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Heydrichia homalopasta sp. nov. (Sporolithaceae, Rhodophyta) from Australia

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Heydrichia homalopasta sp. nov. is described from the east coast of Australia. The new species lacks the prominent pit plug caps found in the two South African species *Heydrichia woelkerlingii* Townsend, Keats *et* Chamberlain and *Heydrichia groeneri* Keats *et* Chamberlain. In habit, *H. homalopasta* grows as a thin crust (to 1 mm thick), similar to *H. groeneri*, but differing from the massive crusts (to 15 mm thick) found in *H. woelkerlingii*. The tetrasporangial nemathecia of *H. homalopasta* are single sporangial complexes whereas those of the South African species are composed of numerous sporangial complexes.

Introduction

Interest in the coralline red algae has ebbed and flowed during the post-Linnaean taxonomic period. The most recent re-evaluation of the taxonomy of the non-geniculate members of this group began in the early 1960s with the publications of Adey (1964, 1965, 1966 a, 1966 b) and continued with those of Cabioc'h (1968, 1971 a, 1971 b, 1972) in the early 1970s, and Chamberlain, Woelkerling and Keats in the 1980s and 1990s (Chamberlain 1986, 1990, 1991 a, 1991 b, 1992, 1993, 1994; Keats and Chamberlain 1993, 1994 a, 1994 b, 1995; see Woelkerling 1988). The works of Adey, Chamberlain and Keats have dealt with specific non-geniculate coralline algal floras whereas those of Cabioc'h dealt with anatomy and those of Woelkerling have dealt with gaining a better understanding of nomenclature and taxonomy of the group. Although Verheij (1993) formally recognised the Sporolithaceae in the late twentieth century, the premise that *Sporolithon* Heydrich (1897) represented an entity separate from other coralline algae had been proposed numerous times before (Setchell 1943, Hamel and Lemoine 1952, Johansen 1969, Cabioc'h 1971 b, Womersley and Bailey 1970). The character states of secondary pit connections and lateral cell fusions in the cortex, tetrasporangia in widely dispersed nemathecia and cruciately divided tetrasporangia were used by Verheij (1993) but had been described previously by Cabioc'h (1972).

The Sporolithaceae contains two genera, *Sporolithon* and *Heydrichia* Townsend, Chamberlain *et* Keats (1994). *Heydrichia* shares character states with *Sporolithon*, such as a calcified sporangial initial wall and proliferation of the tetrasporangia from individual stalk cells but there are also differences such as the numerous stalk cells formed in the sporangial complexes of *Heydrichia* as compared to the single stalk cells observed in *Sporolithon*. *Heydrichia* comprises three species: two have been described from South Africa (Townsend *et al.* 1994, Keats and Chamberlain 1995) and the third, *H. homalopasta* from southeastern Australia is described in this paper.

Materials and Methods

Plants of *Heydrichia homalopasta* were collected using SCUBA and transferred to the laboratory in aerated seawater. They were then processed for transmission electron microscopy (TEM), scanning electron microscopy (SEM) and light microscopy (LM) using a combination of the methods described in Borowitzka and Vesk (1978) and Townsend *et al.* (1994).

The terminology used in this paper is that used by Townsend and Adey (1990) and Townsend *et al.* (1994, 1995) except that the term sorus is replaced by nemathecium. A nemathecium is defined as an area of thallus where the vegetative structure has been modified concurrent with the differentiation of reproductive cells. Under this definition, a nemathecium is found at the site of tetrasporangial, gametophyte and carposporophyte formation in the Sporolithaceae.

Colour codes used in the text and cited '(#)', are those of Kelly and Judd (1976). Herbarium abbreviations follow Holmgren *et al.* (1990).

Heydrichia homalopasta sp. nov.

Diagnosis: *Crustae pagina lucida sed pannis hebetibus. Medulla cellulis 15–20 µm longae et 6–9 µm diametro. Corticis cellulae 5–13 µm longae et 3.5–11 µm diametro. Epithallium cellulis 2–5 µm longis et 2–*

5 μm diametro. Nemathecia turmarum sporangialium singularum 120−170 μm longarum constantia. Sporocyti 75−90 μm longi et 80−110 μm diametro.

Crust surface shiny with dull patches. Medullary cells 15−20 μm long, 6−9 μm diam. Cortical cells 5−13 μm long, 3.5−11 μm diam. Epithallium of cells 2−5 μm long, 2−5 μm diam. Nemathecia as single sporangial complexes, scattered throughout upper cortex; sporangial complexes 120−170 μm long, 110−190 μm diam. Sporocytes 75−90 μm long, 80−110 μm diam.

Holotype: Bongin Bongin Bay, Mona Vale, New South Wales, R. A.Townsend, BB7902, 10 vii 1979, NSW. SEM and LM material housed at LTB/MEL. (Fig. 1); isotype: LTB/MEL

Etymology: The name *homalopasta* is derived from the Greek words homalos (even) and pastos (sprinkled) in reference to the nemathecia (as single sporangial complexes) which are evenly distributed across the tetrasporangial thallus (Fig. 10).

Specimens examined: *Heydrichia homalopasta*: Bongin Bongin Bay, Mona Vale, NSW, Australia., 0−3.5 m, tetrasporic (10 vii 1979, *R. A. Townsend*, NSW, BB7902; MURU BB7901,BB7904-5).

Observations

Habit

Crust are non-geniculate, encrusting and epilithic. They are firmly adherent to the substrate and are glossy, grey red (#19) to dark red (#16) in colour with dull, grey pink (#8) patches. Individual crusts can be quite large (to 15 cm broad) but are always thin, up to 1 mm thick and without protuberances (Figs 1, 2). The crusts often have wound scars caused by urchin grazing visible on the surface.

Vegetative anatomy

This is a monomerous species, in which the cortex is composed of multicellular filaments produced from a sub-apical intercalary initial (Figs 5, 12). The initial produces single epithallial cells outwardly and cortical cells inwardly. The epithallial cells show angular radial walls; they are flared (Fig 9 top left). The initial has wall ingrowths (Fig. 12). The cortex has both secondary pit connections and contiguous lateral cell fusions (Figs 6, 9, 13). Plastids are abundant in the upper ten cells of the cortex and become less common deeper in the thallus. On the other hand, floridean starch grains become more common in the cells of the lower cortex (Figs 6, 7). Osmiophilic spherical bodies, presumed to be lipid deposits, are found throughout the cortex and medulla but are larger and more common deeper in the thallus (Figs 5, 8). The pit plug outer caps (Pueschel 1990) were not seen in *Heydrichia homalopasta* (Figs 6, 7, 11, cf. Townsend *et al*. 1994 fig. 12).

The primary apical initials have not been seen in *H. homalopasta*. The medulla is composed of 1−3 filaments running parallel to the substratum (Figs 5, 7). Medullary filaments, which bend down towards the surface of the substratum, were not seen in this taxon and the transition from medulla to cortex is distinct. Secondary pit connections and lateral cell fusions between contiguous medullary filaments have not been observed.

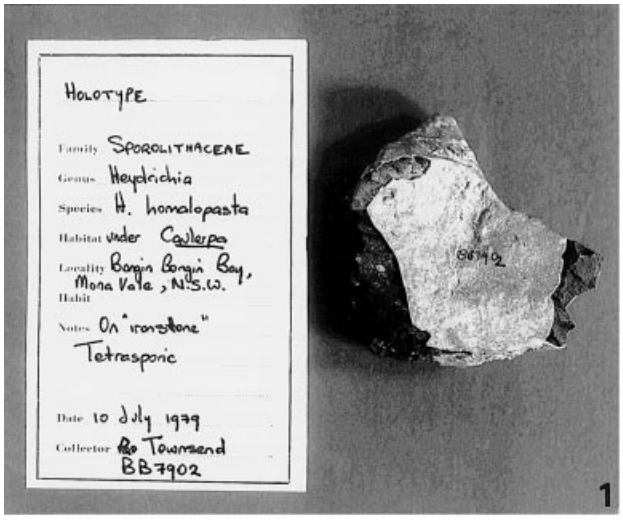
Reproductive anatomy

Tetrasporic plants have been recorded in July. Gametophytic and carposporophytic plants have not been collected. This species differs externally from the other species of *Heydrichia* in that the nemathecia (as single sporangial complexes) are evenly distributed across the tetrasporangial thallus (Fig. 10).

Nemathecial and tetrasporangial development: Tetrasporangia are borne in sporangial complexes in this species. The differences observed in the sporangial complexes of *H. homalopasta* and the type species of the genus, are minor and relate to: (1) the number of stalk cells (usually fewer here than in the type species, cf., Fig. 6 and Townsend *et al*. 1994 fig. 24); (2) the plug above the sporangium may be off-centre to the sporangium; and (3) the planes of

Figs 1−8. *Heydrichia homalopasta*.

Fig. 1. The largest fragment of a single individual representing the holotype of *Heydrichia homalopasta*. Scale: 1 cm = 16 mm. Fig. 2. A paratype specimen of *H. homalopasta*. Scale: 1 cm = 14 mm. Fig. 3. LM of radial thick section through a nemathecium (left) and past reproductive event (right). Note: cruciately arranged spores in sporangium (S) and stalk cell (arrow). Scale: 1 cm = 40 μm. Fig. 4. LM of radial thick section through portion of former nemathecium. Note: cells in this area are joined by fusions and secondary pit connections (arrow). Scale: 1 cm = 30 μm. Fig. 5. LM of radial thick section through thallus. Note: the change in number of lipid bodies (black dots) from thallus surface to deeper in thallus; also note the formation of epithallial cells across the thallus surface (arrows). Scale: 1 cm = 60 μm. Fig. 6. LM of radial thin section through a nemathecium. Note: the stalk cells are not in the plane of section; also the cruciately arranged spores (white arrows show planes of cytokinesis) form by a transaxial division followed by a coaxial division. The pore is occluded by a plug; position of a previous reproductive event (black arrows) and fusion in the cortex (small black arrow). Scale: 1 cm = 37 μm. Fig. 7. LM of radial thin section of medulla (M) and cortex. Note: density of starch grains in these cells compared to the upper cortex (cf., Fig. 6). Scale: 1 cm = 37 μm. Fig. 8. LM of radial thick section of mid- to lower cortex. Note: large bodies in these cells which stain less with Richardson's stain (cf., Fig. 7). Scale: 1 cm = 37 μm. Figs 5, 8 (BB7901); Figs 1, 6 (BB7902); Figs 3, 4, 7 (BB7904); Fig. 2 (BB7905).


HOLOTYPE
Family SPOROLITHACEAE
Genus Heydrichia
Species H. homalopasta
Habitat under Caulerpa
Locality Bongin Bongin Bay, Mona Vale, N.S.W.
Habit
Notes On "ironstone" Tetrasporic
Date 10 July 1979
Collector R. Townsend BB7902
BB7902
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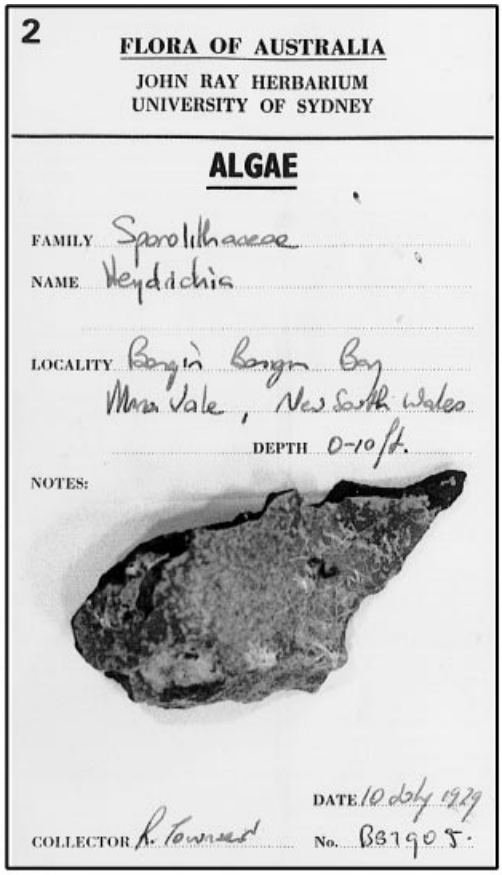
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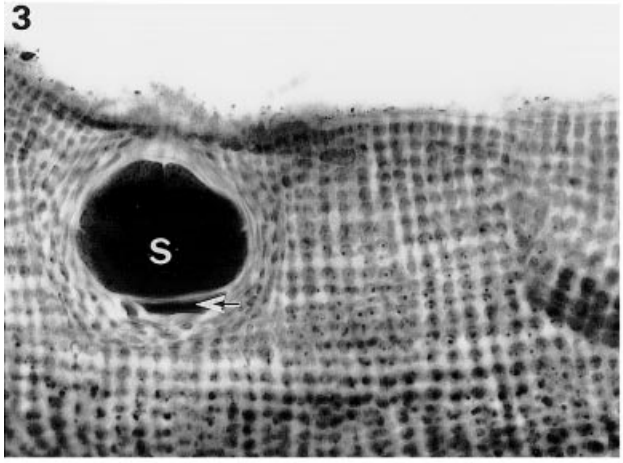
FLORA OF AUSTRALIA
JOHN RAY HERBARIUM
UNIVERSITY OF SYDNEY
ALGAE
FAMILY Sporolithaceae
NAME Heydrichia
LOCALITY Bongin Bongin Bay Mona Vale, New South Wales
DEPTH 0-10 ft.
NOTES:
DATE 10 July 1979
COLLECTOR R. Townsend
No. BB7905.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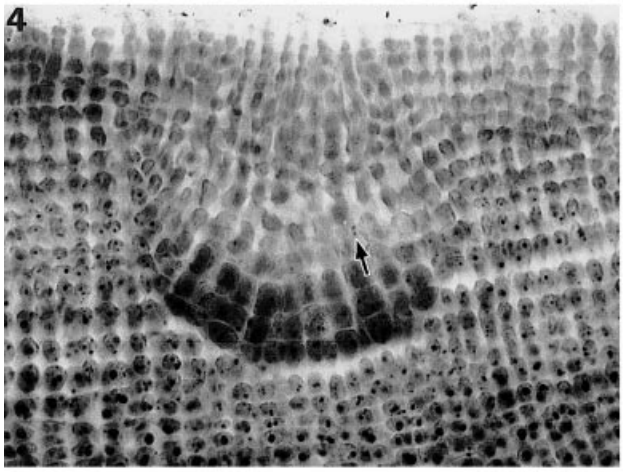
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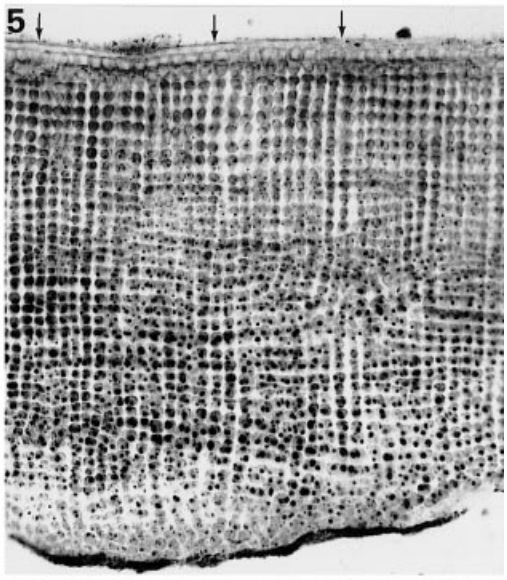
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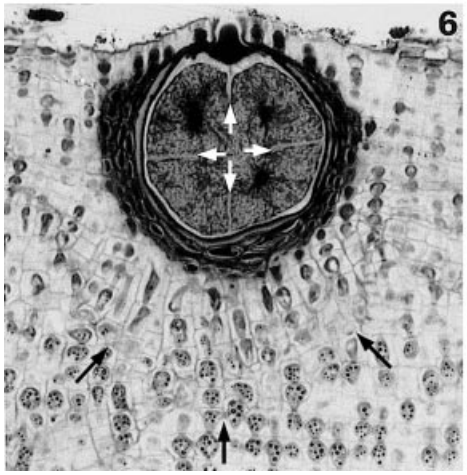
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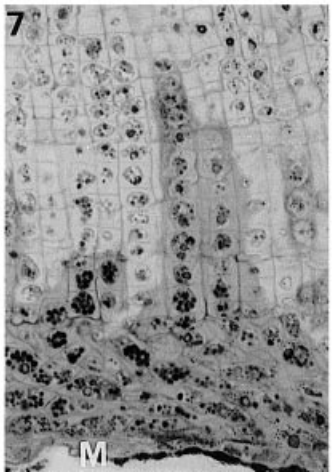
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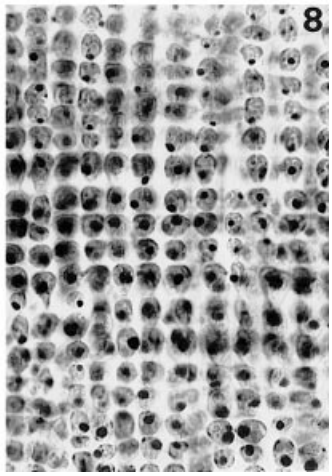
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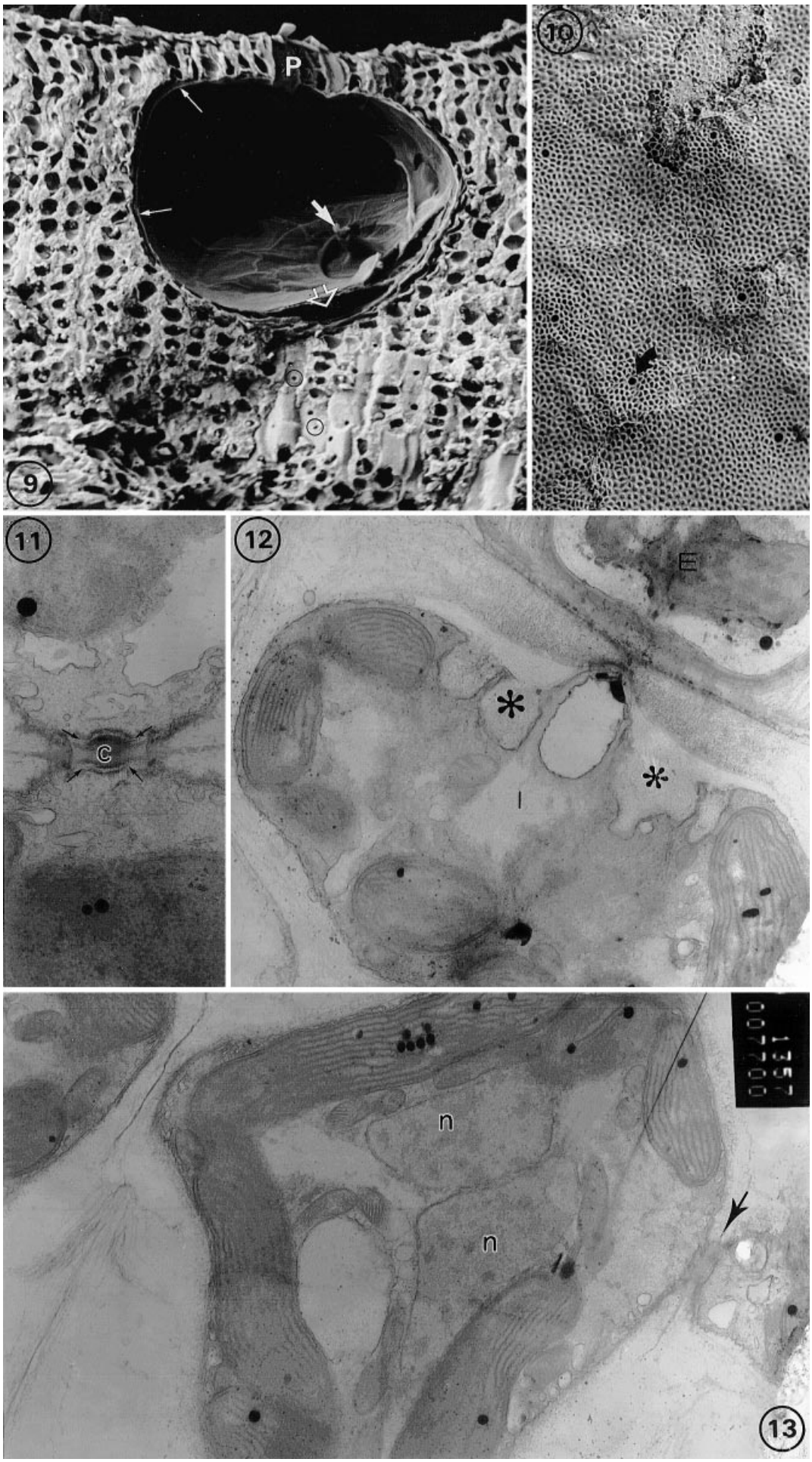
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division in the sporangium are either in the same plane or at right angles to one another (Fig. 6). In either case the resulting pattern is not the 'Y' pattern seen in *H. woelkerlingii*. The contiguous cell filaments forming the sporangial complex wall are interconnected by numerous connections that become more abundant as the sporangial complex matures. The wall filaments are lightly calcified (cf. Figs 3, 9). Bisporangia were not seen in *H. homalopasta*.

The nemathecia of *H. homalopasta* show major differences from those of the other two species of *Heydrichia* in that they consist of single sporangial complexes encircled by modified cortical filaments; the cells are of similar dimensions to the cells in the vegetative cortex. Nemathecia are produced successively in the cortex directly above, and in the same area as the modified cortex of earlier generations of sporangial complexes; i. e., in a vertical section of a thallus, nemathecia are found above evidence of previous reproductive events as shown by the pattern of secondary growth produced after nemathecial dehiscence (Fig. 6). In *H. homalopasta* the senescent nemathecium is sloughed from the thallus and secondary cortical growth occurs to 'fill up' sporangial lumens in the cortex (Fig. 4). New sporangial complexes form within this secondary growth in which pit connections and lateral cell fusions are a prominent feature.
Distribution and habitat: Coast between North Head, Port Jackson and Barrenjoey, New South Wales, Australia. The alga is restricted to ironstone and was itself the substrate for fleshy algae such as *Caulerpa filiformis* (Suhr) Hering.

Discussion

At first glance, *Heydrichia homalopasta* appears similar to many species of *Lithophyllum* (cf. Fig. 10 with Woelkerling and Campbell 1992 fig. 11 a). Upon breaking the thallus open, the differences become obvious, for the large spherical sporangial lumens of *H. homalopasta* are very different in shape from the depressed ovate shaped reproductive structures found in species of *Lithophyllum* (cf. Fig. 9 and Woelkerling and Campbell 1992 figs 3 a, 43 c−d). It is possible, however, that this taxon exists in collections either unnamed or placed with *Lithophyllum*.

Three species of *Heydrichia* have been described in the last five years (Townsend *et al*. 1994, Keats and Chamberlain 1995, this paper). Table I shows a comparison of the taxa based on eight characters. Of the three taxa, *H. woelkerlingii* represents the most robust species. The pit plug caps, so prominent in the cortex of *H. woelkerlingii* (Townsend *et al*. 1994 figs 12, 14, 17), are not found in the Australian species but do occur in the second South African species *H. groeneri* (Keats and Chamberlain 1995 fig 2, Cowan 1995 figs 316, 319, 320). Plug caps are not found in the nemathecial cortex of either *H. homalopasta* or *H. groeneri* whereas they are found in the gametophyte nemathecia of both South African species. The status of this character as a species or generic level character will remain uncertain until gametophyte thalli of *H. homalopasta* are found. Nemathecia in the African taxa have numerous sporangial complexes separated by elongate nemathecial cortex, whereas the nemathecium in *H. homalopasta* is a single sporangial complex surrounded by nemathecial cortex composed of cells no different from those of the vegetative cortex. Nemathecia are sloughed in all three species but the 'scars' from this process are different in each species. In *H. woelkerlingii* the 'scar' is signified by a differential staining property of the cortical cell walls in the area of a scar, associated with a slight change in direction of the secondary cortical filaments (Cowan 1995 fig. 289); in *H. groeneri* the 'scar' appears as a scalloped pattern of the secondary growth (Cowan 1995 fig. 312); and in *H. homalopasta*

Table I. Comparison of the three species of *Heydrichia* in terms of vegetative and reproductive characters. SC: sporangial complexes, PC: plug caps. (Sources: this paper, Townsend *et al*. 1994, Keats and Chamberlain 1995, Cowan 1995).

Character	*H. woelkerlingii*	*H. groeneri*	*H. homalopasta*
Thallus	thick (20 µm −15 mm)	thin (to 800 µm)	thin (to 1 mm)
Cortical PC	present	present	absent
Nemathecia	sloughed	sloughed	sloughed
Nem. cortex	elongate	elongate	absent
Nemathecia	many SC	1−6 SC	1 SC
Nem. PC	visible	not visible	not visible
Gam/te PC	present	present	?
Support cell	small	large	?

Figs 9−13. *Heydrichia homalopasta* (BB7902).
Fig. 9. SEM of sporangial complex. Note: sporangial initial wall (thin white arrows), youngest stalk cell (thick white arrow), older stalk cell (open white arrow) and the pore (P). Note also the fusions (circles) in the lower cortex. Scale: 1 cm = 30 µm. Fig. 10. SEM of surface of a number of nemathecia (indicated by pores, one with black arrow). Note: similarity of the epithallial cells around the pore and of the normal cortex. Scale: 1 cm = 100 µm. Fig. 11. TEM through primary pit connection. Note: inner plug cap (arrows) outside the plug core (c); outer plug caps are not present. Scale: 1 cm = 1.8 µm. Fig. 12. TEM of partial initial (I) and epithallial cell (E). In the epithallial cell the cytoplasm is degenerated. The initial cell has wall ingrowths on its upper tangential wall (*). Scale: 1 cm = 2 µm. Fig. 13. TEM of an initial which has secondary pit connections (arrow) with adjacent cells. Note: bilobed nucleus (n). Scale: 1 cm = 2 µm.

the secondary growth pattern is in the form of lenses of cortex similar to the pattern of scars after loss of the cystocarps in *H. woelkerlingii* (cf. Fig. 4 and Townsend *et al*. 1994 fig. 10). The relationship of the species to one another will become clearer when the yet undiscovered, gametophytes of *H. homalopasta* are described.

Recent palaeontological papers have rekindled the debate on the age of the coralline red algae (Basso *et al*. 1998, Brooke and Riding 1998, Riding *et al*. 1998). At various times in the past 50 years proposals have been put forward regarding the origin of this group (Johnson 1956, 1960, Riding 1977, Wray 1977). By the Cretaceous, calcified red algae with similar structure to present day taxa existed, such that fossil and recent individuals are indistinguishable at generic level. A number of fossil taxa have been described from the Ordovician, many of which have been promoted as possible precursors to the coralline algae. A new family of coralline algae, the Craticulaceae Brooke *et* Riding (1998) has been proposed from the Ordovician. This family includes *Craticula gotlandica* (Rothpletz) Brooke *et* Riding (1998) and possibly *Petrophyton kiaeri* Høeg (1932), which in turn may be an heterotypic synonym of *Solenopora richmondensis* Blackwell, Marak *et* Powell (1982). All of these fossils have vegetative character states in common with the Sporolithaceae and, in the case of *S. richmondensis* and *Craticula gotlandica*, reproductive structures have been recorded. The modern concept of the Sporolithaceae includes those coralline red algae with sporocytes placed in nemathecia. This character state exists in the entirely fossil genus *Craticula*, fossil members of *Sporolithon* and in *Solenopora richmondensis* (Blackwell *et al*. 1982, Brooke and Riding 1998, Vannucci *et al.* 2000. The differentiation of the nemathecia is a generic character within the Sporolithaceae. The differentiation of the sporangial complexes in *Heydrichia* culminates in a complete loss of the complex, however evidence of previous reproductive processes does occur. In all three species of *Heydrichia* there is a change in the orientation of the cortical filaments after a reproductive event. This character state may prove useful in determining whether *Heydrichia* is present in the fossil record. We have not seen published evidence that this is the case, but paleontologists have not looked for the subtle cortical patterns. It is also possible that fossils of *Heydrichia* have been mistaken for *Sporolithon*, since the filaments surrounding the sporangial complexes are decalcified during the process of reproductive differentiation. The recent scanning electron microscopy techniques developed by Braga *et al*. (1993) and used most recently by Rasser and Piller (1999) and Vannucci *et al*. (2000) should detect these filaments.

Heydrichia is apparently a Southern Hemisphere taxon. *Sporolithon* is a Tethyan genus, which has expanded its distribution as a result of tectonic plate movement and climatic changes since the Cretaceous. Its Holocene distribution is from the temperate Northern Hemisphere to temperate Southern Hemisphere. It is difficult to say whether *Heydrichia* is a recently evolved taxon or not, although its distribution and character states, as compared to those in *Sporolithon*, and the lack of fossil evidence indicates that *Heydrichia* is a more recent member of the Sporolithaceae.

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References

Adey, W. H. 1964. The genus *Phymatolithon* in the Gulf of Maine. *Hydrobiologia 24*: 377–420.

Adey, W. H. 1965. The genus *Clathromorphum* (Corallinaceae) in the Gulf of Maine. *Hydrobiologia 26*: 539–573.

Adey, W. H. 1966 a. The genera *Lithothamnium*, *Leptophytum* (nov. gen.) and *Phymatolithon* in the Gulf of Maine. *Hydrobiologia 28*: 321–370.

Adey, W. H. 1966 b. The genus *Pseudolithophyllum* (Corallinaceae) in the Gulf of Maine. *Hydrobiologia 27*: 479–497.

Basso, D., P. Fravega, M. Piazza and G. Vannucci 1998. Biostratigraphic, paleogeographic and paleontological implications in the taxonomic review of Corallinaceae. *Rc. Lincei, Sci. Fis. Nat. 9*: 201–211.

Blackwell, W. H., J. H. Marak and M. J. Powell 1982. The identity and reproductive structures of a misplaced *Solenopora* (Rhodophyta) from the Ordivician of Southwestern Ohio. *J. Phycol. 18*: 477–482.

Borowitzka, M. A. and M. Vesk 1978. Ultrastructure of the Corallinaceae (Rhodophyta) I. Vegetative cells of *Corallina officinalis* and *C. cuvierii*. *Mar. Biol. 46*: 295–304.

Braga, J. C., D. W. Bosence and R. S. Steneck 1993. New anatomical characters in fossil coralline algae and their taxonomic implications. *Palaeontology 36*: 535–547.

Brooke, C. and R. Riding 1998. Ordivician and Silurian coralline red algae. *Lethaia 31*: 187–195.

Cabioc'h, J. 1968. Sur le mode de formation des trichocytes chez le *Neogoniolithon notarisii* (Dufour) Setchell *et* Mason. *C. R. Hébd. Séanc. Acad. Sci. 266*: 333–336.

Cabioc'h, J. 1971 a. Essai d'une nouvelle classification des Corallinacées actuelles. *C. R. Hébd. Séanc. Acad. Sci. 272*: 1616–1619.

Cabioc'h, J. 1971 b. Étude sur les Corallinacées. I. Caractères généraux de la cytologie. *Cah. Biol. mar. 12*: 121−186.

Cabioc'h, J. 1972. Étude sur les Corallinacées. II. La morphogenèse: conséquences systématiques et phylogénétiques. *Cah. Biol. mar. 13*: 137−288.

Chamberlain, Y. M. 1986. A reassessment of the type specimens of *Titanoderma verrucatum* and *T. macrocarpum* (Rhodophyta, Corallinaceae). *Crypto., Algol.* 7: 193−213.

Chamberlain, Y. M. 1990. The genus *Leptophytum* (Rhodophyta, Corallinaceae) in the British Isles with descriptions of *Leptophytum bornetii*, *L. elatum* sp. nov. and *L. laeve*. *Br. Phycol. J. 25*: 179−199.

Chamberlain, Y. M. 1991 a. Historical and taxonomic studies in the genus *Titanoderma* (Rhodophyta, Corallinales) in the British Isles. *Bull. Br. Mus.(Nat. Hist.) 21*: 1−80.

Chamberlain, Y. M. 1991 b. Observations on *Phymatolithon lamii* (Lemoine) Y. Chamberlain comb. nov. (Rhodophyta, Corallinales) in the British Isles and an assessment of its relationship to *P. rugulosum*, *Lithophyllum lamii* and *L. melobesioides*. *Br. Phycol. J. 26*: 219−233.

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 yendoi* (Foslie) comb. nov. in South Africa and its relationship to *S. decipiens* (Foslie) comb. nov. and *Lithophyllum natalense* Foslie. *Phycologia 32*: 100−115.

Chamberlain, Y. M. 1994. *Pneophyllum coronatum* (Rosanoff) D. Penrose comb. nov., *P. keatsii* sp. nov., *Spongites discoideus* (Foslie) D. Penrose *et* Woelkerling and *S. impar* (Foslie) Y. Chamberlain comb.nov. (Rhodophyta, Corallinaceae) from South Africa. *Phycologia 33*: 141−157.

Cowan, R. A. 1995. The Sporolithaceae: Its Place in the Florideophycidae. Ph.D. thesis Sydney University: Australia (*note*: R. A. Cowan = R. A. Townsend).

Hamel, G. and M. Lemoine 1952. Corallinacées de France et d'Afrique du Nord. *Arch. Mus. natn. Hist. nat. 1*: 1−136, pls 1−23.

Heydrich, F. 1897. Corallinaceae, inbesondere Melobesieae. *Ber. Deut. Bot. Ges. 15*: 34−70, pl.3.

Høeg, O. A. 1932. Ordovician algae from the Trondheim area. *Skr. norske Vidensk.-Akad. Mat.-naturv. Kl. 4*: 63−96.

Holmgren, P., N. H. Holmgren and L. C. Bartlett 1990. The Herbaria of the World. *In*: *Index Herbariorum*., 1. (8th. edn). New York Botanical Gardens, New York. x + 693 pp.

Johansen, H. W. 1969. Morphology and systematics of coralline algae with special reference to *Calliarthron*. *Univ. Calif. Publ. Bot. 49*: viii+ 78, 19 pls.

Johnson, J. H. 1956. Ancestry of the coralline algae. *J. Paleontol. 30*: 563−567.

Johnson, J. H. 1960. Paleozoic Solenoporaceae and related red algae. *Colo. Sch. Mines Q. 55*: xiii,1−77.

Keats, D. W. and Y. M. Chamberlain 1993. *Sporolithon ptychoides* Heydrich and *S. episporum* (Howe) Dawson: two coralline red algae (Corallinales, Sporolithaceae) in South Africa. *S. Afr. J. Bot. 59*: 541−550.

Keats, D. W. and Y. M. Chamberlain 1994 a. Three species of *Hydrolithon* (Rhodophyta, Corallinaceae): *Hydrolithon onkodes* (Heydrich) Penrose and Woelkerling, *Hydrolithon superficiale* sp. nov. and *H. samoënse* (Foslie) comb. nov. from South Africa. *S. Afr. J. Bot. 60*: 8−21.

Keats, D. W. and Y. M. Chamberlain 1994 b. Two melobesioid coralline algae (Rhodophyta, Corallinales), *Mesophyllum erubescens* (Foslie) Lemoine and *Mesophyllum funafutiense* (Foslie) Verheij from Sodwana Bay, South Africa. *S. Afr. J. Bot. 60*: 175−190.

Keats, D. W. and Y. M. Chamberlain 1995. *Heydrichia groeneri* sp. nov.: a new species of crustose coralline alga (Rhodophyta, Sporolithaceae) from South Africa and Namibia. *Phycologia 34*: 51−57.

Kelly, K. L. and D. B. Judd 1976. Colour. Universal language and dictionary of names. *National Bureau of Standards*, U.S.A. Special Publication No. 440: 1−158.

Pueschel, C. M. 1990. Cell Structure. *In:* (K. M. Cole and R. G. Sheath, eds) *Biology of the Red Algae.* Cambridge University Press, Cambridge. pp. 7−41.

Rasser, M. W. and W. E. Piller 1999. Application of neontological taxonomic concepts to Late Eocene coralline algae (Rhodophyta) of the Austrian Molasse Zone. *J. Micropalaeontol. 18*: 67−80.

Riding, R. 1977. Problems of affinity in Palaeozoic calcareous algae. *In:* (E. Flügel ed.). *Fossil Algae, Recent Results and Developments.* Springer, Berlin. pp. 202−211.

Riding, R., J. C. W. Cope and P. D. Taylor. 1998. A coralline-like red alga from the lower Ordovician of Wales. *Palaeontology 41*: 1069−1076.

Setchell, W. A. 1943. *Mastophora* and the Mastophoreae: genus and subfamily of Corallinaceae. *Proc. Nat. Acad. Sci. 29*: 127−135.

Townsend, R. A. and W. H. Adey 1990. Morphology of the Caribbean alga: *Goniolithon improcerum* Foslie *et* Howe *in* Foslie (Corallinaceae, Rhodophyceae). *Bot. Mar. 33*: 99−116.

Townsend, R. A., Y. M. Chamberlain and D. W. Keats 1994. *Heydrichia woelkerlingii* sp. et gen. nov. a new nongeniculate coralline alga from South Africa. *Phycologia 33*: 177−186.

Townsend, R. A., W. J. Woelkerling, A. S. Harvey and M. A. Borowitzka 1995. An account of the red algal genus *Sporolithon* (Sporolithaceae, Corallinales) in southern Australia. *Austral. Syst. Bot. 8*: 85−121.

Vannucci, G., M. Piazza, P. Fravega and D. Basso. 2000. Revision and re-documentation of M. Airoldi's species of *Archaeolithothamnium* from the Tertiary Piedmont Basin (NW Italy). *Riv. ital. Paleont. Stratig. 106*: 191−202.

Verheij, E. 1993. The genus *Sporolithon* (Sporolithaceae fam. nov., Corallinales) 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 the Nongeniculate Corallinaceae.* Oxford University Press/British Museum (Nat. Hist.), London. 268 pp.

Woelkerling, W. J. and S. J. Campbell 1992. An account of southern Australian species of *Lithophyllum* (Corallina-

ceae, Rhodophyta). *Bull. Brit. Mus. (Nat. Hist.) Bot. 22*: 1−107.

Womersley, H. B. S. and A. Bailey 1970. Marine algae of the Solomon Islands. *Phil. Trans. R. Soc. 259*: 257−352

Wray, J. L. 1977. *Developments in Paleontology and Stratigraphy: 4. Calcareous Algae.* Elsevier, Amsterdam. 185 pp.