape (UWC) for providing funding and research equipment, the South African Foundation for Research Development (FRD) for a CORE grant to D.W.K., and the Natural Environment Research Council for a grant to Y.M.C. The visit of Y.M.C. to the UWC was made possible through a grant from the joint FRD–UDP/UWC research development programme. Basil Julies of the UWC physics department provided valuable assistance with the operation of the SEM, and Gavin Maneveldt provided technical assistance. The Natal Parks Board helped by providing logistic support, with special thanks due to Dirk Rossouw for providing boat access to the reefs, other local transport when required, and accommodation in his house during a late-night flood. We also thank Simon Chater, Georgina Lambert and Nuno of the Oceanographic Research Institute, Durban, who also helped with field work. We thank the Curator of the New York Botanical Garden for lending specimens, and Eric Verheij for helpful discussions and allowing access to his papers prior to publication.

References

ADEY, W.H. 1979. Crustose coralline algae as microenvironmental indicators for the Tertiart. In: Historical Biogeography, Plate Tectonics, and the Changing Environment, eds. J. Gray & A.J. Boucot, pp. 459 – 464. Oregon State University Press, Corvallis, Oregon.

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.

ADEY, W.H. & MACINTYRE, I.G. 1973. Crustose coralline algae: A re-evaluation in the geological sciences. *Bull. geol. Soc. Am.* 84: 883 – 904.

ADEY, W.H., TOWNSEND, R.A. & BOYKINS, W.T. 1982. The crustose coralline algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands. *Smiths. Contr. mar. Sci.* 15: 1 – 74.

CHAMBERLAIN, Y.M. 1983. Studies in the Corallinaceae with special reference to *Fosliella* and *Pneophyllum* in the British Isles. *Bull. Brit. Mus. nat. Hist. (Bot.)* 11: 291 – 463.

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. 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.

DAWSON, E.Y. 1960. New records of marine algae from Pacific Mexico and Central America. *Pacif. Nat.* 1: 31 – 52.

HEYDRICH, F. 1897. Neue Kalkalgen von Deutsch-Neu-Guinea (Kaiser Wilhelms-Land). *Biblthca bot.* 41: 1 – 11, 1 pl.

HOWE M.A. 1918. On some fossil and recent Lithothamnieae of the Panama Canal Zone. *US Nat. Mus. Bull.* pp. 1 – 13, 11 plates.

KORNERUP, A. & WANSCHER, J.H. 1978. Methuen Handbook of Colour, 3rd edn., Engl. Transl. Methuen, London.

KRISHNAMURTHY, V. & JAYAGOPAL, K. 1985. Studies on the crustose coralline algae of the Tamilnadu coast. I. Melobesioideae. *Seaweed Res. Utiln.* 8: 65 – 73.

LEMOINE, Mme. P. 1911. Structure anatomique des Mélobésiées. Application à la classification. *Ann. Inst. Océanogr. Monaco* 2(2): 1 – 213.

RAMSAY, P.J. & MASON, T.R. 1990. Development of a type zoning model for Zululand coral reefs, Sodwana Bay, South Africa. *J. Coastal Res.* 6: 829 – 852.

ROTHPLETZ, A. 1893. Über eine neue Pflanze (*Lithothamnion erythraeum*) des Rothen Meeres. *Bot. Zbl.* 54: 5 – 6.

SEGONZAC, G. 1982. Algues calcaires de quelques milieux récifaux de l'océan Indien (Rhodophycées et Chlorophycées). *Mém. géol. Univ. Dijon* 7: 249 – 254.

VERHEIJ, E. 1992. Structure and reproduction of *Sporolithon episoredion* (Adey, Townsend et Boykins) comb. nov. (Corallinales, Rhodophyta) from the Spermonde Archipelago, Indonesia. *Phycologia* 31: 500 – 509.

VERHEIJ, E. 1993. The genus *Sporolithon* (Sporolithaceae fam. nov., Corallinales, Rhodophyta) from the Spermonde Archipelago, Indonesia. *Phycologia* 32: 184 – 196.

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