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Non-Geniculate Coralline Algae (Corallinales, Rhodophyta) on Heron Reef, Great Barrier Reef (Australia)

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This is the first modern, comprehensive account of non-geniculate coralline algae (Corallinales, Rhodophyta) occurring on the Great Barrier Reef (Heron Reef). Species were identified in a modern context, using reproductive and vegetative anatomy as diagnostic features. In a collection of 300 specimens, 11 different species were identified. Eight of the species were found exclusively on calcareous substrata, one was exclusively epiphytic, while the remaining two were both epiphytic and found growing on calcareous substrata. Although none of the species are new to science, one is newly recorded for Australia (*Hydrolithon reinboldii*) and 5 are newly recorded for the Great Barrier Reef region (*Spongites fruticulosus*, *Lithophyllum frondosum*, *L. pustulatum*, *Mastophora pacifica* and *Mesophyllum erubescens*). Collections made by A. B. Cribb in the 1960s on Heron Reef were also studied, once again using reproductive and vegetative anatomy as diagnostic features. Illustrations of each species and a tabular key are provided to facilitate non-geniculate coralline algal identification on Heron Reef. Information on their distribution and growth-forms are provided along with references to more detailed morphological accounts and published illustrations. The reported species are compared to findings from other tropical reef systems.

Introduction

Non-geniculate coralline algae (Corallinales, Rhodophyta) are distributed worldwide (Colombo 1888, Johansen 1981, Steneck 1986, Woelkerling 1988). They are the deepest known benthic plants and occur from the upper intertidal to depths exceeding 200 m (Littler *et al.* 1991). Non-geniculate coralline algae (NCA) play a vital role in the construction and maintenance of coral reefs (Dawson 1961, Littler 1972, Wray 1977, Borowitzka 1979, Bjoerk *et al.* 1995, Littler *et al.* 1995), by cementing the reef material together to form a strong and solid structure (Littler 1973) and binding coarse and fine material (Payri 1997).

No modern published accounts of NCA from the Great Barrier Reef region (GBR, Queensland) exist. Extant records are widely scattered and dated. Cribb (1983, 1984) provides information on the algal vegetation of the southern Great Barrier Reef including Heron Reef. He recorded 9 species of NCA and stated that they have received inadequate attention. Consequently there is a critical lack of information on the taxonomy of tropical NCA species occurring on the GBR. Ecological data are limited and data on their distribution and abundance are virtually non-existent.

Recent studies have shown that growth-forms of NCA are generally very variable and a single species may show a variety of different morphotypes (Steneck and Adey 1976, Woelkerling 1988). Previous workers (Lee 1967, Masaki 1968, Chapman and Parkinson 1974, Lawson and John 1987) have, to a large extent, used these differences in growth-form to delimit taxa and to identify specimens. The extent however, to which differences in growth-forms can be used for species identification is still unresolved (Woelkerling *et al.* 1993 a). Published accounts (Woelkerling 1988, Chamberlain 1991, Keats *et al.* 1996, Chamberlain 1997) have shown that species identification based on reproductive structures (tetrasporangial conceptacle anatomy) provide more reliable results. Previous collections from Heron Reef therefore require re-examination and verification.

The aims of the present study are to provide an account of the NCA occurring on Heron Reef by identifying species in a modern context and checking against type material and/or published literature. Remarks about type material examined, growth-form and tetrasporangial conceptacle anatomy are provided for each species with relevant photographs. Data on collections examined, including information on distribution and relative abundance, any distinctive field characters with references to additional information as well as illustrations and pertinent comments are included in the species accounts and a tabular key. Specimens previously collected by A. B. Cribb from Heron Reef are re-examined in a modern context and a key including characters that can be observed in the field is provided. The reported species are compared and discussed in relation to findings from other tropical areas.

Materials and Methods

Random sampling took place on Heron Reef at different months between 1992 and 1998 during which more than 300 collections were obtained. In addition, available specimens collected by A. B. Cribb on Heron Reef (mostly in the 1960s) and lodged in the Queensland Herbarium (BRI), as well as specimens collected on Heron Reef and lodged with the New South Wales Herbarium (NSW) were re-examined and included in the findings of the present study.

Study sites

All fieldwork was conducted on Heron Reef (23°27′ S, 151°55′ E), located in the Capricorn Bunker Group of the southern Great Barrier Reef. Heron Reef is an enclosed elongate lagoonal reef system, approx. 9.5 km by 4.5 km, with a well developed windward rim to the south and a less well-developed northern leeward rim (Smith *et al.* 1998). Six study areas were chosen (Fig. 1) to provide a range of environmental conditions with respect to water movement and light. Sites 1 and 2 were on the northern (leeward) reef slope at 10 m and 5 m depth respectively, site 3 was on the southern (windward) reef slope at 5 m depth, site 4 was in the lagoon at 2.5 m−5 m, site 5 was on the south reef flat and site 6 on the north reef flat. Hereafter, these sites are abbreviated as N 10 m, N 5 m, S 5 m, L 2.5 m, SF and NF. The northern reef slope (N 10 m and N 5 m) is characterised by a gentle slope from the reef crest to about 5 m depth, where it drops to a sandy bottom at 15 m. At the southern site (S 5 m), the reef slope is steeper than on the north side and is dominated by large branching species of the coral *Acropora* to about 7 m depth. Below 7 m, the sandy bottom is covered with small patches of coral rubble. Located in the central lagoon is L 2.5 m, an elongated patch reef ca. 8 × 3 m wide that is subtidal even at extreme spring low tides. Detailed descriptions of the geomorphology of Heron Reef are provided in Mather and Bennet (1993).

Sampling method and laboratory procedures

Collection of algae was done by SCUBA, snorkelling or reef walking. Hammer and chisel were used to remove the algae from the reef and samples were transported to the laboratory in seawater filled containers. In the laboratory, the NCA were fixed in 5% Formalin-seawater solution. After 48 hours collections were thoroughly rinsed in seawater and transferred into a 7:2:1 ethanol:water:glycerol solution.

Prior to species identification fragments containing conceptacles (a cavity which opens to the surface and contains the reproductive structures) were removed under a dissecting microscope using a razor blade, decalcified in 0.6 M HNO_3, rinsed with distilled water, stained in 2% aqueous $KMnO_4$, dehydrated through 30%, 60%, 90% and 100% ethanol and embedded in

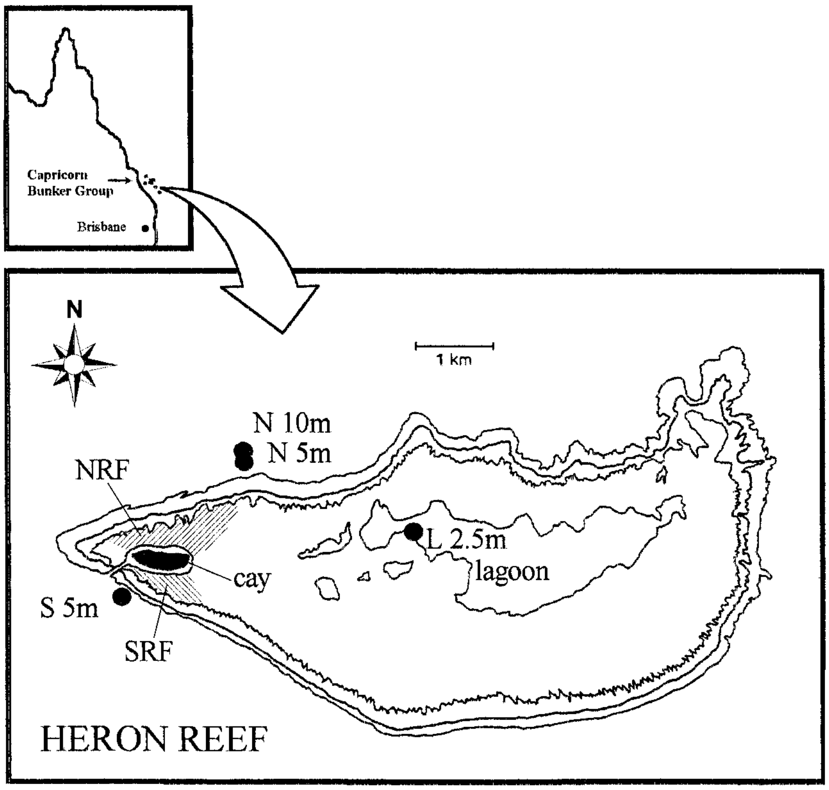


Fig. 1. Map of the study sites on Heron Reef. N 10 m = north slope at 10 m, N 5 m = north slope at 5 m, L 2.5 m = Lagoon 2.5−5 m, S 5 m = south slope at 5 m, NF = north reef flat, SF = south reef flat.

medium grade 'White' resin (London Resin Company Ltd., Basingstoke, England). The embedded material was cut into 6–10 μm sections using a microtome and placed serially on slides for further microscopic analysis. More detailed information on the entire laboratory procedure is published in Woelkerling (1988).

Distribution and relative abundance were determined using a combination of both, collection data and field observations.

Identification

Specimens were identified using tetrasporangial conceptacle anatomy. Where possible, NCA were identified to species level using the taxonomic keys in *Marine Benthic Flora of Southern Australia Part IIIB* (Womersley 1996) and/or compared to appropriate type material and published literature. For species not previously reported from Australia, specimens were compared to the appropriate type material and/or published literature and names applied. All permanent slides and specimens are deposited at the Department of Botany, La Trobe University, Melbourne (LTB). The LTB collections eventually will be transferred to the National Herbarium of Victoria, Royal Botanic Gardens, Melbourne (MEL). The A. B. Cribb specimens examined are currently held by the Queensland National Herbarium (BRI). Herbarium abbreviations follow Holmgren *et al.* (1990).

Subfamily concepts follow Harvey and Woelkerling (1995) and accounts are presented alphabetically by subfamily, genus and species.

Key to species

A tabular key was developed after final taxonomic species identification and assessment of the range in growth-forms of the Heron Reef collections. The key is divided into four different categories: I. Characters that are related to the tetrasporangial conceptacle anatomy. II. Characters that are related to the thallus anatomy. III. Characters that are related to the thallus morphology (growth-form). IV. Characters that are specific in the field.

To identify the characters related to the tetrasporangial conceptacle anatomy, the thallus preparation method described by Woelkerling (1988) was followed.

To recognise the characters related to the thallus anatomy, the following laboratory procedure is required:

a) Carefully detach a small part of the thallus using a razorblade.
b) Decalcify the plant material with 0.6 N HNO_3.
c) Stain plant material in a watch glass with 'Aniline blue' or $KMnO_4$.
d) Place material carefully on a microscopic slide and tease it.

The terminology to describe growth-forms follows Woelkerling *et al.* (1993 a).

Results

Species occurrence and distribution

Eleven species representing seven genera and three subfamilies of non-geniculate coralline algae were found on Heron Reef (Table I). One of these species, *Hydrolithon reinboldii* is newly recorded for Australia and the GBR and five are newly recorded from the GBR region (*Spongites fruticulosus*, *Lithophyllum frondosum*, *L. pustulatum*, *Mastophora pacifica* and *Mesophyllum erubescens*). *Hydrolithon farinosum* was exclusively epiphytic, *Hydrolithon onkodes* and *Lithophyllum pustulatum* grew on both algae and on calcareous substrata, while the remaining 8 species grew on calcareous substrata only.

Species richness and relative abundances (see Table I) were lowest at the south slope (S 5 m) and highest in the lagoonal area (L 2.5 m), although the lagoon has wide areas covered by sand and rubble that are totally devoid of NCA. Five of the 11 species (*Lithophyllum tamiense, Hydrolithon onkodes*, *H. reinboldii*, *Spongites fruticulosus* and *Mesophyllum erubescens*) were found at all 6 collection sites, while *Lithophyllum pustulatum*, *Hydrolithon farinosum, Mastophora pacifica* and *Neogoniolithon brassica-florida* were present at only 3 of the sites. *Lithothamnion prolifer* was collected at one site only (N 10 m), however it was observed to occur at a further 5 sites, particularly under overhangs and in crevices. *Lithophyllum frondosum* occurred at all sites, except on the reef flat (NF and SF). Two species were notably abundant/dominant at specific sites. *Hydrolithon onkodes* was dominant on the south reef flat (SF) towards the reef rim and abundant on the north reef flat (NF) towards the rim. *Neogoniolithon brassica-florida* was found mainly in tide pools on the north reef flat (NF).

The following species accounts contain relevant information required to identify the eleven species of NCA found on Heron Reef. Diagnostic features associated with tetrasporangial conceptacle anatomy are described, along with further references to more detailed morphological accounts and published illustrations, included also are pertinent comments. The range in growth-forms is displayed in relevant photos and information on relevant type material is also presented.

Subfamily Lithophylloideae Setchell 1943: 134 (as 'Lithophylleae').

Lithophyllum frondosum (Dufour) Furnari, Comaci *et* Alongi 1996: 115.

Basionym: *Melobesia frondosa* Dufour 1861: 39.
See also Woelkerling *et al.* (1993 b: 326, figs 12–15) and Woelkerling and Lamy (1998: 372, fig. 326).

Table I. Relative abundance of NCA at the collection sites (1: present; 2: common; 3: abundant; 4: dominant). These results represent data from both specimen collections and field observations.

Species	N 10 m	N 5 m	NF	L 2.5 m	SF	S 5 m
Lithophyllum frondosum	1	1		1		1
Lithophyllum pustulatum (mostly epiphytic)	1		2 (epiphytic)	3 (epiphytic)		
Lithophyllum tamiense	1	1	2	3	1 (tide pools)	1
Hydrolithon farinosum (exclusively epiphytic)			2	2	2	
Hydrolithon onkodes	1	1	3 (reef rim)	2	4 (reef rim)	1
Hydrolithon reinboldii	2	1	2	3	2	1
Mastophora pacifica	1	1		1		
Neogoniolithon brassica-florida			3 (tide pools)	2	1 (tide pools)	
Spongites fruticulosus	1	1	1	3	1	1
Lithothamnion prolifer	2 (cavities)	2 (cavities)	1 (pool cavities)		1 (pool cavities)	2 (cavities)
Mesophyllum erubescens	2	1	2	2	1	2

For additional published records of *Lithophyllum frondosum* and its synonyms see Woelkerling (1996).

Heterotypic synonym: *Lithophyllum bermudense* Foslie *et* Howe 1906: 132, pl. 81 fig. 3, pl. 85 fig. 3, pl. 92.

Additional information and illustrations on this species can be found in Woelkerling and Campbell (1992), Barry and Woelkerling (1995) (both as *L. bermudense*) and Furnari *et al*. (1996).

Heron Reef collections examined. N 5–N 10 m (*P. Ringeltaube* and *S. Daume*: 12.i.1993, LTB 20601). L 2.5 m (5 m) (*P. Ringeltaube*: MAR. 1992, LTB 20799). Reef rim (*P. Ringeltaube*: JAN. 1998, LTB 20817). S 5 m (*P. Ringeltaube*: FEB. 1994, LTB 20735, 20736).

Tetrasporangial conceptacle anatomy and growth-form. Tetrasporangial and carposporangial plants were found on Heron Reef. All features considered diagnostic of *Lithophyllum frondosum* by Woelkerling (1996) were evident in the Heron Reef collections and they were concordant with the holotype.

Tetrasporangial conceptacles (Fig. 2) of Heron Reef collections were uniporate with mature tetrasporangial chambers 230–370 µm in diameter and the chamber floor 9–11 cell layers below the thallus surface. Pore canals were lined with cells projecting somewhat into but not completely occluding the canal.

The growth-form of *L. frondosum* on Heron Reef was encrusting (Fig. 3) to warty (Fig. 4) with individual plants up to 55 mm across.

Comments. *Lithophyllum frondosum* and *L. corallinae* (Crouan *et* Crouan) Heydrich are currently separated taxonomically mainly on size differences of mature tetrasporangial conceptacle chambers (320–410 µm vs 190–235 µm) and the number of cells in the tetrasporangial roofs (4–7 vs 2–4) (Woelkerling 1996). Tetrasporangial conceptacle dimensions and number of cells in the roof of some plants found on Heron Reef approached that of *L. corallinae* (chambers down to 230 µm and roofs 4–5 cells thick). A similar situation was noted by Woelkerling (1996), who concluded that further studies of the relationship between these two species are required. Should further studies of *L. frondosum* and *L. corallinae* provide data that they are the same species *L. corallinae* is an older name and has nomenclatural priority.

Lithophyllum pustulatum (Lamouroux) Foslie 1904 a: 8.

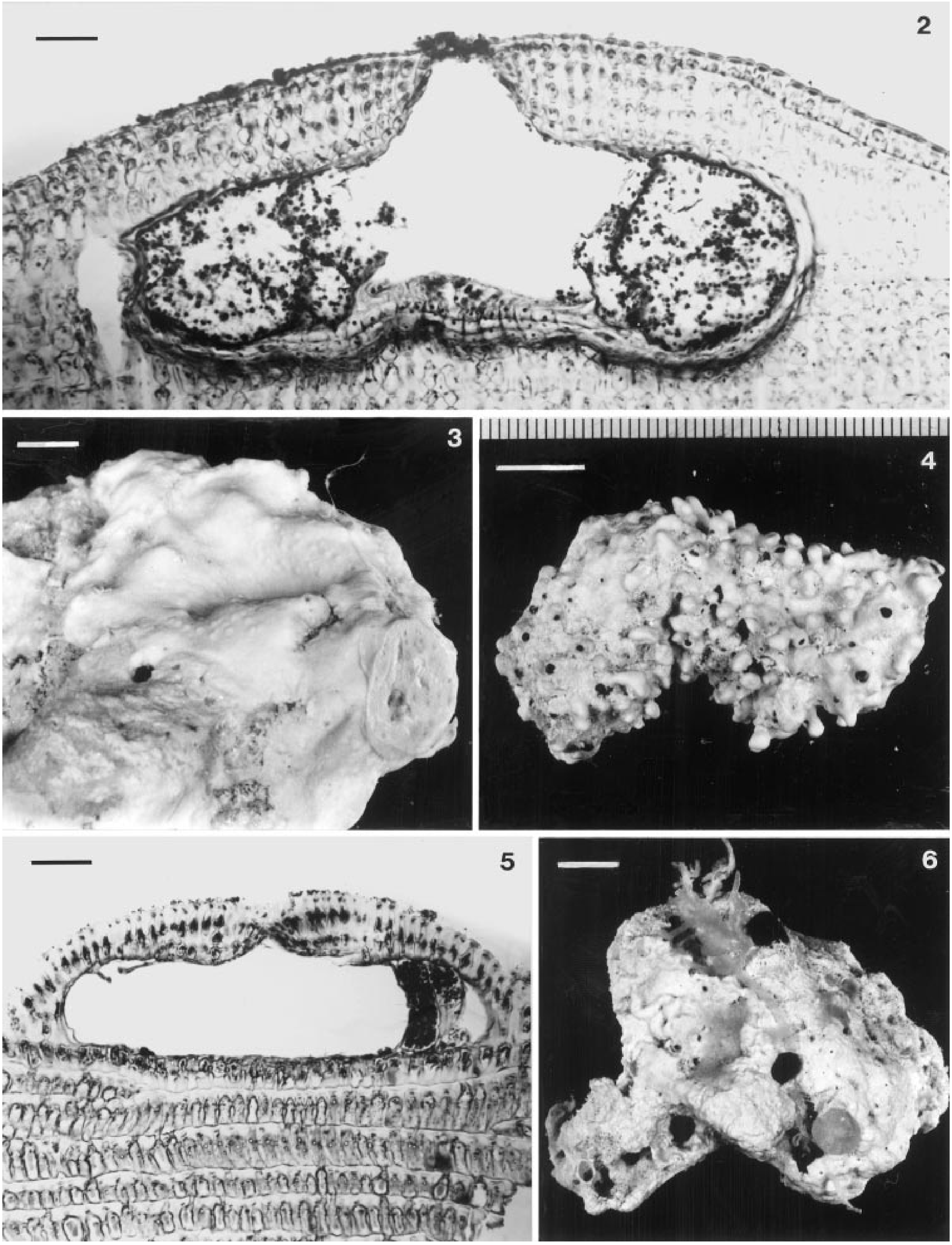
Basionym: *Melobesia pustulata* Lamouroux 1816: 315.

For additional published records of *L. pustulatum* and its synonyms see Woelkerling and Campbell (1992).

Additional information and illustrations on this species can be found in Woelkerling and Campbell (1992), Irvine and Chamberlain (1994) and Barry and Woelkerling (1995).

Heron Reef collections examined. Epiphytic on *Halimeda* sp. L 2.5 m, SF and NF (*P. Ringeltaube*: NOV. 1994, LTB 20767, 20768, 20769, 20772, 20777, 20782, 20783, 20789: JAN, 1998, LTB 20829, 20830). L 2.5 m (5 m) epiphytic on *Halimeda* sp. (*P. Ringeltaube*: 12.i.1993, LTB 20608). N 10 m (*P. Ringeltaube*: FEB. 1994, LTB 20761).

Tetrasporangial conceptacle anatomy and growth-form. Tetrasporangial, female and carposporangial plants were found. All features considered diagnostic of *Lithophyllum pustulatum* by Woelkerling (1996) were evident in the Heron Reef collections and they were concordant with the holotype. Tetrasporangial conceptacles (Fig. 5) of Heron Reef collections were uniporate with mature tetrasporangial chambers 190–250 (–400) µm in diameter. Chamber floors were 1–3 cell layers below the thallus surface with pore canals lined with cells projecting somewhat into but not completely occluding the canal.



Figs 2–4. *Lithophyllum frondosum*.
Fig. 2. Uniporate tetrasporangial conceptacle (LTB 20736, scale is 35 μm). Fig. 3. Encrusting growth-form (LTB 20601, scale is 3 mm). Fig. 4. Warty growth-form (LTB 20799, scale is 10 mm).

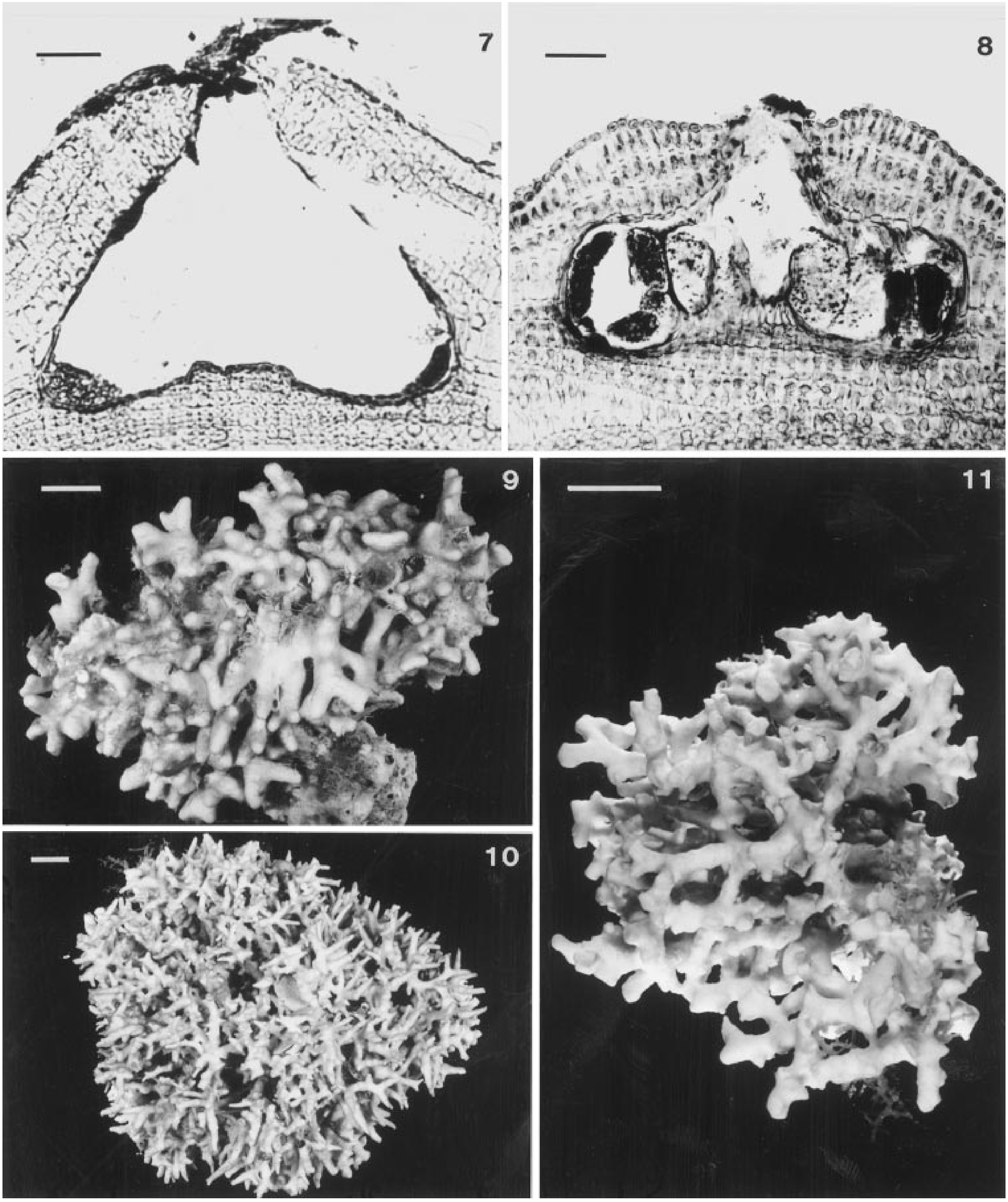
Figs 5 and 6. *Lithophyllum pustulatum*.
Fig. 5. Uniporate tetrasporangial conceptacle (LTB 20761, scale is 50 μm). Fig. 6. Encrusting growth-form (LTB 20761, scale is 10 mm).

All plants on Heron Reef were encrusting in growth-form (Fig. 6). Those epiphytic on *Halimeda* sp. were no more than 4 mm width and a single epizoic collection (LTB 20761) was only 40 mm across.

Lithophyllum tamiense (Heydrich) Foslie 1900 a: 16.

Basionym: *Lithothamnion tamiense* Heydrich 1897 a: 1, figs 4–7.

Published illustration in Heydrich (1897 a, pl. 1, figs 5–7). See also Woelkerling and Lamy (1998: 362, figs 298–300).



Figs 7–11. *Lithophyllum tamiense*.
Fig. 7. Uniporate tetrasporangial conceptacle of lectotype material (C, unnumbered) (scale is 50 μm). Fig. 8. Uniporate tetrasporangial conceptacle (LTB 20708, scale is 50 μm). Fig. 9. Fruticose growth-form with blunt ends and thick branches (LTB 20587, scale is 10 mm). Fig. 10. Fruticose growth-form with pointed ends and thin branches (LTB 20696, scale is 8 mm). Fig. 11. Intermediate fruticose growth-form with relatively thin branches and blunt ends (LTB 20707, scale is 10 mm).

Heterotypic synonym: *Lithophyllum moluccense* Foslie 1897: 12.

Published illustrations of holotype in Printz (1929, pl. 55, fig. 14 as *Lithophyllum moluccense f. typica*). Isolectotypes: PC, unnumbered, Sauvageau Herbarium; C, unnumbered; TRH, unnumbered, includes slide 652.

The isolectotype of *Lithophyllum tamiense* from Copenhagen (C, unnumbered) was examined and found to have uniporate tetrasporangial conceptacles (Fig. 7) with cells projecting into but not occluding the pore canal. Mature tetrasporangial chambers were 330 µm in diameter with the chamber floor 10 cell layers below the thallus surface. Published illustrations of the type show the growth-form to be fruticose with pointed/tapered tips. Additional information and illustrations of this species can be found in Verheij (1994).

Heron Reef collections examined. N 5 m−N 10 m (*P. Ringeltaube*: 12.i.1993, LTB 20586, 20599). L 2.5 m (*P. Ringeltaube*: 12.i.1993, LTB 20595; *P. Ringeltaube and S. Daume:* FEB. 1994, LTB 20696, 20697, 20705, 20706, 20707, 20709, 20708, 20710, 20712, 20714, 20716, 20717, 20718, 20724, 20726, 20727, 20728;). NF (*P. Ringeltaube*: 6.i.1993, LTB 20587; *P. Ringeltaube*: JAN. 1998, LTB 20821). Heron Reef (*A. Cribb*: 1963, BRI 712424). Reef Flat (*A. Cribb*: FEB.1964, BRI 712448). South Platform (*A. Cribb*: JUN. 1961, BRI 712434, *A. Cribb*: 31.i.1963, BRI 712465, *A. Cribb*: 4.xi.1975, BRI 712433).

Tetrasporangial conceptacle anatomy and growth-form. Tetrasporangial, male and carposporangial plants were found on Heron Reef. Vegetative and reproductive anatomy of Heron Reef collections were concordant with that found in the type material of *Lithophyllum tamiense*.

Tetrasporangial conceptacles (Fig. 8) of Heron Reef collections were uniporate with mature tetrasporangial chambers 260−400 µm in diameter and the chamber floor 5−8 cell layers below the thallus surface. Pore canals were lined with cells projecting somewhat into but not completely occluding the canal. Tetrasporangia were peripheral to a central columella or scattered across conceptacle chamber floor.

Heron Reef specimens were fruticose in growth-form and up to 95 mm across. Individual plants varied from fruticose with blunt ends and relatively thicker branches (Fig. 9), to fruticose with pointed ends and relatively thinner branches (Fig. 10).

Comments. Cribb (1983) identified specimens of *Lithophyllum tamiense* as *Lithophyllum moluccense*. In addition he distinguished plants of *Lithophyllum* with different growth-forms as two different species. He identified plants with branches that were strongly flattened with blunt apices (Cribb 1983, plate 53, fig. 2) as *Lithophyllum kotschyanum* (Unger) Foslie and plants with tapered branches and relatively sharp apices (Cribb 1983, plate 54, fig. 1) as *Lithophyllum tamiense (moluccense)* respectively. The Heron Reef collections, however, showed a continuum in both, branch thickness and morphology of branch tips. Illustrated plants measured 5 mm from the branch tip and branch thickness ranged from 1.4−2.5 mm (see Fig. 10) to 2.0−3.0 mm (Fig. 11) through to 3.0−5.5 mm across (see Fig. 9). In addition, the branch tip morphology showed a continuum from pointed to blunt with varying branch thickness (not illustrated). As plants of both growth-forms were anatomically and reproductively concordant the present authors have referred all plants to the one species (*L. tamiense*) which shows a varied fruticose habit.

Specimens referred to *Lithophyllum tamiense* from Heron Reef were found to be vegetatively and reproductively concordant with type material of *L. tamiense* examined during the present study (see Figs 7 and 8). Type material of *L. kotschyanum* was not examined during the present study however, should further studies of *L. tamiense* and *L. kotschyanum* provide data that they are the same species *L. kotschyanum* is an older name and has nomenclatural priority.

In addition vegetative and reproductive anatomy of Heron Reef *L. tamiense* collections, are concordant with that found in southern Australian plants of *L. frondosum*. The distinct fruticose growth-form however, of Heron Reef collections has no southern Australian counterparts. Heron Reef collections therefore have been maintained as a distinct species pending further detailed investigations.

Subfamily Mastophoroideae Setchell 1943: 134 (as 'Mastophoreae')

Hydrolithon farinosum (Lamouroux) Penrose *et* Chamberlain 1993: 295.

Basionym: *Melobesia farinosa* Lamouroux 1816: 315.

For additional published records of *Hydrolithon farinosum* and its synonyms see Penrose (1996).

Additional information and published illustrations on this species can be found in Penrose and Chamberlain (1993) and Penrose (1996).

Heron Reef collections examined. NF and SF (*P. Ringeltaube*: JAN. 1998, LTB 20824, 20825, 20827, 20828, 20832). L 2.5 m, NF and SF epiphytic on *Halimeda* sp. (*P. Ringeltaube*: JUN. 1994, LTB 20781). L 2.5 m (5 m) on *Halimeda* sp. (*P. Ringeltaube*: 12.i.1993, LTB 20592).

Tetrasporangial conceptacle anatomy and growth-form. Only tetrasporangial plants were found on Heron Reef. All features considered diagnostic of *Hydrolithon farinosum* by Penrose (1996) were evident in the Heron Reef collections and they were concordant with the holotype.

Tetrasporangial conceptacles (Fig. 12) of Heron Reef collections were uniporate with pore canals lined by cells that were orientated more of less perpendicular to the roof surface. Mature tetrasporangial chambers were 40–65 μm in diameter.

The growth-form of *H. farinosum* on Heron Reef was entirely encrusting (Fig. 13). The plants were epiphytic (usually on *Halimeda sp.*), their thalli were no more than 2 cell layers thick and measured up to 2 mm across.

Hydrolithon onkodes (Heydrich) Penrose *et* Woelkerling 1992: 81, figs 4, 5.

Basionym: *Lithothamnion onkodes* Heydrich 1897 b: 6, pl. 1, figs 11 a, 11 b.

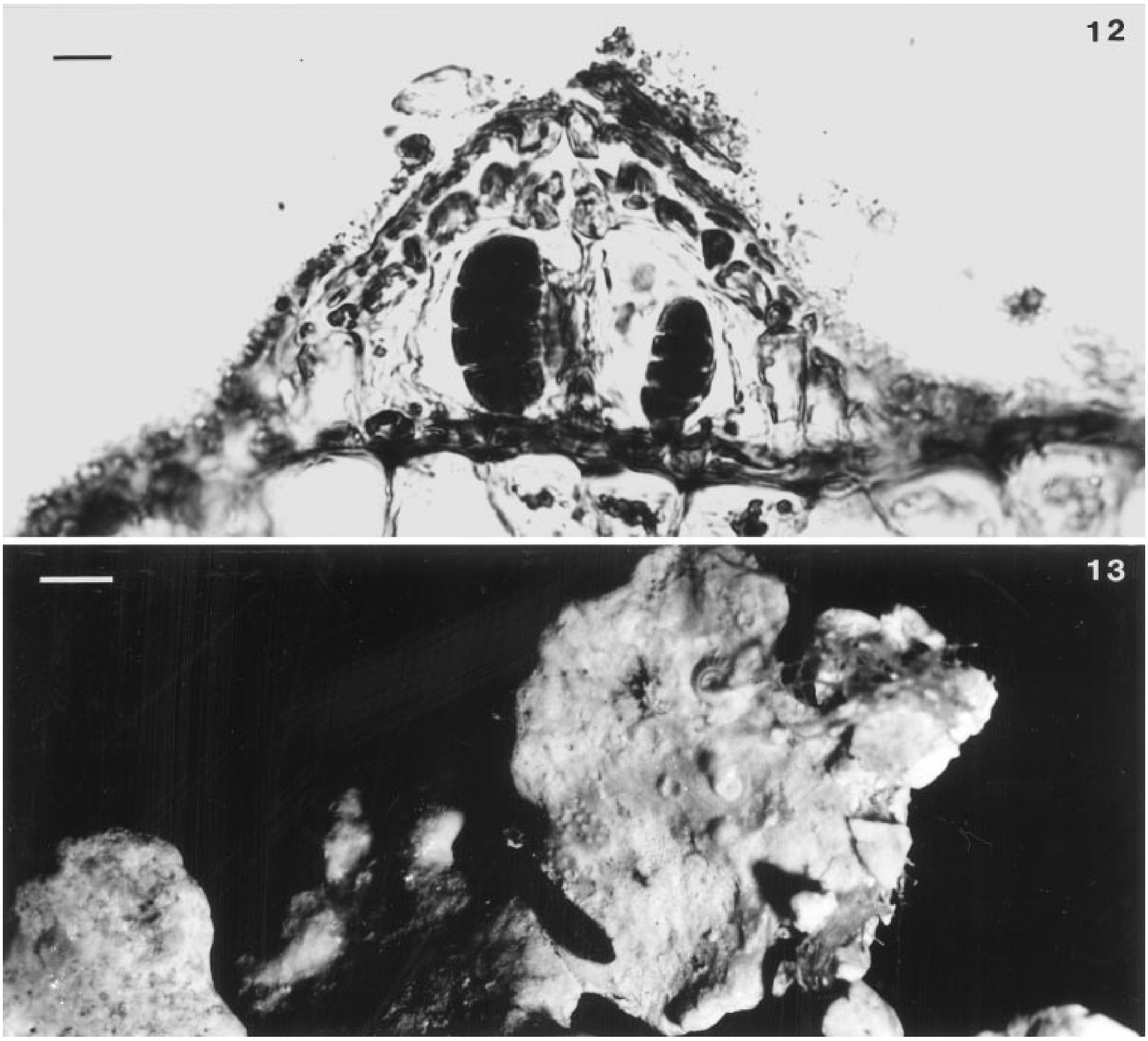
See also Woelkerling (1993) and Woelkerling and Lamy (1998: 357, figs 287–288).

Further published records of *Hydrolithon onkodes* and its synonyms are in Woelkerling (1996).

Additional illustrations and information on this species can be found in Keats and Chamberlain (1994), Verheij (1994) and Penrose (1996).

Heron Reef collections examined. NF, SF and N 5 m epiphytic species (*P. Ringeltaube*: JAN. 1998 LTB 20836, 20837). N 5 m–N 10 m (*P. Ringeltaube and S. Daume*: 12.i.1993, LTB 20597). L 2.5 m and NF, SF epiphytic on *Halimeda* sp. (*P. Ringeltaube*: JAN. 1994, LTB 20771, 20791, 20818, 20786). NF, SF (*P. Ringeltaube and S. Daume*: 09.i.1993, LTB 20579). SF (*P. Ringeltaube*: JAN. 1992, LTB 20795). SF (Reef Rim Zone) (*P. Ringeltaube*: JAN. 1998, LTB 20809, 20812, 20813, 20814, 20815, 20816).

Tetrasporangial conceptacle anatomy and growth-form. Tetrasporangial, female, carposporangial and male plants were found on Heron Reef. All features



Figs 12 and 13. *Hydrolithon farinosum*.
Fig. 12. Uniporate tetrasporangial conceptacle (LTB 20592, scale is 10 μm). Fig. 13. Encrusting growth-form (LTB 20592, scale is 1 mm). Specimen is growing on *Halimeda* sp.

considered diagnostic of *Hydrolithon onkodes* by Penrose (1996) were evident in the Heron Reef collections and they were concordant with the holotype.

Tetrasporangial conceptacles (Fig. 14) of Heron Reef collections were uniporate and contained two or more upright sporangia. Pore canals were lined by cells that are orientated more or less perpendicular to the roof surface with mature tetrasporangial chambers 130–260 µm in diameter. The thallus commonly contained horizontal rows of trichocytes (Fig. 15) occurring at the surface and buried within the thallus.

The growth-form of *H. onkodes* was encrusting (Fig. 16), with epiphytic plants up to 3 mm across, and most epizoic plants up to 33 mm across. A single epizoic collection (LTB 20597, see Fig. 16) however, was 10 mm thick and 90 mm across.

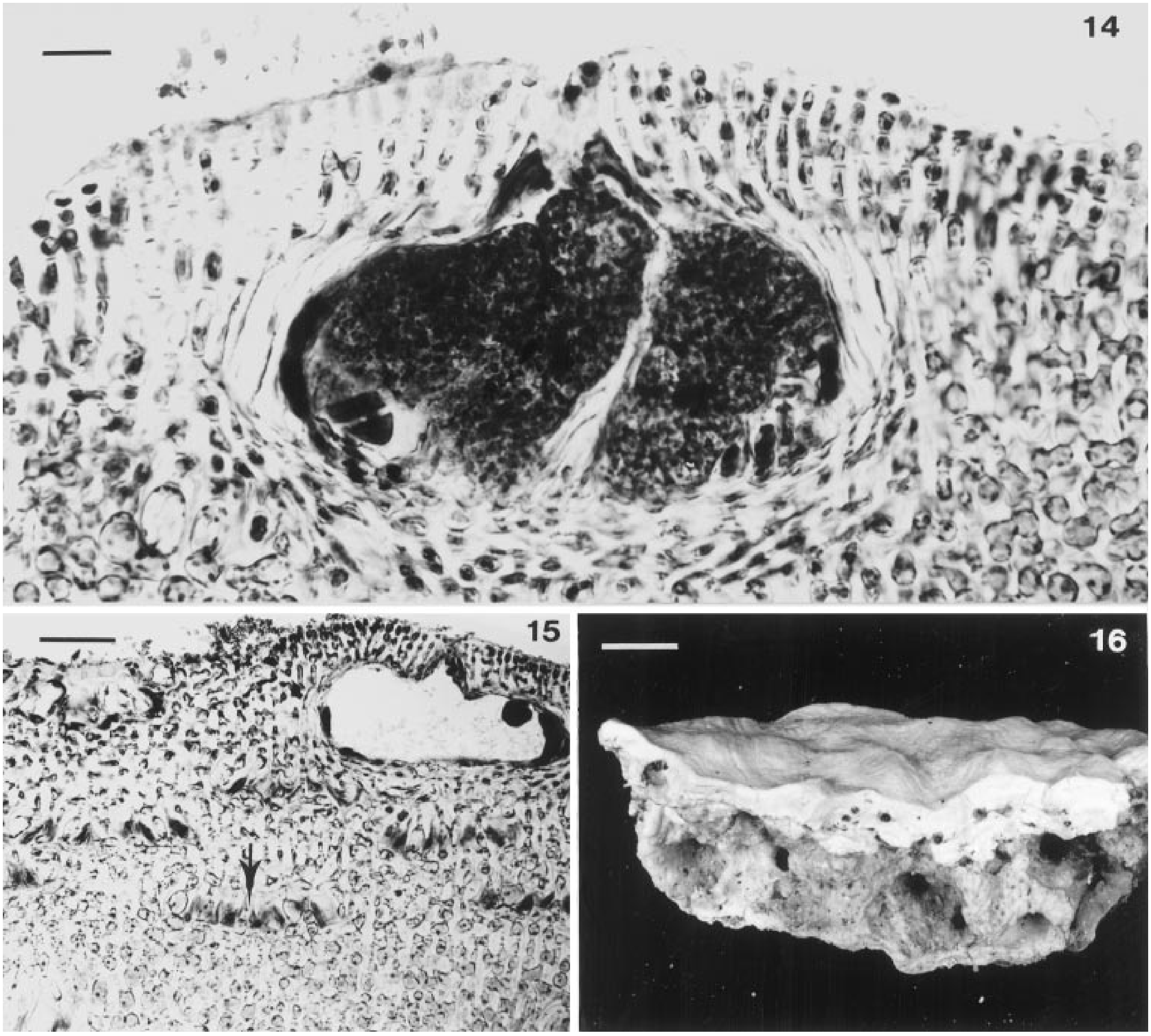
Hydrolithon reinboldii (Weber van Bosse *et* Foslie) Foslie 1901 a: 5.

Basionym: *Lithophyllum reinboldii* Weber van Bosse *et* Foslie *in* Foslie 1901 a.

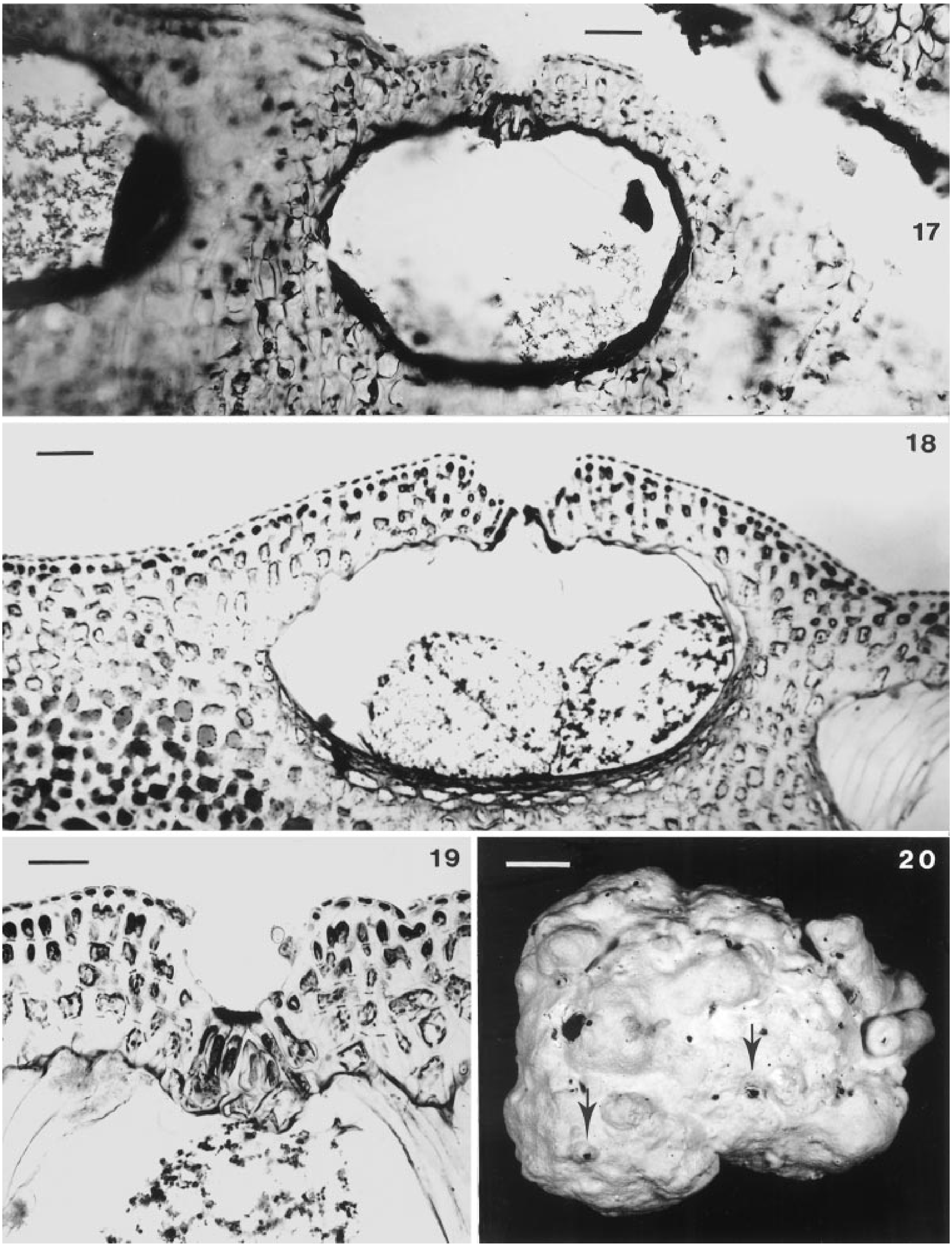
Lectotype: TRH (unnumbered, Siboga Expedition collection 38).

Additional information and published illustrations of lectotype are in Penrose and Woelkerling (1988, figs 1–9; 1992, fig. 3). See also Woelkerling (1993) and Woelkerling and Verheij (1995).

Lectotype material of *H. reinboldii* from Trondheim (TRH, unnumbered, collection 38) was examined and was found to possess uniporate tetrasporangial conceptacles (Fig. 17). Pore canals were lined by elongate cells orientated more or less perpendicular to the roof surface, and the pore canal opening was slightly sunken below the surrounding thallus sur-



Figs 14–16. *Hydrolithon onkodes*.
Fig. 14. Uniporate tetrasporangial conceptacle (LTB 20725, scale is 20 µm). Fig. 15. Thallus containing horizontal rows of trichocytes (arrow), (LTB 20791, scale is 50 µm). Fig. 16. Encrusting growth-form (LTB 20597, scale is 10 mm).



Figs 17−20. *Hydrolithon reinboldii.*
Fig. 17. Uniporate tetrasporangial conceptacle of lectotype material (TRH, unnumbered, collection 38) (scale is 50 μm). Fig. 18. Uniporate tetrasporangial conceptacle (LTB 20758, scale is 50 μm). Fig. 19. Structure of the pore canal. (LTB 20758, scale is 30 μm). Fig. 20. Encrusting growth-form (LTB 20699, scale is 10 mm) with numerous holes made by burrowing polychaetes (arrows).

face. Mature tetrasporangial conceptacle chambers were 300 μm in diameter.

Heron Reef collections examined. L 2.5 m (*P. Ringeltaube*: FEB. 1994, LTB 20694, 20699; *P. Ringeltaube*: JAN. 1994, LTB 20725). L 2.5 m, N 10 m (*P. Ringeltaube*: JAN. 1994, LTB 20756, 20758, 20759). S 5 m (*P. Ringeltaube*: JAN. 1994, LTB 20747). Heron Reef (*R. Townsend*: JAN. 1982, NSW 410952).

Tetrasporangial conceptacle anatomy and growth-form. Tetrasporangial plants only were found on Heron Reef. Vegetative and reproductive anatomy of Heron Reef collections were concordant with that found in the lectotype of *Hydrolithon reinboldii.*

Tetrasporangial conceptacles (Fig. 18) of Heron Reef collections were uniporate, containing two or more upright sporangia. The pore canals were lined by cells that are orientated more or less perpendicular to the roof surface with the pore canal opening slightly sunken below the surrounding thallus surface (Fig. 19). Mature tetrasporangial conceptacle chambers were 210−370 μm in diameter.

The growth-form on Heron Reef was encrusting (Fig. 20) with individual plants up to 65 mm across.

Comments. Penrose (1996) currently distinguishes *Hydrolithon onkodes* from other species of *Hydrolithon* on the presence of numerous trichocyte fields in the vegetative thallus. *Hydrolithon reinboldii* however, has not been reported from Australia previously and is not included in the Penrose (1996) species accounts or key. Heron Reef collections of *H. reinboldii* and *H. onkodes* were examined for vegetative and reproductive differences and distinguished using two distinct features. Plants of *H. reinboldii* possessed a slightly sunken/depressed tetrasporangial pore canal (see Fig. 19) and lack numerous trichocyte fields. Plants of *H. onkodes* however, possess a pore canal that is flush with the surrounding thallus surface (see Fig. 14) and numerous trichocyte fields both buried within the thallus and at the thallus surface (see Fig. 15). Although trichocytes may be present in *H. reinboldii* these are not usually numerous, nor arranged in groups called 'fields'.

Hydrolithon reinboldii has been described and illustrated in numerous publications and although the sunken pore canal is evident in previously published illustrations (e. g.: Verheij 1994 fig. 34, Penrose and Woelkerling 1992 figs 1−3 and lectotype material in Penrose and Woelkerling 1988 fig. 4) it has not been noted or described by previous authors. The slightly sunken/depressed tetrasporangial pore canal was also present in both, lectotype and isolectotype material examined by the present authors (see Fig. 17) as well as the Heron Reef collections. Although this pore canal feature and the lack of obvious trichocyte fields were consistent in the Heron Reef collections further detailed taxonomic studies of *H. reinboldii* are needed to fully evaluate these characters.

Mastophora pacifica (Heydrich) Foslie 1901 b: 19.

Basionym: *Melobesia pacifica* Heydrich 1901: 529.

For additional published records of *M. pacifica* and its synonyms see Woelkerling (1996). See also Woelkerling (1993) and Woelkerling and Lamy (1998: 378, figs 334−335).

Additional information and illustrations of this species can be found in Woelkerling (1988, 1996), Verheij (1993, 1994).

Heron Reef collections examined. N 5 m−N 10 m (*P. Ringeltaube and S. Daume*: 12.i.1993, LTB 20602). L 2.5 m (*P. Ringeltaube*: FEB. 1994, LTB 20723).

Tetrasporangial conceptacle anatomy and growth-form. Both tetrasporangial and carposporangial plants were found on Heron Reef. All features considered diagnostic of *Mastophora pacifica* by Woelkerling (1996) were evident in the Heron Reef collections and they were concordant with the holotype.

Tetrasporangial conceptacles (Fig. 21) of Heron Reef collections were uniporate and usually visible to the naked eye or with a hand lens (Fig. 22). Conceptacles roof protruded above the surrounding thallus surface and mature tetrasporangial chambers were 670 μm in diameter. Pore canals were lined with cells projecting somewhat into the canal.

The growth-form of *M. pacifica* on Heron Reef was encrusting (see Fig. 22).

Neogoniolithon brassica-florida (Harvey) Setchell *et* Mason 1943: 91.

Basionym: *Melobesia brassica-florida* Harvey 1849: 110.

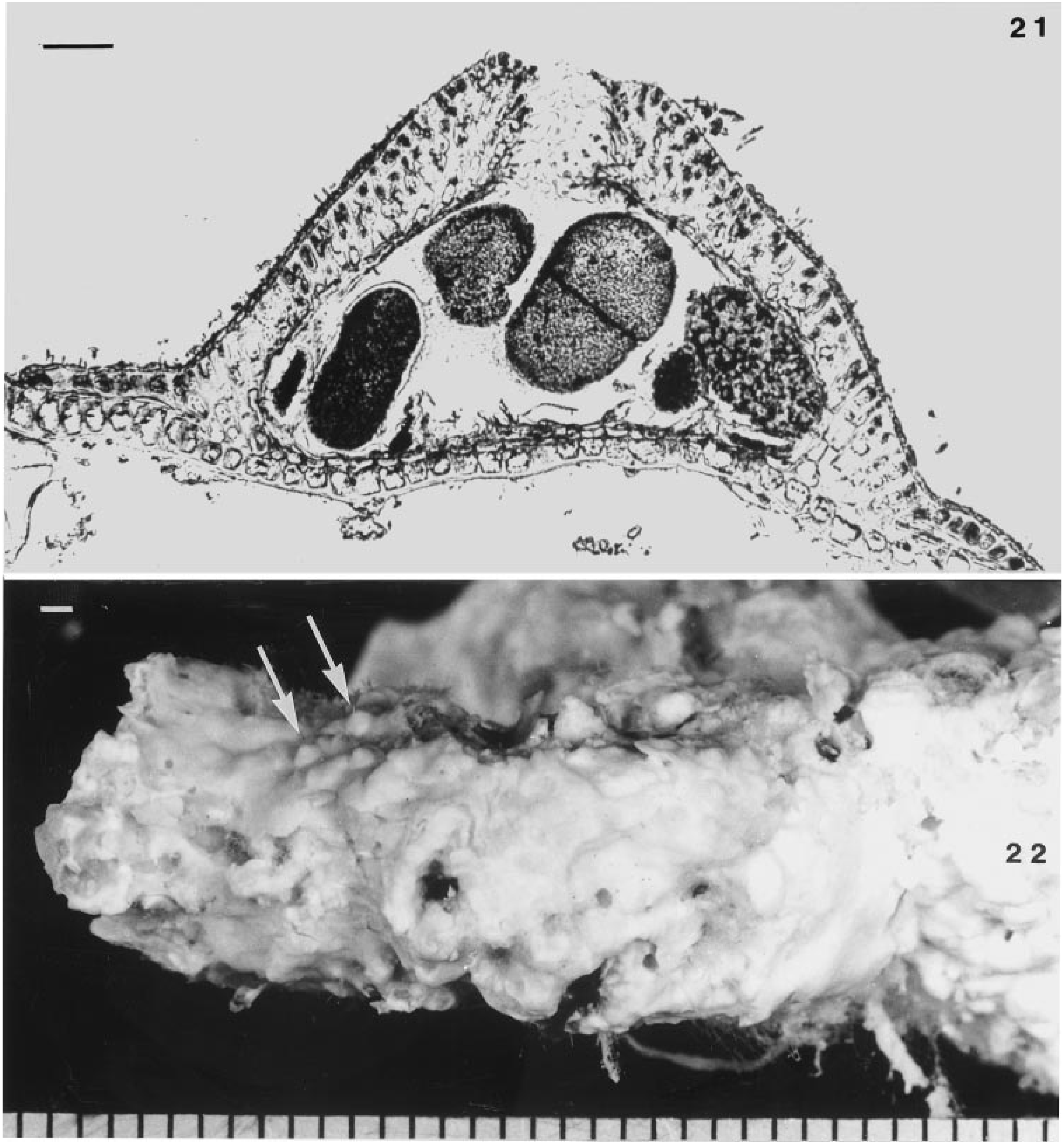
For additional published records of *N. brassica-florida* and its synonyms see Woelkerling (1996). See also Woelkerling (1993).

Additional information and illustrations of this species can be found in Penrose (1992), Woelkerling *et al.* (1993 b), Verheij (1993, 1994) and Penrose (1996).

Heron Reef collections examined. L 2.5 m (5 m) (*P. Ringeltaube and S. Daume*: 09.i.1993, LTB 20607; 12. i.1993, LTB 20593). L 2.5 m (*P. Ringeltaube*: FEB. 1994, LTB 20692, 20693, 20698). NF (*P. Ringeltaube and S. Daume*: 09.i.1993, LTB 20581, 20583.

Tetrasporangial conceptacle anatomy and growth-form. Only tetrasporangial plants were collected from Heron Reef. All features considered diagnostic of *Neogoniolithon brassica-florida* by Penrose (1996) were evident in the Heron Reef collections and they were concordant with the holotype.

Tetrasporangial conceptacles (Fig. 23) of Heron Reef collections were uniporate, extremely large and usually visible to the naked eye (Fig. 24). Conceptacle roofs protruded above the surrounding thallus surface, and the mature tetrasporangial chambers were 670−1050 μm in diameter. The pore canals were lined with cells projecting somewhat into the canal.



Figs 21 and 22. *Mastophora pacifica*.
Fig. 21. Uniporate tetrasporangial conceptacle (LTB 20723, scale is 80 μm). Fig. 22. Encrusting growth-form. Note uniporate conceptacles (arrows), usually visible with a hand lense or to the naked eye (LTB 20723, scale is 20 mm).

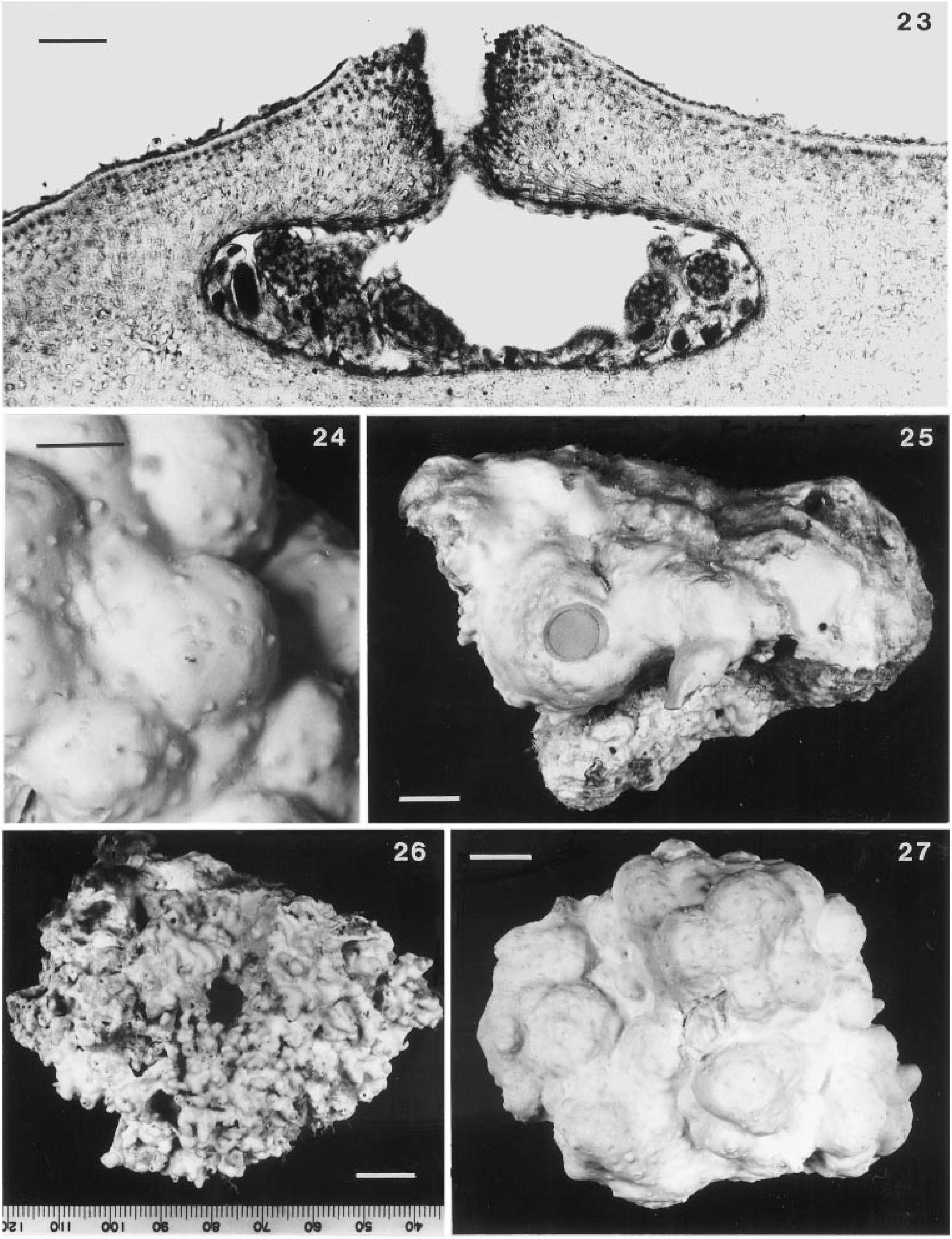
The growth-form in *N. brassica-florida* on Heron Reef varied from encrusting (Fig. 25) through warty (Fig. 26) to lumpy (Fig. 27). Individual plants ranged from relatively small and thin specimens, through to very thick and large plants (> than 70 mm across).

Spongites fruticulosus Kützing 1841: 33.

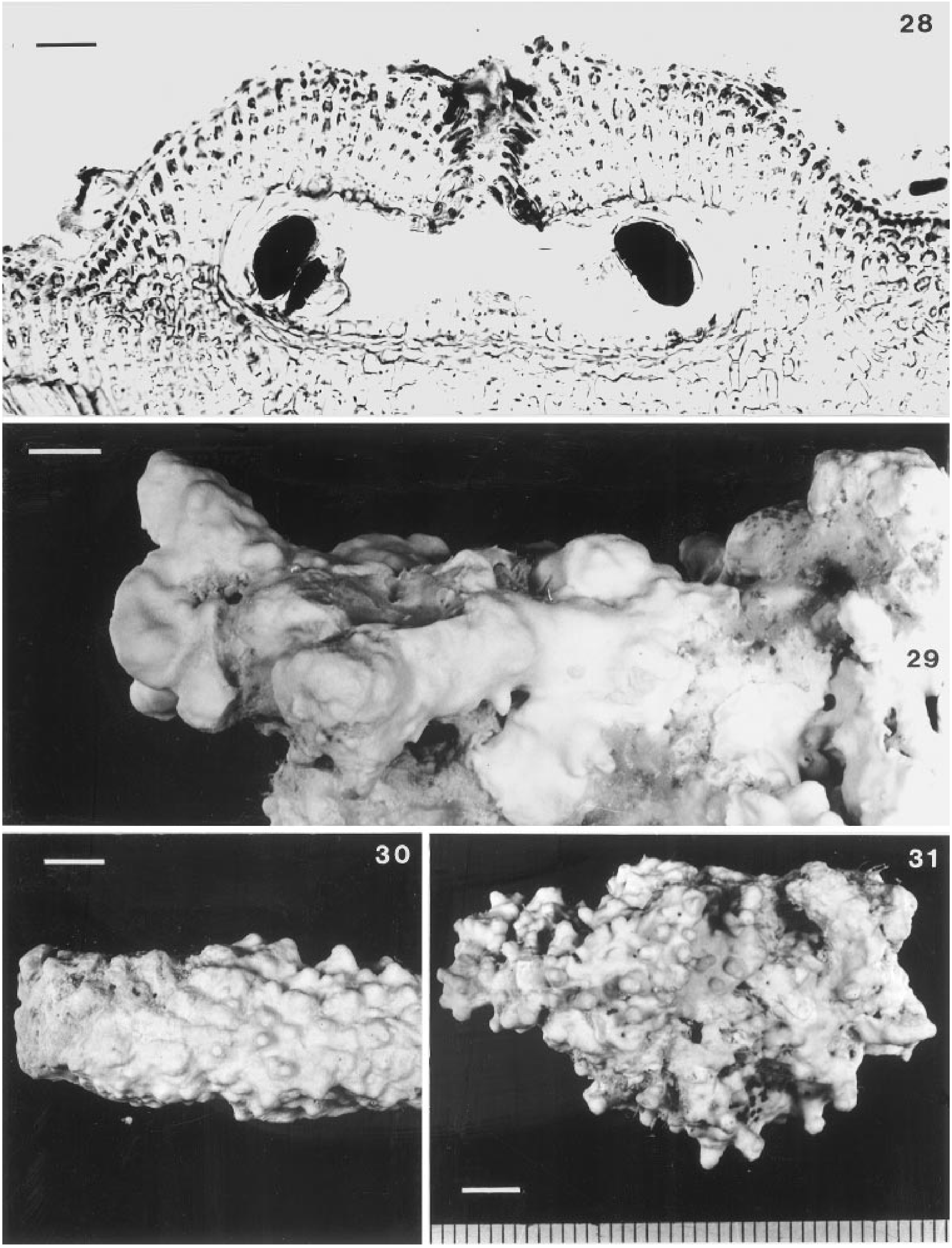
Basionym: *Spongites fruticulosus* Kützing 1841: 33.
For additional published records of *S. fruticulosus* and its synonyms see Woelkerling (1996). See also Woelkerling (1993) and Woelkerling and Verheij (1995).

Additional information and illustrations of this species can be found in Woelkerling (1985), Penrose (1991) and Penrose (1996).

Heron Reef collections examined. N 5 m−N 10 m (*P. Ringeltaube and S. Daume*: 12.i.1993, LTB 20567, 20600, 20629). L 2.5 m (5 m) (*P. Ringeltaube*: 08.i.1993, LTB 20589, 20590). L 2.5 m (*P. Ringeltaube*: FEB. 1994, LTB 20695, 20700, 20701, 20702, 20703, 20704, 20713, 20722, 20744). N 10 m (*P. Ringeltaube*: FEB. 1994, LTB 20753, 20755). SF (*P. Ringeltaube and S. Daume*: 06.i.1993, LTB 20588). NF (*P. Ringeltaube and S. Daume*: 10.i.1993, LTB



Figs 23−27. *Neogoniolithon brassica-florida*.
Fig. 23. Uniporate tetrasporangial conceptacle (LTB 20607, scale is 100 μm). Fig. 24. Numerous large uniporate conceptacle which are visible to the naked eye (LTB20693, scale is 5 mm). Fig. 25. Encrusting growth-form (LTB 20581, scale is 9 mm). Fig. 26. Warty growth-form (LTB 20607, scale is 12 mm). Fig. 27. Lumpy growth-form (LTB 20693, scale is 9 mm).



Figs 28–31. *Spongites fruticulosus*.
Fig. 28. Uniporate tetrasporangial conceptacle (LTB 20600, scale is 35 µm). Fig. 29. Encrusting growth-form (LTB 20753, scale is 5 mm). Fig. 30. Warty growth-form (LTB 20755, scale is 5 mm). Fig. 31. Fruticose growth form (LTB 20802, scale is 5 mm).

20565). S 5 m (*P. Ringeltaube*: FEB. 1994, LTB 20741, 20743; *P. Ringeltaube*: APR. 1992, LTB 20802).

Tetrasporangial conceptacle anatomy and growth-form. Tetrasporangial and female plants only were found on Heron Reef. All features considered diagnostic of *Spongites fruticulosus* by Penrose (1996) were evident in the Heron Reef collections and they were concordant with the holotype.

Tetrasporangial conceptacles (Fig. 28) of Heron Reef collections were uniporate, protruding above or flush with surrounding thallus surface. Mature tetrasporangial chambers were 230–520 μm in diameter.

The growth-form in *S. fruticulosus* on Heron Reef was mostly encrusting (Fig. 29), however a few populations were warty (Fig. 30) to almost fruticose (Fig. 31). Individual plants were 10 mm to 75 mm in width.

Comments. Penrose (1996) currently distinguishes *Spongites fruticulosus* and *S. yendoi* (Foslie) Chamberlain mainly on the disparate size of mature tetrasporangial conceptacle chambers (> 450 μm vs < 250 μm in diameter). Tetrasporangial conceptacle chambers from plants found on Heron Reef however, were intermediate in size (230–560 μm). As plants were unable to be split into two definite groups on conceptacle chamber size the authors have retained the plants found on Heron Reef as a single species (*S. fruticulosus*). Should detailed taxonomic re-examination of *S. fruticulosus* and *S. yendoi* provide data that they are the same species *S. fruticulosus* is an older name and has nomenclatural priority.

Subfamily Melobesioideae Bizzozero, 1885: 109 (as 'Melobesiea')

Lithothamnion prolifer Foslie 1904 b: 18, figs 1–36.

Basionym: *Lithothamnion prolifer* Foslie 1904 b: 18.

Additional information and illustrations of this species can be found in Verheij (1994) and Keats *et al.* (1996).

Heron Reef collections examined. N 10 m (*P. Ringeltaube and S. Daume*: 12.i.1993, LTB 20568, *P. Ringeltaube*: JAN. 1998, LTB 20757, 20763, 20807, 20808, *P. Ringeltaube*: APR. 1992, LTB 20797).

Tetrasporangial conceptacle anatomy and growth-form. Tetrasporangial and male plants only were collected from Heron Reef. The combination of characters used to distinguish this species by Keats *et al.* (1996: 195) were evident in the Heron Reef collections.

Tetrasporangial conceptacles (Fig. 32) of Heron Reef collections were multiporate with mature tetrasporangial conceptacles large, often irregular in shape, flush with or slightly raised above the surrounding thallus surface. These multiporate conceptacles mainly occurred on the tips of the protuberances. Rosette cells seen in surface SEM view were slightly sunken into the pore. Tetrasporangial chambers were 660–1100 μm in diameter, with old conceptacles persisting and becoming buried within the thallus, eventually filled in by irregularly arranged cells.

The growth-form in *Lithothamnion prolifer* on Heron Reef was fruticose with markedly flattened protuberances emerging from the encrusting thalli at an angle (Fig. 33). Individual plants were up to 70 mm wide, protuberances measured 5–15 mm long and 5–25 mm wide.

Mesophyllum erubescens (Foslie) Lemoine 1928: 252.

Basionym: *Lithothamnion erubescens* Foslie 1900 b: 9.

Published illustrations of holotype are in Foslie (1904 a, pl. 3, fig. 20, as Lithothamnion).

Additional information and published illustrations of holotype material are in Verheij (1993) and Keats and Chamberlain (1994, figs 31–34). See also Woelkerling (1993) and Woelkerling and Lamy (1998).

Additional information and illustrations on this species can be found in Keats and Chamberlain (1994) and Verheij (1994).

Heron Reef collections examined. N 5 m–N 10 m (*P. Ringeltaube and S. Daume*, 12.i.1993, LTB 20598, 20603). L 2.5 m (5 m) (*P. Ringeltaube and S. Daume*: 09.i.1993, LTB 20606). L 2.5 m (*P. Ringeltaube*: FEB. 1994, LTB 20719, 20720, 20721). N 10 m (*P. Ringeltaube*: FEB. 1994, LTB 20751, 20752, 20754, 20762, 20764). S 5 m (*P. Ringeltaube*: FEB. 1994, LTB 20729, 20730, 20733, 20734, 20738, 20746). SF (*P. Ringeltaube*: APR. 1992, LTB 20805; *P. Ringeltaube and S. Daume*: 10.01.1993, LTB 20566).

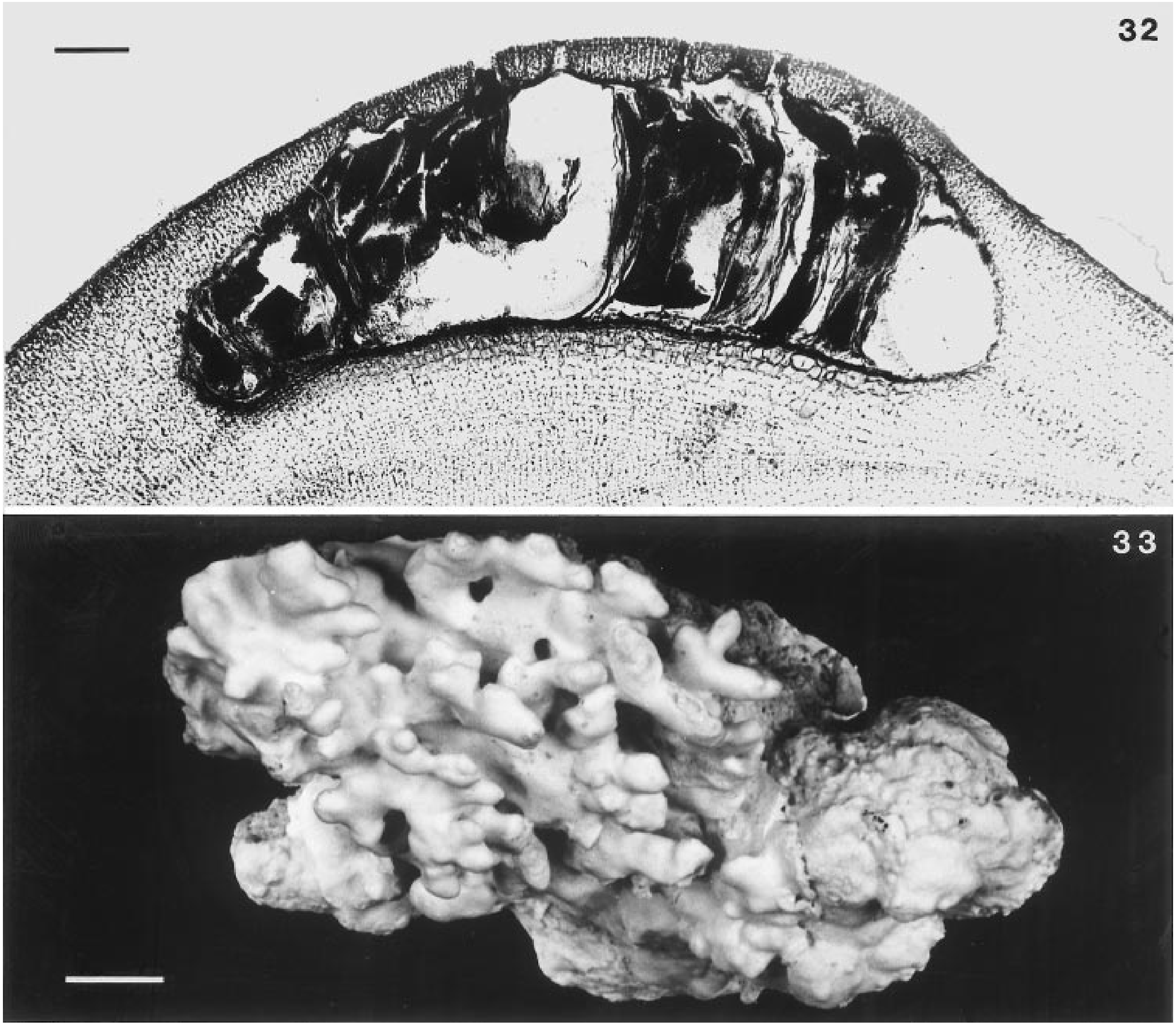
Tetrasporangial conceptacle anatomy and growth-form. Tetrasporangial, carposporangial, female and male plants were found on Heron Reef. Vegetative and reproductive anatomy of Heron Reef collections were concordant with that described by Keats and Chamberlain (1994).

Tetrasporangial conceptacles (Fig. 34) of Heron Reef collections were multiporate with mature tetrasporangial chambers 230–480 μm in diameter. Filaments lining the pore canal differed from normal roof filaments in having elongate cells present at the base of the pore canal (Fig. 35). Male plants containing uniporate conceptacles with simple (unbranched) spermatangial filaments on the floor, walls and roof of the conceptacle chambers.

The growth-form in *Mesophyllum erubescens* on Heron Reef was initially encrusting, becoming warty (Fig. 36) with larger plants fruticose (Fig. 37). Individual plants were 20 mm to 65 mm in width.

Re-examination of A. B. Cribb's collection

Over a period of 20 years A. B. Cribb collected and identified numerous algae (including NCA) from the Capricorn Bunker Group, publishing his findings in



Figs 32 and 33. *Lithothamnion prolifer.*
Fig. 32. Multiporate tetrasporangial conceptacle (LTB 20807, scale is 100 μm). Fig. 33. Fruticose growth-form (LTB 20757, scale is 10 mm) with markedly flattened protuberances.

Marine Algae of the Southern Great Barrier Reef (1983). Only a few of these algal specimens were NCA from Heron Reef and of these collections many could not be found, thus were not available for re-examination. Available specimens however, were re-examined in a modern context and compared to both the current Heron Reef collections and type material where necessary. Of the 5 available species identified by A. B. Cribb we could positively identify three species *Lithophyllum tamiense* (as *L. moluccense* by Cribb), *L. frondosum*, and *Spongites fruticulosus* (Table II).

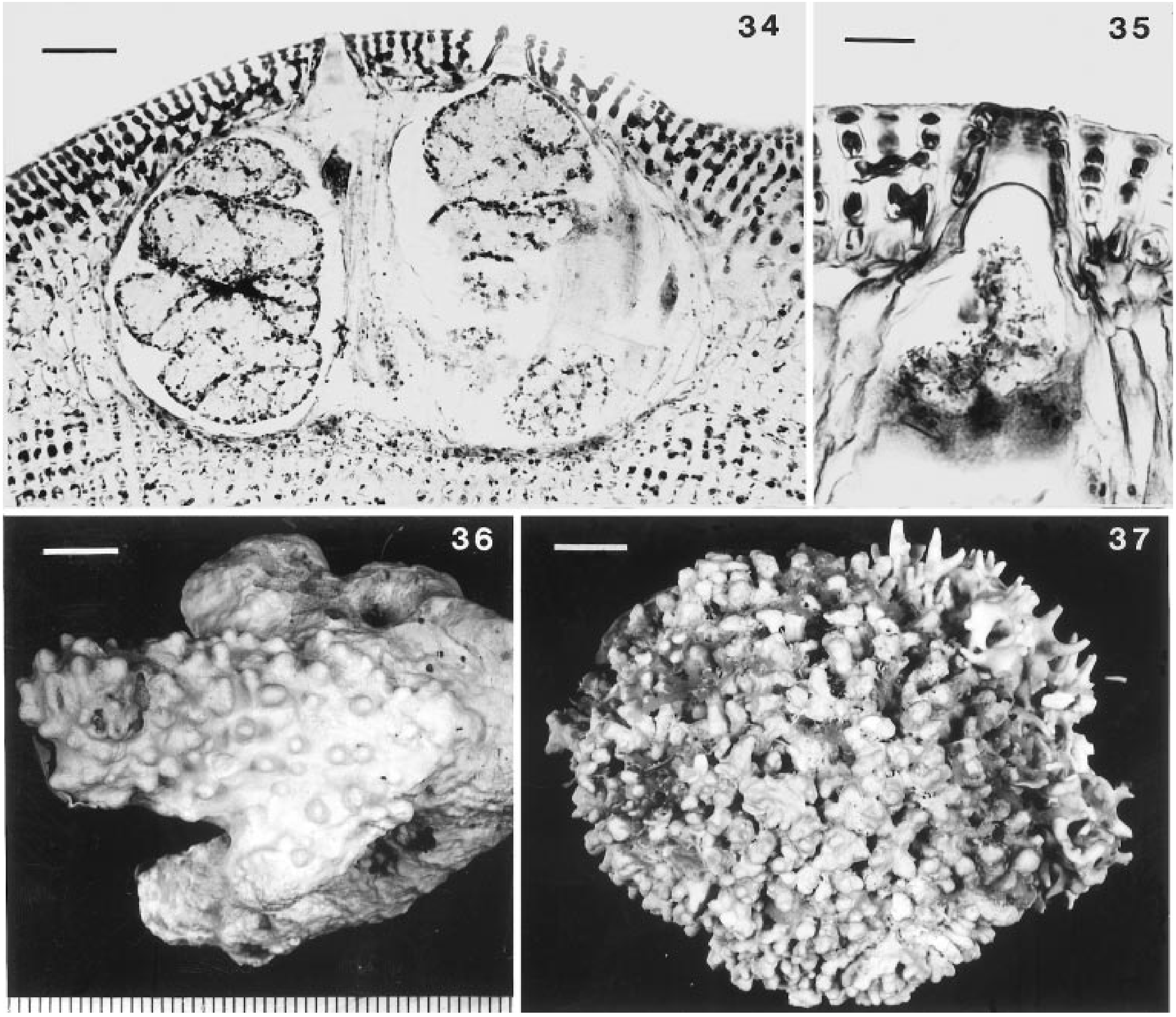
Key

Field and taxonomic laboratory work on Heron Reef revealed that certain specimens could be identified in the field as they display very distinct morphotypes and/or distinct field characters. Other species however, show the same growth-form or a single species exhibits more than one growth-form. As a result a divided tabular key was developed (Table III and Table IV). This key includes the large variations in growth-forms, distinct field characters as well as characteristic cellular features (e. g. tetrasporangial conceptacle anatomy and cellular connections) required to identify specimens in a modern context.

Discussion

Species occurrence and distribution

The present study provides the first modern account of NCA species occurring on Heron Reef and the first modern account for the GBR region. Most species occurring on Heron Reef were found at all experimental sites with varying relative abundances (see Table I). Within this study, it has not been evaluated which factors might influence the distribution and abundance of a single species. Personal observations however, suggest that micro-environmental factors such as light intensity and/or desiccation might influ-

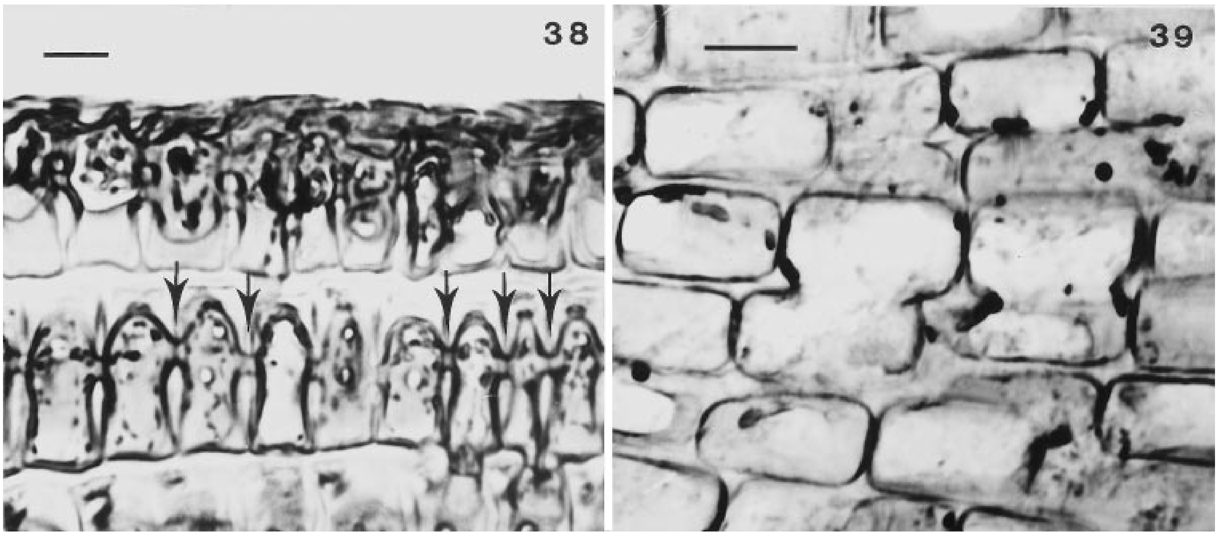


Figs 34–37. *Mesophyllum erubescens*.
Fig. 34. Multiporate tetrasporangial conceptacle (LTB 20606, scale is 40 μm). Fig. 35. Pore canal lined with elongated cells (LTB 20719, scale is 15 μm). Fig. 36. Warty growth-form (LTB 20738, scale is 7 mm). Fig. 37. Fruticose growth-form (LTB 20606, scale is 9 mm).

ence the distribution and abundance of particular species. *Lithothamnion prolifer* for instance, was principally found in low light environments such as in crevices or under overhangs. This was also observed by Keats *et al.* (1996) in Fiji and on Lizard Island (GBR), where it mainly grew on vertical surfaces in caves, crevices and under overhangs. *Neogoniolithon brassica-florida* and *Hydrolithon onkodes* occurred in areas of high light intensity. *Neogoniolithon brassica-florida* was common at L 2.5 m and in tide pools on the reef flat. *Hydrolithon onkodes* was abundant on the reef flat towards the rim. It seems however, that *H. onkodes* can withstand desiccation better than *Neogoniolithon brassica-florida,* as it occurred in areas, which may be emerged at low tide, whereas, *N. brassica-florida* occurred in areas which are always completely submerged. Certain species such as *Mesophyllum erubescens, Spongites fruticulosus* and *Mastophora pacifica* occurred in both, high light and low light conditions, as they were found to grow on the top and underneath coral rubble. *Hydrolithon farinosum* was the only species that was exclusively epiphytic on *Halimeda sp.* and on some red algae. This is in accordance with Cribb (1983), who found *Hydrolithon farinosum* [as *Fosliella farinosa* (Lamouroux) Howe] on the southern Great Barrier Reef growing epiphytically on *Laurencia sp.* and other algae. Penrose and Chamberlain (1993) reported *Hydrolithon farinosum* from the Red Sea, where it grew on *Padina* and *Zostera*.

A. B. Cribb's collection

Only a few specimens of NCA from the A. B. Cribb collection were from Heron Reef, most of them were collected on the reef flat and none were from deeper waters. As a result the number of species from Heron Reef and the data related to these species (depth, distribution, growth-form, data etc.) prior to this account were very poor. After reassessment of the avail-



Figs 38 and 39. Sections showing secondary pit connection and cell fusion.
Fig. 38. Section showing secondary pit connections (arrows) (LTB 20761, scale is 10 µm). Fig. 39. Section showing cell fusion (center of fig.) (LTB 20741, scale is 10 µm).

able A. B. Cribb specimens we can confirm that 3 of the 11 species found on Heron Reef (*Lithophyllum tamiense*, *L. frondosum* and *Spongites fruticulosus)* were also collected by A. B. Cribb. Prior to this study only 4 species were known to occur on Heron Reef (see Table II). The current study has increased the number of species by nearly four times and further studies may well turn up more taxa. This comparison highlights the need for rigorous monographic work before any biogeographic comparison can be made of the NCA occurring in Australia.

Key

The extent to which the thallus morphology and field characters (character states 9–11) in the tabular key are applicable to NCA occurring on other tropical reef systems or other reefs within the GBR has yet to be examined. Growth-forms of NCA are generally very variable. Particular species on Heron Reef displayed distinct morphotypes, in other geographical areas they may display a range of growth-forms. *Hydrolithon reinboldii* for example is encrusting on Heron Reef, but in Indonesia its growth-form was lumpy (Verheij 1993). On the other hand, other species such as *Lithothamnion prolifer* display the same growth-forms over large geographical areas. *Lithothamnion prolifer* develops horizontally orientated protuberances on Heron Reef as well as on Fiji (Keats *et al*. 1996). In addition the range in growth-forms and the number of species occurring on Heron Reef may well be larger than what is represented in the key. The combination of both field and taxonomic characters however, provide the first available

Table II. Comparison of species collected and identified by A. B. Cribb with findings of this study

Plants collected by A. B. Cribb	Herbarium number (BRI)	Growth form	Species name following reassessment	Collection date and collection site (if available)
Lithophyllum sp.	712449	?	*Spongites fruticulosus*	31. 01. 1963
	712448	fruticose	*Lithophyllum tamiense*	01. 02. 1964, Reef flat
Lithophyllum moluccense var.	712435	fruticose	*Lithophyllum tamiense*	01. 02. 1964, East end of Heron
Lithophyllum moluccense	712433	fruticose	*Lithophyllum tamiense*	04. 11. 1975, South platform
	712434	fruticose	*Lithophyllum tamiense*	June 1961, South platform
	712424	fruticose	*Lithophyllum tamiense*	1963
Mesophyllum mesomorphum	712656	foliose	(*)	03. 11. 1983, under surface of coral rubble
	712475	foliose	*Mesophyllum sp.*	31. 01. 1963, under surface of coral rubble
Lithothamnion sp.	709344	encrusting	(*)	04. 11. 1975, Reef flat
	712465	encrusting	*Lithophyllum frondosum*	31. 01. 1963, South reef platform

(*) Not possible to identify, because the plant did not bear tetraspores.

Table III. List of characters and character codes used in the tabular key in Table IV. Characters are numbered in the sequence used in Table IV.

I: Characters relating to tetrasporangial conceptacles

1: Tetrasporangial/bisporangial conceptacles
M − Multiporate (Figs 32 and 34).
U − Uniporate (Figs 2, 8, 12, 21).

2: Number of cell layers to uniporate conceptacle chamber floor
1−3 1 to 3 cell layers (Fig. 5).
6+ 6 or more cell layers (Fig. 2).

3: Cells lining uniporate conceptacle pore canal
P − Cells orientated more or less perpendicular to roof surface (Figs 12 and 18).
I − Cells projecting somewhat into but not occluding pore canal (Figs 23 and 28).

4: Uniporate conceptacle pore
S − Pore slightly sunken below thallus surface (Fig. 19).
R − Pore raised above or flush with thallus surface (Figs 12 and 14).

5: Elongate cells at the base of the multiporate pore canal
P − Present (Fig. 35).
A − Absent.

II: Characters relating to thallus anatomy

6: Epithallial cells
R − Rounded or flattened but not flared.
F − Flared.

7: Cell connections
S − Secondary pit connections (Fig. 38).
F − Cell fusions (Fig. 39).

8: Trichocytes fields
P − Present (Figs 15).
A − Absent.

III: Characters relating to thallus morphology

9: Growth form mainly
E − Encrusting (Figs 16, 22, 29).
W − Warty (Fig. 4).
L − Lumpy (Fig. 27).
F − Fruticose (Figs 9−11 and 37).
FP − Fruticose thallus with markedly flattened protuberances (Fig. 33).

10: Substratum
E − Epiphytic growth (Fig. 13).
C − Growing on calcareous substrata.

IV: Distinctive characters observable in the field

11: Additional features of vegetative thallus
NAF − No additional features.
PC − Conceptacles have a pustulose appearance.
ELCB − Thallus forms branches (thin or thick) which are elongated and laterally coherent, the tips of the branches either rounded or pointy (Figs 9−11).
BP − Thallus associated with burrowing polychaetes, visible as large pores in the thallus surface (Fig. 20).
CCS − Thallus thin (generally < 1 mm) conforming to the contours of the substratum; conceptacles generally visible with a hand lens (Fig. 22).
DLC − Thallus thick (generally > 2 mm) with very distinct and large conceptacles, visible to the naked eye (Fig. 24).
GS − Thallus is extremely glossy and smooth with a 'velvet' texture.

NA − not applicable.

Table IV. Tabular key to facilitate the identification of non-geniculate coralline algae from Heron Reef. Characters and character codes are listed in Table III.

Species	Tetrasporangial conceptacles				Thallus anatomy				Thallus morphology		Field characters
	1	2	3	4	5	6	7	8	9	10	11
Lithophyllum frondosum	U	6+	I	R	NA	R	S	A	E-W	C	NAF
Lithophyllum pustulatum	U	1−3	I	R	NA	R	S	A	E	E / C	PC
Lithophyllum tamiense	U	6+	I	R	NA	R	S	A	F	C	ELCB
Hydrolithon farinosum	U	NA	P	R	NA	R	F	A	E	E	NAF
Hydrolithon onkodes	U	NA	P	R	NA	R	F	P	E	E / C	NAF
Hydrolithon reinboldii	U	NA	P	S	NA	R	F	A	E	C	BP
Mastophora pacifica	U	NA	I	R	NA	R	F	A	E	C	CCS
Neogoniolithon brassica-florida	U	NA	I	R	NA	R	F	A	E-W-L	C	DLC
Spongites fruticulosus	U	NA	I	R	NA	R	F	A	E-W-F	C	NAF
Lithothamnion prolifer	M	NA	NA	NA	A	F	F	A	FP	C	GS
Mesophyllum erubescens	M	NA	NA	NA	P	R	F	A	E-W-F	C	NAF

Table V. Species records in tropical reef systems: synonyms may have been cited in the literature. (Note: not all listings are confirmed records).

Species	Locality and reference
Lithophyllum frondosum	– Abrolhos Islands, Western Australia (Huisman 1997 as *L. bermudense*)
Lithophyllum pustulatum	– French Polynesia (Payri and N'Yeurt 1997)
	– Shark Bay, Western Australia (Barry and Woelkerling 1995)
Lithophyllum tamiense	– Capricornia Section, GBR (Cribb 1973 as *L. moluccense* and 1984 as *L. moluccense*)
	– Guam (Gordon *et al.* 1976, Pitlik and Paul 1997 both as *L. moluccense*)
	– Heron Island, GBR (Cribb 1966 as *L. moluccense*)
	– Lizard Island, GBR (Price *et al*. 1976 as *L. moluccense*)
	– Mauritius (Ballesteros and Afonso-Carillo 1995)
	– One Tree Island, GBR (Borowitzka and Larkum 1986 as *L. molluccense*)
	– Queensland (Cribb 1996 as *L. moluccense*)
	– Rotuma Island, Fiji (N'Yeurt 1996)
	– Ryukyu Islands, Japan (Iryu *et al*. 1995 as *L. moluccense*)
	– Solomon Islands (Littler 1972 as *L. moluccense*)
	– Southern Great Barrier Reef (Cribb 1983 as *L. moluccense*)
	– Spermonde Archipelago, SW Sulawesi, Indonesia (Verheij 1993)
Hydrolithon farinosum	– Brampton Island (May 1951 as *Fosliella farinosa* (Lamouroux) Howe)
	– Capricornia Section, GBR (Cribb 1984 as *Fosliella farinosa*)
	– Eniwetok Atoll, Marshall Islands (Dawson 1957 as *Fosliella farinosa*)
	– French Polynesia (Payri and N'Yeurt 1997)
	– Guam (Gordon *et al.* 1976 as *Fosliella farinosa*)
	– Red Sea (Penrose and Chamberlain 1993)
	– Rotuma Island, Fiji (N'Yeurt 1996)
	– Shark Bay, Western Australia, (Barry and Woelkerling 1995)
	– Southern Great Barrier Reef, GBR (Cribb 1983 as *Fosliella farinosa*)
Hydrolithon onkodes	– Fiji (Keats 1995, Keats *et al.* 1997)
	– French Polynesia (Payri and N'Yeurt 1997)
	– Guam (Gordon *et al.* 1976 as *Porolithon onkodes* (Heydrich) Foslie)
	– Hawaiian Islands (Adey *et al*. 1982 as *Porolithon onkodes*)
	– Indian and Pacific Oceans (Foslie 1907 in Littler 1972 as *Porolithon onkodes*)
	– Maledives (Womersley and Bailey 1969, in Littler 1972 as *Porolithon onkodes*)
	– Marshall Islands (Dawson 1957, Lee 1967 (Rongelap Atoll), Littler 1972 as *Porolithon onkodes*)
	– Mauritius (Ballesteros and Afonso-Carrillo 1995)
	– Northern Red Sea (Rasser and Piller 1997)
	– One Tree Island, GBR (Borowitzka and Larkum 1986 as *Porolithon onkodes*)
	– Ryukyu Islands, Japan (Iryu *et al.* 1995)
	– Shark Bay, Western Australia (Barry and Woelkerling 1995)
	– Society Islands, French Polynesia (Guilcher *et al.* 1966 in Littler 1972 *as Porolithon onkodes*)
	– Sodwana Bay, Natal, South Africa (Keats and Chamberlain 1994)
	– Solomon Islands (Littler 1972 as *Porolithon onkodes*)
	– South India (Krishnamurthy and Jayagopal 1987 a as *Porolithon onkodes*)
	– Southern Great Barrier Reef (Cribb 1983 as *Porolithon onkodes*)
	– Spermonde Archipelago, SW Sulawesi, Indonesia (Verheij 1993)
	– Tahiti (Setchell 1926 in Littler 1972 as *Porolithon onkodes*)
Hydrolithon reinboldii	– French Polynesia, (Payri and N'Yeurt 1997)
	– Guam (Gordon *et al*. 1976)
	– Hawaiian Islands (Adey *et al*. 1982)
	– Ryukyu Islands, Japan (Iryu *et al*. 1995)
	– South India (Krishnamurthy and Jayagopal 1987 a)
	– Spermonde Archipelago, SW Sulawesi, Indonesia (Verheij 1993)
Mastophora pacifica	– French Polynesia (Payri and N'Yeurt 1997)
	– Ryukyu Islands, Japan (Iryu *et al.* 1995)
	– Spermonde Archipelago, SW Sulawesi, Indonesia (Verheij 1993)
Neogoniolithon brassica-florida	– Capricornia Section, GBR (Cribb 1984 as *N. fosliei* (Heydrich) Setchell and Mason)
	– Fiji (Keats *et al.* 1997 as N. fosliei)
	– Great Barrier Reef (Cribb 1983 as *N. fosliei*)
	– Guam (Gordon *et al.* 1976 as *N. fosliei*)
	– Hawaiian Islands (Adey *et al.* 1982 as *N. fosliei*)

Table V. Continued.

Species	Locality and reference
Neogoniolithon brassica-florida	– Lizard Island GBR (Price *et al*. 1976 as *N. fosliei*) – Northern Red Sea (Rasser and Piller 1997) – Ryukyu Islands, Japan (Iryu *et al.* 1995 as *N. fosliei*) – Shark Bay, Western Australia (Barry and Woelkerling 1995) – South India (Krishnamurthy and Jayagopal 1987 b as *N. fosliei*) – Spermonde Archipelago, SW Sulawesi, Indonesia (Verheij 1993) – Queensland (Cribb 1996 as *N. fosliei*)
Spongites fruticulosus	– no records from tropical reef systems
Lithothamnion prolifer	– Fiji, Australia (Lizard Island GBR, Palm Isles, Whitsundays and Capricorn Group), Kiribati and Indonesia (Keats *et al.* 1996) – Spermonde Archipelago, SW Sulawesi, Indonesia (Verheij 1993)
Mesophyllum erubescens	– Abrolhos Islands, Western Australia (Huisman 1997) – French Polynesia (Payri and N'Yeurt 1997) – Guam (Gordon *et al.* 1976) – Hawaiian Islands (Adey *et al.* 1982) – Indonesia (Verheij 1994) – Mauritius (Ballesteros and Afonso-Carillo 1995) – Sodwana Bay, Natal, South Africa (Keats and Chamberlain 1994) – Spermonde Archipelago, SW Sulawesi, Indonesia (Verheij 1993)

guide for scientists to enable identification of this difficult algal group on Heron Reef.

Comparison with species found on other reef systems

The taxonomy of NCA has undergone many changes in recent years (Keats and Maneveldt 1997) and very few modern taxonomic accounts of NCA from tropical reef systems currently exist in the literature. Species records of NCA from these areas are therefore based on identifications of uncertain accuracy and many must be treated as unconfirmed records (Keats *et al*. 1996). Despite these shortcomings however, certain comparisons among species occurring on Heron Reef and other tropical reef systems can be made.

Eleven species were found on Heron Reef, ten of which have previously been reported from other tropical reef systems (Table V). The total number of species found on Heron Reef was also similar to more recent accounts. Verheij (1993) identified 16 different species on the reefs of the Spermonde Archipelago and 7 of these species (see Table V) were also found on Heron Reef. Ballesteros and Afonso-Carillo (1995) reported 7 NCA species from the eastern coast of Mauritius and 3 of these species (see Table V) were also collected on Heron Reef.

Certain distributional patterns of some species appear to be similar in different reef systems. *Hydrolithon onkodes*, for example, is dominant on the reef flat towards the rim on Heron Reef and also appears to dominate the reef edges in the Hawaiian Islands, [Adey *et al*. 1982, as *Porolithon onkodes*, (Heydrich) Foslie], Indonesia (Verheij 1994) and on Mauritius, (Ballesteros and Afonso-Carrillo 1995). *Lithophyllum tamiense* is abundant in the lagoonal area on Heron Reef and similar information regarding its distribution and abundance was reported by Verheij (1994) and Ballesteros and Afonso-Carrillo (1995). *Mesophyllum erubescens* is common, but nowhere abundant, on Heron Reef. The same has been reported for *M. erubescens* in the southernmost coral reefs in the western Indian Ocean at Sodwana Bay (Keats and Chamberlain 1994). *Neogoniolithon brassica-florida* and *Hydrolithon reinboldii* appear to be generally common in tropical waters throughout the world (used see Table V).

The current lack of modern taxonomic accounts for most tropical reef areas highlights the need for further detailed modern studies of tropical NCA.

Without these studies it is far too early for conclusions to be drawn regarding worldwide biographical species distributions and biodiversity.

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