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# NONGENICULATE CORALLINACEAE (CORALLINALES, RHODOPHYTA) FROM THE SPERMONDE ARCHIPELAGO, SW SULAWESI, INDONESIA[1]

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SUMMARY

A critical study of the nongeniculate Corallinaceae (Corallinales, Rhodophyta) from the Spermonde Archipelago, Southwest Sulawesi, Indonesia, has been carried out. More than 750 collections, including type- and other relevant collections, were examined. In total 16 taxa belonging to 7 genera of nongeniculate Corallinaceae are reported. These are *Lithophyllum* (4 species), *Hydrolithon* (3 species), *Mastophora* (2 species), *Neogoniolithon* (1 species), *Spongites* (2 species), *Lithothamnion* (1 species), and *Mesophyllum* (3 species). The synonymy, type collection(s), type locality(ies), specimens examined, a detailed description, and remarks are given for each taxon. Two collections are referred to an unidentified taxon, probably belonging to the genus *Spongites*.

## INTRODUCTION

Although hermatypic corals of the tropical Indo-Pacific have been the subject of many studies (e.g. Veron, 1986; Moll, 1984; Randall & Meyers, 1983; Hoeksema, 1990), Indo-Pacific nongeniculate coralline red algae (Corallinales, Rhodophyta) are poorly known. Nongeniculate coralline algae contribute to the biomass and sediment of the reef ecosystem, and are also the main consolidating component of the reef systems. Reefs could not survive without these algae.

The only modern studies of nongeniculate coralline red algae from Indonesia involve *Sporolithon* (family Sporolithaceae) (Verheij, 1992, 1993a, c), the description of a new species, *Spongites sulawesiensis* (Verheij, 1993b), and the typification of the taxa collected during the Siboga Expedition of 1899–1900 (Verheij & Woelkerling, 1992). The Siboga Expedition reports provided by Foslie (1901c, 1904) and Weber-van Bosse (1926) are dated and require critical review in relation to recent taxonomic developments. Only a few other papers deal with the coralline algae from the remaining parts of the tropical Indo-Pacific (e.g. Gordon et al., 1976; Adey et al., 1982).

The taxonomy of nongeniculate Corallinales has many difficulties and has been subject to many changes. Most of the difficulties concerning names of taxa date back to the period of the Foslie–Heydrich rivalry (Woelkerling, 1988: ix–xi). Within some of Foslie's publications the nomenclature is chaotic and combined with the fact that a major part of his writings is in old Norwegian language, confusions are easily created. Occasionally Foslie changes within one publication the name of a single

[1] Previously published in PhD Thesis, Leiden University (1993) Chapter 2.2, pp. 35–77. Here partly emended.

taxon two times. One of the examples of this way of changing names is Foslie's 1909 paper 'Algologiske Notiser VI'. In that paper, on page 53, Foslie gives an additional description of *Mastophora* (*Lithoporella*) *pacifica* (Heydrich) Foslie which he transferred in 1902 from the genus *Melobesia* to the genus *Mastophora*. In the same paper on page 58 he describes a new genus *Lithoporella* and transfers *Mastophora pacifica* (Heydrich) Foslie to this new genus, making the combination *Lithoporella pacifica* (Heydrich) comb. nov.

During the Buginesia-III Project (October 1988–November 1990), extensive collections of nongeniculate Corallinales were made from the Spermonde Archipelago, SW Sulawesi, Indonesia (Verheij, 1992: fig. 1), and 20 species were found. Four species of Sporolithaceae have been dealt with previously (Verheij, 1992, 1993a, c). The present paper contains accounts of the 16 nongeniculate species of Corallinaceae found. For each species the synonymy, the distribution, a description, and some remarks are given. A dichotomous key to the species of the Spermonde Archipelago is provided.

## MATERIAL AND METHODS

Specimens were collected at depths of 0–65 m by snorkeling and/or by SCUBA diving from October 1988 to September 1990. The specimens were preserved in a 7% formalin-seawater solution for at least 48 h prior to transfer to a 70% ethanol/2% glycerol solution. The material is deposited in the Rijksherbarium, Leiden, The Netherlands (L), and specimens are referred by collector number. Type collections and other collections were studied at or borrowed from C, LTB, PC, TRH, US and USNC. [Herbarium abbreviations as in Holmgren et al. (1990).] This material is referred to by herbarium number. Each number represents one or several plants belonging to the same population. In total over 750 collections, containing more than 1200 plants from 224 localities, were examined.

For light microscopy, selected fragments of liquid-preserved specimens were decalcified in 0.6 M $HNO_3$, rinsed with distilled water, stained in 5% aqueous $KMnO_4$ for 25–30 min, rinsed with distilled water, dehydrated through a series of 30, 60, 90 and 100% ethanol at a minimum of 30 min intervals prior to embedding in 'LR White medium' resin (London Resin Company Ltd., Basingstoke, England) according to the method described by Penrose (1991: 438–439). Serial sections, 5–10 µm in thickness, were made using a steel knife, hardness d+. The sections were placed on a slide and a drop of Histoclear (National Diagnostics, Manville, New Jersey 08835, USA) was added to clear the resin prior to mounting in Eukitt (O. Kindler, Freiburg, Germany), and then hardened on a 40°C heating-plate. Small modifications in the duration of the different steps were made to prevent adverse tropical influences on the preserving and embedding processes. All prepared permanent slides are deposited at L. Morphological and anatomical terms are those of Woelkerling (1988: 58–75). Terms describing the external form and appearance have been taken from Woelkerling & Campbell (1992), with one category added: Branched: cylindrical to compressed, length of branches more than 3 times diameter. The abbreviation ICBN is used for the International Code of Botanical Nomenclature (Greuter, 1988) and the abbreviation SE is used for Siboga Expedition, the Dutch expedition to the Indonesian Archipelago (1899–1900).

## OBSERVATIONS

**Family Corallinaceae** Lamouroux, 1812: 185 (as 'Corallineae')

Remarks – Verheij (1993a) described a new family, Sporolithaceae, belonging to the Corallinales. The description of the Corallinaceae, as given by Woelkerling (1988: 85), has been modified in relation to the family Sporolithaceae. A modified diagnostic description of the Corallinaceae follows below.

Diagnosis – Thalli epogenous, semi-endophytic or free-living; thalli geniculate or non-geniculate, almost entirely calcified; internal organisation diffuse or pseudoparenchymatous; cells of adjacent filaments laterally connected by mainly secondary pit-connections or mainly cell fusions; gametangial and tetrasporangial structures in conceptacles; tetrasporangia cleaving simultaneously into zonate arranged spores. In some genera pores blocked by apical plug prior to spore release.

### KEY TO THE NONGENICULATE GENERA OF THE CORALLINACEAE FROM THE SPERMONDE ARCHIPELAGO, INDONESIA

a. Tetrasporangial conceptacles multiporate ..... 2
b. Tetrasporangial conceptacles uniporate ..... 5
2a. Epithallial cells flattened *and* eared ..... **13. Lithothamnion prolifer**
b. Epithallial cells sometimes flattened but *not* eared ..... 3
3a. Elongated basal pore cell in tetrasporangial conceptacles present **14. Mesophyllum erubescens**
b. Elongated basal pore cell in tetrasporangial conceptacles absent ..... 4
4a. Internal diameter tetrasporangial conceptacles large ≥ 450 µm; tetrasporangial roof ≥ 8 cell layers ..... **15. Mesophyllum funafutiense**
b. Internal diameter tetrasporangial conceptacles small ≤ 350 µm; tetrasporangial roof ≤ 6 cell layers ..... **16. Mesophyllum syrphetodes**
5a. Cells of adjacent filaments joined by means of secondary pit connections ... 6
b. Cells of adjacent filaments joined by means of cell fusions ..... 9
6a. Tetrasporangial conceptacle chamber floor ≥ 10 cell layers below thallus surface; internal height of tetrasporangial chamber ≥ 175 µm ..... 7
b. Tetrasporangial conceptacle chamber floor ≤ 9 cell layers below thallus surface; internal height of tetrasporangial chamber ≤ 175 µm ..... 8
7a. Tetrasporangial conceptacle chamber less than 15% raised above thallus surface; tetrasporangial conceptacle chamber floor > 15 cell layers below thallus surface **2. Lithophyllum kotschyanum**
b. Tetrasporangial conceptacle chamber more than 25% raised above thallus surface; tetrasporangial conceptacle chamber floor 10–12 cell layers below thallus surface ..... **1. Lithophyllum bamleri**
8a. Tips of branches rounded, never pointed; tetrasporangial roof ≥ 4 cell layers thick ..... **3. Lithophyllum okamurai**
b. Tips of branches pointed, never rounded; tetrasporangial roof ≤ 4 cell layers thick ..... **4. Lithophyllum tamiense**

9a. Plants, except where conceptacles or branches arise, two layered, dimerous; basal layer composed of palisade cells, trichocytes present ..... 10
b. Plants multi layered, dimerous and/or monomerous; no basal layer of palisade cells ..... 11
10a. Internal diameter tetrasporangial conceptacle chambers 700–900 µm) **8. Mastophora pacifica**
b. Internal diameter tetrasporangial chambers 350–500 µm **9. Mastophora rosea**
11a. Roof of tetrasporangial conceptacles formed by filaments interspersing tetrasporangia *and* filaments surrounding the fertile region ..... 12
b. Roof of tetrasporangial conceptacles only formed by filaments surrounding the fertile region ..... 14
12a. Tetrasporangial conceptacles without central columella **7. Hydrolithon reinboldii**
b. Tetrasporangial conceptacles with central columella ..... 13
13a. Thalli predominantly branched; tetrasporangial conceptacle chamber floor more than 10 cell layers below thallus surface; diameter tetrasporangial conceptacle pores ≥ 65 µm ..... **5. Hydrolithon gardineri**
b. Thalli predominantly encrusting; tetrasporangial conceptacle chamber floor ≤ 9 cell layers below thallus surface; diameter tetrasporangial conceptacle pores ≤ 55 µm ..... **6. Hydrolithon onkodes**
14a. Gonimoblast filaments arising only from the periphery of the continuous fusion cell ..... **11. Spongites sulawesiensis**
b. Gonimoblast filaments arising from dorsal side of the discontinuous fusion cell ..... 15
15a. Simple spermatangia restricted to the floor of the male conceptacles; internal diameter female conceptacle 900–1100 µm ..... **12. Spongites** spec.
b. Simple spermatangia on both floor and roof of male conceptacles; internal diameter female conceptacles 250–450 µm **10. Neogoniolithon brassica-floridum**

**Subfamily Lithophylloideae** Setchell, 1943: 134 (as 'Lithophylleae')

Remarks – Subfamily concept following Woelkerling (1988: 92).

**Lithophyllum** Philippi, 1837: 389

Remarks – Genus concept follows Woelkerling & Campbell (1992). They presented an account of southern Australian species of *Lithophyllum*. Most species reported by Woelkerling & Campbell are at least partly dimerous. The ventral regions of these dimerous parts are usually composed of filaments of palisade cells, paralleling the substratum. During the present study four *Lithophyllum* species were found. However, these species are mainly monomerous.

Woelkerling & Campbell (1992) considered seven characters having diagnostic value for the southern Australian species. Three of these characters, associated with

the tetrasporangial conceptacles (position of the floor, roof elevation and internal chamber dimensions) can be used for delimiting *Lithophyllum* species from the Spermonde Archipelago. The other four characters used by Woelkerling & Campbell are not applicable to the species from the Spermonde Archipelago. None of the species from the Spermonde Archipelago have tetrasporangial conceptacles with pores occluded by a cluster of large cells, nor do they have terrassing thalli, or applanate branches, and all species have thalli with dorsal regions (postigenous filaments) composed of multicellular filaments.

## 1. **Lithophyllum bamleri** (Heydrich) Foslie — Figs. 1–6

Basionym: *Lithothamnion bamleri* Heydrich, 1897c: 4–6.

Homotypic synonyms: *Goniolithon bamleri* (Heydrich) Foslie, 1898: 9. — *Lithophyllum bamleri* (Heydrich) Foslie, 1900b: 20; Foslie, 1904: 64–66.

Type collection: lectotype: PC, no number (designated in the present paper).

Type locality: Tami Island, Gulf of Huon, Papua New Guinea.

Distribution: Tropical Indo-Pacific.

Representative specimens examined: lectotype, PC no number; Kudingareng Keke Island, depth 5–10 m (*Verheij B36, B37 & B48*, 27-vi-1985; *Verheij B98a*, 05-vii-1985; *Verheij B126*, 14-vii-1985; *Verheij B143 & B145*, 16/17-vii-1985; *Verheij B162*, 20/21-vii-1985; *Verheij 0021*; *Verheij 0067*), Langkai Island, depth 1–10 m (*Verheij B218*, 24/29-vii-1985; *Verheij 0101*, 23-iii-1989; *Verheij 0192, 0248 & 0263*, 13/15-iv-1989; *Verheij 0806 & 0816*, 27/29-xi-1989), Lanyukang Island, 0–5 m (*Verheij B259*, 24/29-vii-1985), Bone Tambung Island, depth 2 m, (*Verheij 0719*, 26-x-1989), Gusung Island, depth 1 m (*Verheij 0730*, 01-xi-1989), all from the Spermonde Archipelago, SW Sulawesi, Indonesia; Bira, South Sulawesi, Indonesia, depth 2–5 m (*Verheij 0057*, 20-xii-1988).

Description – Young parts of plants encrusting, older parts branched; branches flattened to plate-like, not cylindrical; crustose parts attached to substratum. Crustose parts 0.5–1.0 mm thick. Thallus pseudoparenchymatous; cells of adjacent filaments laterally connected by secondary pit connections.

Crustose parts of thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized in a coaxial manner (cells 5–15 µm in diameter and 10–30 µm long); dorsal region composed of portions of filaments curving outwardly from the ventral region towards the surface (cells 5–12 µm in diameter and 5–10 µm long). Branched parts radial and monomerous; central core composed of filaments arising from the ventral region, organized in a coaxial manner (cells 7–15 µm in diameter and 8–25 µm long); peripheral region (cells 5–10 µm in diameter and 5–12 µm long) composed of portions of filament curving outwardly from the central core towards the surface.

Trichocytes not observed. Filaments terminated by a single, rounded epithallial cell (cell 5–12 µm in diameter and 3–5 µm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Tetrasporangial development on the side of the plate-like branches not exposed to direct sunlight. Conceptacles 300–400 µm internal diameter and 200–275 µm internal height). Conceptacle floor 10–12 cells below thallus surface. Conceptacle roof 3–7 cells thick, arising from filaments surrounding the tetrasporangial disc; 25–50% of the conceptacle raised above thallus surface, old and empty conceptacles becoming

buried. A well developed columella present; filaments of columella protruding into the pore.

Male conceptacles not observed. Female conceptacle 175–225 µm internal diameter and 40–65 µm internal height. Carposporangial conceptacles 350–425 µm internal diameter and 100–150 µm internal height.

Diagnostic features – *Lithophyllum bamleri* is distinguished from other species of *Lithophyllum* examined in having the following combination of features:

— Tetrasporangial conceptacle height usually > 225 µm.
— Tetrasporangial roof filaments 3–7 cells long.
— Tetrasporangial chamber usually 25–50% raised above thallus surface.
— Tetrasporangial conceptacle floor usually 10–12 cell layers below thallus surface.

Remarks – *Lithophyllum bermudense* Foslie & Howe (1906) as described by Woelkerling & Campbell (1992), agrees partly with specimens of *Lithophyllum bamleri*. However, the dimensions of the conceptacles, tetrasporangial and female/ carposporangial, of *L. bamleri* are smaller and the roof filaments are longer.

A detailed study of types and of relevant collections is needed to elucidate the relationships of *Lithophyllum bamleri* and *Lithophyllum bermudense*. If *Lithophyllum bamleri* and *Lithophyllum bermudense* are conspecific, the epithet *bamleri* has priority (ICBN art. 9, 10 and 11.3).

*Lithophyllum bamleri* and *Lithophyllum tamiense* are the two most important lithophylloid species in the Spermonde Archipelago. They form, together with *Hydrolithon onkodes*, the major part of the coralline algal biomass on the reef edges of the southern and eastern reefs. They occur in between the branches of corals, generally belonging to the genus *Acropora*.

## 2. **Lithophyllum kotschyanum** Unger — Figs. 7–9

Basionym: *Lithophyllum kotschyanum* Unger, 1858: 22; Foslie, 1909: 34; Gordon et al., 1976: 267–269; Adey et al., 1982: 37–40.
Type collection: holotype: TRH, no number, leg. Kotschy; see also Woelkerling (1993: 133)
Type locality: *Lithophyllum kotschyanum*: Gulf of Bahrein, Persian Gulf.
Distribution: Persian Gulf, Tropical Indo-Pacific.
Representative specimens examined: holotype, Gulf of Bahrein, Persian Gulf, (*Kotschy*, TRH no number); Bone Tambung Island, Spermonde Archipelago, SW Sulawesi, Indonesia, depth 2 m (*Verheij 1133*, 07-iv-1990); Hilo Bay, Hawaii Island (*Child*, iii-1971, USNC: 71-58-72, 71-59-8, 71-59-10 & 71-59-25), Kawaihae, Hawaii Island (*Child*, iii-1971, USNC: 71-54-1, 71-57-2), Lagoon, Midway Islands (*Child*, iii-1971, USNC: 71-62-21), South Island, Midway Islands (*Child*, viii-1971, USNC: 71-82-60).

Description – Young parts of plants encrusting, older parts branched, branches compressed to plate-like, not cylindrical; crustose parts attached to substratum. Crustose parts 0.5–1.0 mm thick. Thallus pseudoparenchymatous; cells of adjacent filaments laterally connected by secondary pit connections.

Crustose parts of thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized in a noncoaxial manner (cells 5–15 µm in diameter and 10–30 µm long); dorsal region composed of

portions of filaments curving outwardly from the ventral region towards the surface (cells 5–12 µm in diameter and 5–10 µm long). Branched parts radial and monomerous; central core composed of filaments arising from the ventral region, organized in a nonaxial manner (cells 5–15 µm in diameter and 10–25 µm long); peripheral region (cells 5–10 µm in diameter and 5 -12 µm long) composed of portions of filament curving outwardly from the central core towards the surface.

Trichocytes not observed. Filaments terminated by a single, rounded epithallial cell (cells 5–10 µm in diameter and 3–6 µm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Tetrasporangial development on the side of the plate-like branches not exposed to sunlight. Conceptacles 300–400 µm internal diameter and 175–225 µm internal height. Conceptacle floor > 15 cells below thallus surface. Conceptacle roof 5–10 cells thick, arising from filaments surrounding the tetrasporangial disc, < 15 % of the conceptacle raised above thallus surface. Old and empty conceptacles buried. A well developed columella present, filaments of columella protruding into the pore.

Gametangial conceptacles not found.

Diagnostic features – *Lithophyllum kotschyanum* is distinguished from other species of *Lithophyllum* examined in having the following combination of features:

- Tetrasporangial roof filaments 5–10 cells long.
- Less than 15% of the conceptacle chamber is raised above the thallus surface.
- Tetrasporangial conceptacle floor more than 15 cell layers below the thallus surface.

Remarks – *Lithophyllum kotschyanum* can easily be recognized by the anatomy of the tetrasporangial conceptacles. They are not or only slightly raised above the thallus surface and the conceptacle floor is situated more than 15 cell layers below the thallus surface.

### 3. **Lithophyllum okamurai** Foslie — Figs. 10–18

Basionym: *Lithophyllum okamurai* Foslie, 1900c: 4; Foslie, 1904: 59, pl. 11, fig. 11.

Heterotypic synonyms: *Lithophyllum okamurai* f. *trincomaliensis* Foslie, 1906: 23. — *L. okamurai* f. *valida* Foslie, 1906: 23.

Type collections: *Lithophyllum okamurai* lectotype: TRH no number, leg. K. Yendo, 1899, no. 408; see also Woelkerling (1993: 163). — *L. okamurai* f. *trincomaliensis* holotype: TRH no number, leg. N. Svedelius, 17-iv-1903; see also Woelkerling (1993: 225). — *L. okamurai* f. *valida* holotype: TRH no number, leg. N. Svedelius, 16-iii-1903; see also Woelkerling (1993: 231).

Type localities: *Lithophyllum okamurai*: Marine Laboratory, Sagami Province, Japan. — *L. okamurai* f. *trincomaliensis*: Trincomalee, Sri Lanka. — *L. okamurai* f. *valida*: Dondra Head, Sri Lanka.

Distribution: Tropical Indo-Pacific.

Representative specimens examined: lectotype *Lithophyllum okamurai*, TRH no number, leg. K. Yendo, 1899, no. 408; holotype *L. okamurai* f. *trincomaliensis*, TRH no number, leg. N. Svedelius, 17-iv-1903; holotype *L. okamurai* f. *valida*: TRH no number, leg. N. Svedelius, 16-iii-1903; Langkai Island, the Spermonde Archipelago, SW Sulawesi, Indonesia, depth 10–15 m (*Verheij, 0217*, 14-iv-1989; *Verheij, 1284*, 10-ix-1990); Snellius-II Expedition, no. 10911A.

Description – Young parts of plants encrusting, older parts lumpy or warty and becoming often free-living and forming rhodoliths; crustose parts attached to substratum. Crustose parts 1.0–2.0 mm thick, excrescences up to 5 mm thick. Thallus pseudoparenchymatous; cells of adjacent filaments laterally connected by secondary pit connections.

Crustose parts of thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized in a noncoaxial manner (cells 5–15 μm in diameter and 10–30 μm long); dorsal region composed of portions of filaments curving outwardly from the ventral region towards the surface (cells 5–12 μm in diameter and 5–10 μm long). Branched parts radial and monomerous; central core composed of filaments arising from the ventral region, organized in a noncoaxial manner (cells 5–15 μm in diameter and 5–20 μm long); peripheral region (cells 5–10 μm in diameter and 5 -15 μm long) composed of portions of filament curving outwardly from the central core towards the surface.

Trichocytes not observed in specimens examined. Filaments terminated by a single, rounded epithallial cell (cells 4–8 μm in diameter and 3–5 μm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Tetrasporangial development on the side of the plate-like branches not exposed to sunlight. Conceptacles 250–350 μm internal diameter and 125–150 μm internal height. Conceptacle floor 6–8 cells below thallus surface. Conceptacle roof 4–6 cells thick, arising from filaments surrounding the tetrasporangial disc, 25–50% of conceptacle raised above thallus surface. Old and empty conceptacles buried. A well developed columella present, filaments of columella protruding into the pore.

Male conceptacles slightly raised above thallus surface. Conceptacle roof 4–7 cells thick. Simple spermatangia occurring only on the floor of the male conceptacle, 225–375 μm internal diameter and 75–175 μm internal height. Female conceptacles not observed.

Carposporangial conceptacles 250–400 μm internal diameter and 100–175 μm internal height.

Diagnostic features – *Lithophyllum okamurai* is distinguished from other species of *Lithophyllum* examined in having the following combination of features:

— Thallus not branched, only warty.
— Tetrasporangial conceptacle height less than 150 μm.
— Tetrasporangial roof filaments 4–6 cells long.
— 25–50% of the conceptacle chamber is raised above the thallus surface.
— Tetrasporangial conceptacle floor 6–8 cell layers below the thallus surface.

Remarks – Gametangial measurements were taken from the type collection; no gametangial plants were collected in the Spermonde Archipelago.

This species is the only lithophylloid species in the Spermonde Archipelago that becomes free-living and forms rhodoliths.

During the present study the type collections of *Lithophyllum okamurai* f. *trincomaliensis* Foslie, 1906 and *L. okamurai* f. *valida* Foslie, 1906 were found to be conspecific with *L. okamurai* f. *okamurai* and therefore are regarded as heterotypic synonyms.

Foslie described an additional form of *L. okamurai*. A critical examination during the present study of the type collection of *L. okamurai* f. *ptychoides* Foslie, 1907a, in 1909 raised to species level, *L. ptychoides*, showed that it does not belong in the Lithophylloideae but has to be referred to the Melobesioideae or Mastophoroideae on basis of the presence of lateral cell fusions instead of secondary pit connections (see also Fig. 16).

## 4. Lithophyllum tamiense Heydrich — Figs. 19–26

Basionym: *Lithophyllym tamiense* Heydrich, 1897c: 1, figs. 4–7.

Homotypic synonym: *Lithophyllym tamiense* Heydrich, 1897c: 1; Heydrich, 1901: 419; Foslie, 1900b: 16; Foslie, 1901d: 17.

Heterotypic synonyms: *Lithothamnion moluccense* Foslie, 1897: 12. — *Lithophyllum moluccense* (Foslie) Foslie, 1901a: 12; Foslie, 1901b: 17; Foslie, 1904: 65–69; Gordon et al., 1976: 270–272. — *Goniolithon moluccense* (Foslie) Foslie, 1898: 8; Foslie, 1900d: 10, 11; Foslie, 1901b: 17. — *Lithothamnion pygmaeum* Heydrich, 1897: 3. — *Goniolithon pygmaeum* (Heydrich) Foslie, 1898: 8. — *Lithophyllum torquescens* Foslie, 1901a: 11; Foslie, 1901d: 23–24. — *Lithophyllum moluccense* f. *torquescens* Foslie, 1904: 69–70.

Type collections: *Lithophyllum moluccense* holotype: TRH, no number, leg. Kukenthal; see also Woelkerling (1993: 152). — *L. tamiense* lectotype: PC no number, Heydrich specimen from Tami Island, Papua New Guinea (designated in this paper); see also Woelkerling (1993: 220). — *L. tamiense* isolectotype: C no number, Heydrich specimen (designated in this paper). — *L. tamiense* isolectotype: TRH no number, Heydrich specimen (designated in this paper); see also Woelkerling (1993: 220). — *L. pygmaeum* lectotype: PC no number, Heydrich specimen from Tami Island, Papua New Guinea (designated in this paper). — *L. torquescens* lectotype: TRH no number, leg. Agassiz; see also Woelkerling (1993: 224).

Type localities: *Lithophyllum tamiense*: Tami Island, Papua New Guinea. — *L. moluccense*: Moluccas, Indonesia. — *L. pygmaeum*: Tami Island, Papua New Guinea. — *L. torquescens*: Mauritius (?).

Distribution: Tropical Indo-Pacific, West Indies (?).

Representative specimens examined: lectotype *Lithophyllum tamiense*, PC no number; isolectotypes *L. tamiense* C and TRH no number; holotype *L. moluccense*, TRH no number; lectotype *L. pygmaeum*, PC no number; lectotype *L. torquescens*, TRH no number; SE station 47, Bay of Bima, Flores Island, Indonesia, depth 55 m (SE collection 1287, 8/12-iv-1899, L 943.7-1); SE station 78, Lumu Lumu shoal, Borneo Bank, Indonesia, depth 34 m (SE Collections 135, 136 & 1199, L 943.7-81); SE station 91, Moeras Reef, east coast Borneo, Indonesia, depth up to 54 m (SE collections 105 & 121, TRH no number, SE collection 100, L 943.7-1 and SE collections 7, 23, 95–98, 101, 102, 104, 107-109, 112–115, 120, 122, L 943.7-81, 22-vi-1899); SE station 93, Sanguisiapo Island, Sulu Archipelago, Philippines, depth 12 m (SE collections 1050, 1052–1055, 24/25-vi-1899, L 943.7-1); SE station 129, Anchorage off Kawio and Kamboling Islands, Indonesia (SE collection 903, TRH no number and SE collections 907 and 908, L 943.7-81, 22/23-vii-1899); SE station 131, Karakelang Islands, Indonesia, depth 13 m (SE collections 1139–1141, 24/25-vii-1899, L 943.7-81); SE station 149, Fau anchorage, west coast of Gebe Island, Indonesia, depth 31 m (SE collections 412 & 413, 10/11-viii-1899, L 943.7-1); SE station 193, Sanana bay, Sula Besi Island, depth 22 m (SE collection 706, 13/14-ix-1899, L 943.7-81); SE station 213, 26-x-1899, L 943.7-81); Salayer Island, Indonesia, depth up to 36 m (SE collections 985–988 station 220, anchorage off Pasir Pandjang, west coast of Binongka, Indonesia (SE collections 1179 1180, 1182, 1185, 1187 & 1193, TRH no number, and SE collections 1181, 1183, 1184, 1186, 1187, 1189, 1190, 1192–1194, 1196, L 943.7-1, 1/3-xi-1899); SE station 240, Banda anchorage, Indonesia, depth 9–45 m (SE collections 181–183, 186–188, 190–195, 22-xi/01-xii-1899, L 943.7-81); SE station 248, anchorage off Rumah Lusi, north point of Tiur Island, Indonesia, depth up to 54 m (SE collections

1070–1072, 4/5-xii-1899, L 943.7-1); SE station 303, Haingsisi, Samau Island, Indonesia, depth up to 36 m (SE collection 16, 2/5-ii-1900, L 943.7-81); SE station 311, Sapeh bay, north coast of Sumbawa, depth up to 36 m (SE collection 945, 12/13-ii-1900, L 943.7-1); SE station 313, Dangar Besar Island, Indonesia, depth up to 36 m (SE collection 1286, 14/16-ii-1900, L 943.7-1); Kudingareng Keke Island, depth 2–5 m (*Verheij 0021*, 08-xii-1988; *Verheij 0512*, 28-viii-1989; *Verheij 0546*, 19-ix-1989), Langkai Island, depth 5–10 m (*Verheij 0249*, 15-iv-1989; *Verheij 0807*, 29-xi-1989; *Verheij 1017*, 08-v-1990), Lanyukang Island, depth 1–5 m (*Verheij 0323*, 05-v-1989; *Verheij 1039*, 09-v-1990), Gusung Island, depth 1–2 m (*Verheij 0622*, 29-ix-1989; *Verheij 0731*, 01-xi-1989; *Verheij 1224*, 23-viii-1990), Bone Tambung Island, depth 1–2 m (*Verheij 0718*, 26-x-1989; *Verheij 0793*, 16-xi-1989; *Verheij 0976*, 09-iv-1990), Kapoposang Island, depth 2 m (*Verheij 1191*, 15-vii-1990), all Spermonde Archipelago, SW Sulawesi, Indonesia; Bira, South Sulawesi, Indonesia, depth 2 m (*Verheij 0047*, 17-xii-1988); Guadalcanal, Honiara, Solomon Islands (*Womersley & Bailey 202*, 09-viii-1965, L 975.350-9 & L 975.350-14); Guadalcanal, Komimbo, Solomon Islands (*Womersley & Bailey 291*, 18-viii-1965, L 977. 350-49); Guadalcanal, Mamara, Solomon Islands (*Womersley & Bailey 168*, 07-viii-1965, L 977.350-84).

Description – Young parts of plants encrusting, older parts branched; branches cylindrical, not flattened or plate-like; crustose parts attached to substratum. Crustose parts 0.5–1.0 mm thick. Thallus pseudoparenchymatous; cells of adjacent filaments connected laterally by secondary pit connections.

Crustose parts of thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized in a coaxial manner (cells 5–15 µm in diameter and 15–45 µm long); dorsal region composed of portions of filaments curving outwardly from the ventral region towards the surface (cells 4–10 µm in diameter and 5–20 µm long). Branched parts radial and monomerous; central core composed of filaments arising from the ventral region, organized in a coaxial manner (cells 5–15 µm in diameter and 5–30 µm long); peripheral region (cells 4–10 µm in diameter and 5–15 µm long) composed of portions of filament curving outwardly from the central core towards the surface.

Trichocytes not observed. Filaments terminated by a single, rounded epithallial cell (4–10 µm in diameter and 3–5 µm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Tetrasporangial conceptacle development at all sides of the cylindrical branches. Conceptacles 300–450 µm internal diameter and 125–175 µm internal height. Conceptacle floor 7–9 cells below thallus surface. Conceptacle roof 2–4 cells thick, arising from filaments surrounding the tetrasporangial disc, > 50% of conceptacle raised above thallus surface. Old and empty conceptacles buried. A well developed columella present, filaments of columella protruding into the pore.

Gametangial conceptacles not found during the present study.

Diagnostic features – *Lithophyllum tamiense* is distinguished from other species of *Lithophyllum* examined in having the following combination of features:

- — Tetrasporangial conceptacle height usually less than 150 µm.
- — Tetrasporangial roof filaments 2–4 cells long.
- — More than 50% of the conceptacle chamber is raised above the thallus surface.
- — Tetrasporangial conceptacle floor 7–9 cell layers below the thallus surface.

Remarks – During the present study a critical examination was carried out of the type collections of *Lithophyllum moluccense* Foslie, 1897 (holotype in TRH), *L. tamiense* Heydrich, 1897c (lectotype in PC, isolectotypes in C and TRH), *L. pygmaeum* Heydrich, 1897c (lectotype in PC) and *L. torquescens* Foslie, 1901a (lectotype in TRH). All four type collections belong to the same taxon. *Lithophyllum moluccense*, *L. tamiense* and *L. pygmaeum* were described in 1897. The latter two were published by Heydrich in the same paper in 'Bibliotheca Botanica', which was issued in February 1897 (see page 11 of the volume). *Lithophyllum moluccense* was published in 'Det Kgl. Norske Videnskabers Selskabs Skrifter 1897 (1)', which was printed between July 1897 and December 1897 [pers. comm. S. Johansen, University library TRH; see also Woelkerling (1993: 278)]. Consequently *L. tamiense* and *L. pygmaeum* have priority over *L. moluccense*. *Lithophyllum tamiense* is chosen here as the legitimate name for the taxon because *L. tamiense* has the largest lectotype collection, containing thalli with a large number of tetrasporangial conceptacles.

Figures 22–26 show different stages of tetrasporangial conceptacle development. During the earliest stage of development seen, the submeristematic cells in the fertile region become elongated (Fig. 22). Subsequently, the overlaying meristematic cells continue producing vegetative cells inwardly, forming the future conceptacle roof (Fig. 23). When the developing conceptacle roof has become two to four cells thick, tetrasporangial initials are formed in between the elongated cells (Figs. 24, 25). During maturation a pore is formed above the center of the fertile region, probably due to autolysis of the cells (Fig. 25). Until the spores are matured the pore remains covered by a thin layer of cells, probably the remains of the overlaying epithallial cells (Fig. 25). After spore release the conceptacle remains intact and becomes overgrown by the developing thallus (Fig. 26).

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

Remarks – Subfamily concept follows Woelkerling (1988: 115).

Several genera of the Mastophoroideae (e.g. *Hydrolithon*, *Mastophora*, *Neogoniolithon*, and *Spongites*) have been the subject of detailed taxonomic studies (e.g. Penrose, 1990, 1991, 1992a; Penrose & Woelkerling, 1992; Turner & Woelkerling, 1982a, 1982b). These revised generic concepts are adopted in the present paper, although, one taxon from the Spermonde Archipelago, *Spongites* spec., does not fully agree with the generic circumscription of *Spongites* provided by Penrose (1991). See further the remarks of the taxa involved.

**Hydrolithon** (Foslie) Foslie, 1909: 55

Remarks – Generic concept following Penrose & Woelkerling (1992: 87). Penrose & Woelkerling (1988) and Penrose & Woelkerling (in Woelkerling 1988) concluded that the genera *Porolithon* Foslie (1909: 57) and *Hydrolithon* could not be separated from *Spongites* Kützing (1841: 30), a genus resurrected by Woelkerling

(1985), based on vegetative features previously used to separate those genera. However, they realized that a broad range of taxa was included in *Spongites* (sensu lato) and that after studying reproductive structures some taxa might be separated from *Spongites*. Penrose & Woelkerling (1992) presented the results of a detailed study of the generic type collections of the genera *Spongites*, *Porolithon* and *Hydrolithon*, previously included in *Spongites* (sensu lato). They concluded that two different types of tetrasporangial conceptacle development occur. One type occurs in *Spongites* and another type occurs in *Porolithon* and *Hydrolithon*. Subsequently they characterized *Spongites* (sensu stricto) and *Hydrolithon*; *Porolithon* is regarded as a heterotypic synonym of *Hydrolithon*. In the present paper the Penrose & Woelkerling (1992) concept of *Hydrolithon* is followed.

## 5. **Hydrolithon gardineri** (Foslie) Verheij & Prud'homme van Reine — Figs. 27–30

Basionym: *Lithophyllum gardineri* Foslie, 1907a: 30.

Homotypic synonyms: *Lithophyllum gardineri* Foslie f. *gardineri* (as f. *typica*) Foslie, 1907a: 30. — *Hydrolithon gardineri* (Foslie) Verheij & Prud'homme van Reine, 1993: 451. — *Porolithon gardineri* (Foslie) Foslie, 1909: 57; Littler, 1971; Adey et al., 1982: 7–9.

Heterotypic synonyms: *Lithophyllum gardineri* f. *obpyramidata* Foslie, 1907a: 30. — *Lithophyllum coarctatum* f. *coarctatum* Foslie, 1907a: 31 (as f. *typica*). — *Porolithon coarctatum* (Foslie) Adey, 1970: 10.

Type collections: *Lithophyllum gardineri* f. *gardineri* lectotype: TRH no number, leg. Gardiner, Indian Ocean, Coevity, 9.1905, LM70(8), Lith. Sealark Exp. 2(4); see also Woelkerling (1993: 102 & 103). — *L. gardineri* f. *obpyramidata* lectotype: TRH no number, Gardiner, Indian Ocean, Coevity, 9.1905, LM70(11), Lith. Sealark Exp. 2 (7); see also Woelkerling (1993: 160). — *L. coarctatum* holotype: TRH no number, Cocos-Keeling Islands, Josephine Exp; see also Woelkerling (1993: 52, 53).

Type localities: *L. gardineri* f. *gardineri*: Coevity, Seychelles Islands, Indian Ocean. — *L. gardineri* f. *obpyramidata*: Coevity, Seychelles Islands, Indian Ocean. — *L. coarctatum* f. *coarctatum*: Cocos–Keeling Islands.

Representative specimens examined: lectotype *L. gardineri* f. *gardineri*, TRH no number; lectotype *L. gardineri* f. *obpyramidata*, TRH no number; lectotype *L. coarctatum* f. *coarctatum*, TRH no number; Lanyukang Island, Spermonde Archipelago, SW Sulawesi, depth 5–10 m (*Verheij B228*, 24/29-vii-1985, L 986.106-492).

Description – Plants initially encrusting and attached to the substratum, but soon becoming branched. Crustose parts up to 1–2 mm thick, branches 3–5 mm thick. Thallus pseudoparenchymatous; cells of adjacent filaments connected laterally by cell fusions connections.

Crustose parts of thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized in a coaxial manner (cells 5–15 µm in diameter and 10–25 µm long); dorsal region composed of portions of filaments curving outwardly from the ventral region towards the surface (cells 5–25 µm in diameter and 5–20 µm long). Branches radial and monomerous; central core composed of filaments arising from the ventral region, organised in a coaxial manner (cells 5–15 µm in diameter and 5–20 µm long); peripheral region (cells 5–15 µm in diameter and 5–15 µm long) composed of portions of filaments curving outwardly from the central core towards the surface.

Trichocytes (cells 10–18 µm in diameter and 15–25 µm long) common, occurring solitary, in short vertical rows, or in horizontal fields at the thallus surface, in general becoming buried.

Filaments terminated by a single, rounded epithallial cell (cells 5–12 µm in diameter and 3–6 µm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Tetrasporangial conceptacles 175–250 µm internal diameter and 50–100 µm internal height. Conceptacle roof 5–7 cells thick, formed by filaments surrounding and interspersing the tetrasporangia. Conceptacle not or slightly raised above thallus surface. Conceptacle floor more than 10 cells below the thallus surface. Pore canal lined by elongated cells not protruding into the canal and orientated perpendicularly to the roof surface. Diameter conceptacle pore: 65–75 µm. Old and empty conceptacles buried. A central columella present.

Gametangial plants not found.

Diagnostic features – *Hydrolithon gardineri* is distinguished from other species of *Hydrolithon* examined in having the following combination of features:

- — Thallus usually branched.
- — Central columella present in tetrasporangial conceptacles.
- — Tetrasporangial conceptacles usually less than 100 µm in height.
- — Tetrasporangial conceptacle floor more than 10 cell layers below the thallus surface.
- — Diameter tetrasporangial pore usually more than 65 µm.

Remarks – *Hydrolithon gardineri* is a characteristic species from the very exposed, deeper (5–10 m) reef flats. It has only been observed on the deeper reef flats on the west side of the islands Langkai, Lanyukang and Kapoposang.

### 6. **Hydrolithon onkodes** (Heydrich) Penrose & Woelkerling — Figs. 31–35

Basionym: *Lithothamnion onkodes* Heydrich, 1897c: 6; Foslie, 1901b: 533.

Homotypic synonyms: *Goniolithon onkodes* (Heydrich) Foslie, 1898: 8. — *Porolithon onkodes* (Heydrich) Foslie, 1909: 57; Gordon et al., 1976: 266, 267; Adey et al., 1982: 7, 8. — *Hydrolithon onkodes* (Heydrich) Penrose & Woelkerling, 1992: 173.

Type collections: *Hydrolithon onkodes* lectotype: TRH, no number, Heydrich, specimen no. 97; see also Woelkerling (1993: 164). — *Hydrolithon onkodes* isolectotype: PC, no number, Heydrich.

Type locality: Tami Island, Papua New Guinea.

Distribution: Tropical Indo-Pacific, southern Australia.

Representative specimens examined: lectotype, TRH no number; syntype, PC no number; SE station 91, Moeras reef, east coast Borneo, Indonesia, depth up to 45 m (SE collection 130, 22-vi-1899, TRH no number); SE station 225, south of Lucipara Islands, depth 894 m (?) (SE collection 534 & 535a, 08-xi-1899, TRH no number); SE station 215, Kambia Island, Indonesia, depth unknown (SE collection 891, 28/29-x-1899, TRH no number); Kudingareng Keke Island, depth 0–5 m (*Verheij B49*, 27-vi-1985; *Verheij B95*, 05-vii-1985; *Verheij B135*, 14-vii-1985; *Verheij 0516*, 28-viii-1989; *Verheij 0583*, 26-ix-1989), Bone Baku, depth 0–5 m (*Verheij B120*, 12-vii-1985, L 986.106-509), Langkai Island, depth 1–15 m (*Verheij B183, B192, B198 & B221*, 24/29-vii-1985, L 986.106-509; *Verheij 0100*, 23-iii-1989; *Verheij 0198*, 13-iv-1989; *Verheij 0250*, 15-iv-1989; *Verheij 1134*, 04-vii-1990), Lanyukang Island, depth 0–5 m (*Verheij B246 & B253*, 24/29-vii-1985, L 986.106-509), Samalona Island, depth 1 m (*Verheij*

*0169*, 07-iv-1989; *Verheij 0870*, 25-xi-1989), Barang Lompo Island, depth 1 m (*Verheij 0917*, 18-xii-1989), all from the Spermonde Archipelago, SW Sulawesi, Indonesia; Bira, South Sulawesi, Indonesia, depth 2 m (*Verheij 0056*, 17-xii-1988); Hilo Bay, Hawaii Island (*Child*, iii-1971, USNC: 71-58-38 & 71-59-28), Kawaihae, Hawaii Island (*Child*, iii-1971, USNC: 71-57-20), South Island, Midway Islands (*Child*, viii-1971, USNC: 71-82-76, 71-82-84 & 71-82-85), Kaneohe Bay, Oahu Island (*Child*, USNC: 71-54-4, iii-1971), Wainae, Oahu Island (*Child*, iii-1971, USNC: 71-52-9), all Hawaiian Archipelago.

Description – Plants encrusting, attached to the substratum; plants sometimes enclosing substratum and becoming free-living. Thalli up to several mm thick. Thallus pseudoparenchymatous; cells of adjacent filaments connected laterally by cell fusions connections.

Thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized in a noncoaxial manner (cells 5–20 µm in diameter and 10–30 µm long); dorsal region composed of portions of filaments curving outwardly from the ventral region towards the surface (cells 5–10 µm in diameter and 5–15 µm long).

Trichocytes (cells 14–25 µm in diameter and 25–35 µm long) common, occurring solitary and/or in horizontal fields, in general becoming buried. Vertical rows of trichocytes were not found.

Filaments terminated by a single, rounded epithallial cell (cells 5–10 µm in diameter and 3–5 µm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Tetrasporangial conceptacles 200–350 µm internal diameter and 100–250 µm internal height. Tetrasporangial conceptacle roof 3–6 cells thick, formed by filaments surrounding and interspersing the tetrasporangia. Tetrasporangial conceptacle not or slightly raised above thallus surface. Conceptacle floor 8–9 cells below thallus surface. Pore canal lined by large, elongated cells, not protruding into pore canal and orientated perpendicularly to the roof surface. Diameter of conceptacle pore 40–55 µm. Old and empty tetrasporangial conceptacles buried. A central columella present.

Gametangial and carposporangial plants not observed.

Diagnostic features – *Hydrolithon onkodes* is distinguished from other species of *Hydrolithon* examined in having the following combination of features:

— Thallus usually encrusting.
— Central columella present in tetrasporangial conceptacles.
— Tetrasporangial conceptacles usually more than 100 µm in height.
— Tetrasporangial conceptacle floor 8–9 cell layers below the thallus surface.
— Diameter tetrasporangial pore 40–50 µm.

Remarks – *Hydrolithon onkodes* is, together with *Lithophyllum bamleri* and *L. tamiense*, the most important coralline algal component of the reef edges of the eastern and southern parts of the reefs of the Spermonde Archipelago.

### 7. **Hydrolithon reinboldii** (Weber-van Bosse & Foslie) Foslie — Figs. 36–38

Basionym: *Lithophyllum reinboldii* Weber-van Bosse & Foslie in Foslie, 1901c: 5.
Homotypic synonyms: *Goniolithon reinboldii* (Weber-van Bosse & Foslie) Foslie, 1904: 49; Johnson, 1964: 26. — *Hydrolithon reinboldii* (Weber-van Bosse & Foslie) Foslie, 1909: 55; Gordon

et al., 1976: 255–257; Adey et al., 1982: 25–26; Penrose & Woelkerling, 1992: 83. — *Paragoniolithon reinboldii* (Weber-van Bosse & Foslie) Lemoine, 1911: 166. — *Spongites reinboldii* (Weber-van Bosse & Foslie) Penrose & Woelkerling in Woelkerling, 1988: 173.

Type collections: lectotype: TRH no number, Siboga Expedition, stat. 91, collection 38; see also Verheij & Woelkerling (1992: 284) and Woelkerling (1993: 188); isolectotypes: L 943.5-149, Siboga Expedition, stat. 91, collections 43–46, 53, 56, 59, 61, 62, 67, 78 & 128; see also Verheij & Woelkerling (1992: 284) and Woelkerling (1993: 188).

Type locality: Mocaras reef, east coast of Kalimantan, Indonesia.

Distribution: tropical Indo-Pacific, southern Australia.

Representative specimens examined: lectotype, TRH no number; isolectotypes L 943.5-149; Leiden Island (Pulau Nyamuk Besar), Pulau Seribu, bay of Jakarta, Indonesia (L 986.106-495); Tual, Kei Islands, Indonesia (L 943.10-29); SE station 19, Labuan Tring Bay, Lombok, Indonesia, depth 18–27 m (SE collection 947, 19/21-iii-1899, TRH no number); SE station 91, Moeras reef, east coast Borneo, Indonesia, depth up to 54 m (SE collections 38 & 74, 22-vi-1899, TRH no number); SE station 93, Sanguisiapo Island, Sulu Archipelago, Philippines, depth 12 m (SE collection 1061, 24/25-vii-1899, TRH no number); SE station 193, Sanana Bay, east coast of Sula Besi Island, Indonesia, depth 22 m (SE collection 709, 13/14-ix-1899, TRH no number); SE station 213, Saleyer Island, Indonesia, depth up to 36 m (SE collection 1277, 26-ix/26-x-1899, TRH no number); SE station 252, Taam Island, Indonesia, depth 9–36 m (SE collection 19, 8/9-xii-1899, TRH no number); SE station 282, anchorage between Nusa Besi Island and NE point of Timor Island, Indonesia, depth 27–54 m (SE collection 682, 15/17-i-1900, TRH no number); Barang Lompo Island, depth 1–25 m (*Verheij 0040*, 13-xii-1988; *Verheij 0130*, 29-iii-1989; *Verheij 0778*, 15-xi-1989; *Verheij 0896*, 18-xii-1989), Kudingareng Keke Island, depth 1–2 m (*Verheij 0066*, 24-xii-1988; *Verheij 0901*, 20-xii-1989), Samalona Island, depth 1 m (*Verheij 0171*, 07-iv-1989), Langkai Island, depth 1–15 m (*Verheij 0191, 0216, 0235, 0251, 0272, 0274, 0275 & 0276*, 13/16-iv-1989; *Verheij 0863, 0873 & 0891*, 27/29-xi-1989; *Verheij 1013, 1041 & 1076*, 08/10-v-1990; *Verheij 1146*, 03-vii-1990; *Verheij 1206*, 13-vii-1990), Lanyukang Island, depth 1–5 m (*Verheij 0332*, 05-v-1989; *Verheij 1019, 1034 & 1036*, 09-v-1990), Lae Lae Island, depth 1 m (*Verheij 0386*, 02-vi-1989; *Verheij 0762*, 14-xi-1989; *Verheij 1210 & 1234*, 15-vii-1990), Bone Tambung Island, depth 2–15 m (*Verheij 0706 & 0792*, 16-xi-1989, Kapoposang Island, depth 2 m (*Verheij 1192*, 15-vii-1990), all from the Spermonde Archipelago, SW Sulawesi, Indonesia; Bira, South Sulawesi, Indonesia, depth 2 m (*Verheij 0055*, 17-xii-1988); Kawaihae, Hawaii Island (*Child*, iii-1971, USNC: 71-57-9), Kaneohe, Oahu Island (*Child*, iii-1971, USNC: 71-54-11, & 71-54-19), all from the Hawaiian Archipelago.

Description – Young parts of plants encrusting, older parts encrusting to protuberant or lumpy; plants initially attached to the substratum, older plants sometimes enclosing substratum; older plants or fragments of older plants in general free-living. thalli up to several cm thick. Thallus pseudoparenchymatous; cells of adjacent filaments connected laterally by cell fusions connections.

Crustose parts of thalli dorsiventral and monomerous or dimerous; ventral region unistratose composed of a filament of nonpalisade cells or composed of filaments more or less paralleling the substratum and organized in a noncoaxial manner (cells 8–20 µm in diameter and 15–30 µm long); dorsal region composed of portions of filaments arising from the unistratose ventral region or portions of filaments curving outwardly from the ventral region towards the surface (cells 5–25 µm in diameter and 5–20 µm long). Excrescences radial and monomerous; central core composed of filaments arising from the ventral region, organized in a coaxial to noncoaxial manner (cells 5–25 µm in diameter and 5–25 µm long); peripheral region (cells 5–15 µm in diameter and 5–15 µm long) composed of portions of filament curving outwardly from the central core towards the surface.

Trichocytes (cell 18–23 µm in diameter and 25–40 µm long) common, occurring solitary, in horizontal fields, or vertical rows at the thallus surface, in general becoming buried.

Filaments terminated by a single, rounded epithallial cell (cell 5–12 µm in diameter and 3–6 µm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Tetrasporangial development on the crustose parts or on the excrescences. Conceptacles 150–300 µm internal diameter and 100–200 µm internal height. Conceptacle roof 3–7 cells thick, formed by filaments surrounding and interspersing the tetrasporangia. Conceptacles not or slightly raised above thallus surface. Conceptacle floor 7–9 cells below thallus surface. Pore canal lined by large, elongated cells, not protruding into the canal and orientated perpendicularly to the roof surface. Diameter of the pore 30–50 µm. Old and empty conceptacles buried. A central columella absent.

Gametangial thalli not found.

Diagnostic features – *Hydrolithon reinboldii* is distinguished from other species of *Hydrolithon* examined in having the following combination of features:

— Thallus usually encrusting or protuberant.
— Central columella absent in tetrasporangial conceptacles.
— Tetrasporangial conceptacles usually more than 100 µm in height.
— Tetrasporangial conceptacle floor 7–9 cell layers below the thallus surface.
— Diameter tetrasporangial pore 30–50 µm.

Remarks – Penrose & Woelkerling (1988, 1992) discussed clearly the species delimitation of *Hydrolithon reinboldii*. This is one of the most common species on the reefs of the Spermonde Archipelago. It is found on the reefs in the four zones and it shows a vertical distribution from intertidal to 25 m, with the highest density, locally up to > 100 rhodoliths per $m^2$, on the reef flats.

**Mastophora** Decaisne, 1842: 365

Remarks – The generic concept follows Turner & Woelkerling (1982a, 1982b) and Woelkerling (1988: 129–133). Turner & Woelkerling (1982a, 1982b) carried out a detailed historical study and a study of the type species of *Mastophora*. Their results and conclusions were used for a more complete characterization of the genus, using both vegetative and reproductive characters.

**8. Mastophora pacifica** (Heydrich) Foslie — Figs. 39–41

Basionym: *Melobesia pacifica* Heydrich, 1901: 529; Foslie, 1901d: 19.

Homotypic synonyms: *Mastophora pacifica* (Heydrich) Foslie, 1903b: 25; Foslie, 1904: 73, 75; Foslie, 1905: 4; Foslie, 1909: 53. — *Lithoporella pacifica* (Heydrich) Foslie, 1909: 59; Dawson, 1954: 428; Gordon et al., 1976: 259.

Type collection: *Melobesia pacifica* holotype: PC no number, Heydrich no. 49a; see also Woelkerling (1993: 167). A fragment of the holotype is present in TRH.

Type locality: Sandwich Islands.

Distribution: Tropical western Australia, Indonesian Archipelago.

Representative specimens examined: holotype, Sandwich Islands, PC no number; Kudingareng Keke Island, Spermonde Archipelago, SW Sulawesi, Indonesia, depth 30 m (*Verheij 0020*, 08-xii-1988); Jeannie's Lookout, west of Parker Point, Rottnest Island, Western Australia (*Woelkerling*, 12-ii-1978, LTB 10948); north Point Reef, Rottnest Island, Western Australia (*Woelkerling*, 10-ii-1978, LTB 11053).

Description – Plants applanate branched; plants locally attached to the substratum by cell cohesion or rhizoids. Plants less than 0.5 mm thick; cells of adjacent filaments connected laterally by cell fusions connections.

Thalli dorsiventral and dimerous; ventral region unistratose, filaments of palisade cells paralleling the substratum (cells 25–40 µm in diameter and 15–25 µm long); dorsal region composed of a unistratose epithallial layer (cells 15–25 µm in diameter and 4–8 µm long), where applanate branches arise or where conceptacles are formed, a small, multi-layered, dorsal region arise from the ventral region.

Trichocytes (20–30 µm in diameter and 30–45 µm long) very rare, occurring mainly solitary.

Tetrasporangial conceptacles on the dorsal side, 700–900 µm internal diameter and 300–400 µm internal height. Conceptacle roof 4–7 cells thick, formed by filaments peripheral to the tetrasporangial. Cells, surrounding the pore canal, more or less parallel to the thallus surface orientated and protruding into pore canal. A central columella present.

Gametangial plants not observed.

Diagnostic features – *Mastophora pacifica* is distinguished from other species of *Mastopora* examined in having the following combination of features:

— Thallus applanate branched.
— Trichocytes absent or very rare.
— Tetrasporangial conceptacle 700–900 µm in diameter.

Remarks – The single lectotype conceptacle examined was probably gametangial but was in poor conditions. Conceptacles in specimens from the Spermonde Archipelago, on the other hand, were all tetrasporangial. However, their vegetative structure fully agrees with the vegetative structure of the lectotype. The tetrasporangial conceptacle anatomy fully agrees with the tetrasporangial conceptacle anatomy of specimens from western Australia and identified by Woelkerling (1988: 130 & 132) as *Mastophora pacifica* (Heydrich) Foslie, non *Melobesia pacifica* Masaki, 1968: 8 (nom. illeg.).

### 9. **Mastophora rosea** (C. Agardh) Setchell — Figs. 42–50

Basionym: *Zonaria rosea* C. Agardh, 1824: 264.

Homotypic synonym: *Mastophora rosea* (C. Agardh) Setchell, 1943.

Heterotypic synonyms: *Mastophora licheniformis* Descaisne, 1842: 359, 365. — *M. macrocarpa* f. *condensata* Foslie, 1907b: 30. — *M. rosea* f. *condensata* (Foslie) Setchell, 1943. — *M. affinis* Foslie, 1904: 71.

Type collections: *Zonaria rosea* lectotype: LD no. 50714. — *Mastophora affinis* holotype: L 943.7-29. — *M. macrocarpa* f. *condensata* holotype: L 943.10-60. — *M. licheniformis* isotype: PC, Montagne herbarium, no. 2232.

Type localities: *Zonaria rosea*: Guam. — *Mastophora affinis*: Tual, Kei Islands, Indonesia. — *M. macrocarpa* f. *condensata*: Sula Besi Islands, Indonesia. — *M. licheniformis*: Manila Philippines.
Distribution: Indo-Pacific (Guam, Philippines, Indonesian Archipelago).
Representative specimens examined: Isotype *Mastophora licheniformis*, Manila, Philippines (PC, Montagne herbarium, *Cuming 2232*); lectotype *Z. rosea*, Guam (LD 50714); holotype *M. macrocarpa* f. *condensata*, SE station 193, Sula Besi Island, Indonesia, depth 22 m (SE collection number 1334, L 943.10-60); holotype *M. affinis*, SE station 258, Tual anchorage, Kei Islands, depth unknown (SE collection number 1262, L 943.7-29); holotype fragment *M. affinis*, Sikka, Flores Island, depth unknown (no SE collection number, TRH no number); Barang Lompo Island, Spermonde Archipelago, SW Sulawesi, Indonesia, depth 3 m (*Verheij 0008*, 03-xii-1988), Bira, South Sulawesi, Indonesia, depth 2 m (*Verheij 0046 & 0049*, 17-xii-1988); Gili Air, Lombok, Indonesia, depth 1 m (*Verheij 0941*, 28-xii-1989).

Description – Plants taeniform; plants locally attached to the substratum by cell cohesion or rhizoids, sometimes occurring as free-living balls. Plants less than 0.5 mm thick; cells of adjacent filaments connected laterally by cell fusions connections.

Thalli dorsiventral and dimerous; ventral region unistratose, filaments of palisade cells paralleling the thallus surface (cells 35–70 µm in diameter and 15–40 µm long); dorsal region composed of a unistratose epithallial layer (cells 10–30 µm in diameter and 5–10 µm long). A small multi-layered dorsal region arising from ventral region or where conceptacles developed.

Trichocytes (cells 20–30 µm in diameter and 35–45 µm long) common, occurring solitary or in horizontal fields, and in general bearing a hair.

Tetrasporangial conceptacles on the dorsal side, 350–500 µm internal diameter and 300–450 µm internal height. Conceptacle roof 3–6 cells thick, formed by filaments peripheral to the tetrasporangial. Cells, surrounding the pore canal, more or less parallel to the thallus surface orientated and protruding into pore canal. A central columella present.

Gametangial plants monoecious. Male conceptacles raised above thallus surface. Conceptacle roof 4–8 cells thick. Simple spermatangia occurring only on the floor of the male conceptacle, 450–650 µm internal diameter and 200–300 µm internal height. Female conceptacles raised above thallus surface. Conceptacle roof 6–10 cells thick. Female conceptacles 250–350 µm internal diameter and 200–300 µm internal height.

Carposporangial conceptacles 400–550 µm internal diameter and 300–400 µm internal height.

Diagnostic features – *Mastophora rosea* is distinguished from other species of *Mastophora* examined in having the following combination of features:

— Thallus taeniform.
— Trichocytes common.
— Tetrasporangial conceptacle 350–500 µm in diameter.

Remarks – Woelkerling (1988) discussed the synonymy of *Mastophora rosea*. *Mastophora rosea* is in general found in shallow water and is widespread in the central Indo-Pacific. In the South Sulawesi region it is commonly growing as an epiphyte on macroalgae and stems of larger seagrasses, like *Thalassodendron ciliatum*, but also on dead coral branches or on volcanic rock.

**Neogoniolithon** Setchell & Mason, 1943: 89

Remarks – The generic concept follows Penrose (1992a: 348). Penrose (1992a) emended the generic description of *Neogoniolithon* after a study of the generic type and other collections, and she discussed the affinities with closely related genera.

## 10. Neogoniolithon brassica-floridum (Harvey) Setchell & Mason — Figs. 51–57

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

Homotypic synonyms: *Lithothamnion brassica-florida* (Harvey) Areschoug, 1852: 523. — *Goniolithon brassica-floridum* (Harvey) Foslie, 1898: 9 (as *G. brassica-florida*). — *Neogoniolithon brassica-floridum* (Harvey) Setchell & Mason, 1943: 91; Woelkerling et al., 1993 (as *N. brassica-florida*).

Heterotypic synonyms: *Lithothamnion fosliei* Heydrich, 1897a: 58. — *Archaeolithothamnion fosliei* (Heydrich) Foslie, 1898: 4; Foslie, 1900b: 9; Heydrich, 1901: 185. — *Goniolithon fosliei* (Heydrich) Foslie, 1903b: 470; Foslie, 1904: 46. — *Lithophyllum fosliei* (Heydrich) Heydrich, 1897b: 410; Lemoine, 1911: 142. — *Neogoniolithon fosliei* (Heydrich) Setchell & Mason, 1943: 90; Womersley & Bailey, 1970: 310; Gordon et al., 1976: 261; Townsend, 1981: 409; Adey et al., 1982: 23, 24; Woelkerling, 1985: 148; Penrose, 1992a. — *Goniolithon frutescens* Foslie, 1900d: 9. — *Neogoniolithon frutescens* (Foslie) Setchell & Mason, 1943: 91; Lemoine, 1965: 7; Gordon et al., 1976: 263. — *Goniolithon frutescens* f. *subtilis* Foslie, 1904: 53. — *Goniolithon brassica-floridum* f. *laccadivicum* Foslie, 1903b: 469 (as *G. brassica-florida* f. *laccadivica*). — *Goniolithon laccadivicum* (Foslie) Foslie, 1904: 50.

Type collections: *Melobesia brassica-florida* lectotype: BM, algal box collection 78 (specimen not seen). A fragment of the lectotype is present in TRH; see also Woelkerling (1993: 43). — *Goniolithon brassica-floridum* f. *laccadivicum* lectotype: TRH, no number, leg. Gardner; see also Woelkerling (1993: 134). — *Goniolithon frutescens* lectotype: TRH, no number; see also Woelkerling (1993: 99). — *Goniolithon frutescens* f. *subtilis* lectotype: L 991.239-232; see also Verheij & Woelkerling (1992: 287) and Woelkerling (1993: 216). — *Goniolithon frutescens* f. *subtilis* isolectotypes: L 991.239-244 & -245; TRH, no number; see also Verheij & Woelkerling (1992: 287) and Woelkerling (1993: 216). — *Lithothamnion fosliei* lectotype: TRH, no number, Heydrich, specimen no. 59; see also Woelkerling (1993: 97).

Type localities: *Melobesia brassica-florida*: Algola Bay, South Africa. — *Goniolithon brassica-floridum* f. *laccadivicum*: Laccadives. — *Goniolithon frutescens*: Funafuti Island. — *Goniolithon frutescens* f. *subtilis*: south of the Lucipara Islands, Indonesia. — *Lithothamnion fosliei*: El Tor, Red Sea.

Distribution: Red Sea, Indian Ocean, Indonesian Archipelago, South Australia, Victoria, Western Australia.

Representative specimens examined: lectotype *Lithothamnion fosliei*, El Tor, Red Sea (*Heydrich, no. 59*, TRH no number); lectotype *Goniolithon brassica-floridum* f. *laccadivicum*, Laccadives; lectotype *G. frutescens*, Funafuti Island, TRH no number; lectotype *G. frutescens* f. *subtilis*, south of the Lucipara Islands, Indonesia, L 991.237-244/-245; SE station 78, Lumu Lumu Shoal, Borneo Bank, Indonesia, depth 34 m (SE collection 134, 10/11-vi-1899, L 943.7-9); SE station 91, Moeras Reef, east coast Borneo, Indonesia, depth up to 54 m (SE collections 80, 81 & 84, 22-vi-1899, L 943.7-9); SE station 93, Sanguisiapo Island, Sulu Archipelago, Philippines, depth 12 m (SE collection 1051b, L 943.7-8); SE station 220, Pasir Pandjang Anchorage, west coast of Binongka Island, depth 55 m (SE collections 1163, 1165–1167, 1169 & 1174, 1/3-xi-1899, L 943.7-8); SE station 225, Lucipara Islands, depth unknown (SE collections 553, 554, 556–559 & 565, 8/11-xi-1899, L 943.7-8); SE station 240, Banda anchorage, Indonesia, depth 9–45 m (SE collection 167, 22-xi/01-xii-1899, L 943.7-8); SE station 261, Elat, west of Kei Besar Island, Indonesia, depth 27 m (SE collections 509, 510 & 521, 16/18-xii-1899); SE station 277, Dammer Island, Indonesia, depth 45 m (SE collection 133, 9/11-i-1900, L 943.7-8);

SE station 303, Haingsisi, Samau Islands, depth up to 36 m (SE collections 270 & 273); Barang Lompo Island, depth 2–10 m (*Verheij 0005*, 03-xii-1988; *Verheij 0072*, 22-i-1989; *Verheij 0560*, 20-ix-1989; *Verheij 0796*, 15-xi-1989), Kudingareng Keke Island, depth 1–25 m (*Verheij 0059*, 27-xii-1988; *Verheij 0088*, 18-iii-1989; *Verheij 0440*, 24-viii-1989; *Verheij 0903*, 20-xii-1989; *Verheij 1172*, vii-1990; *Verheij 1211*, 16-vii-1990), Samalona Island, depth 1 m, 07-iv-1989; Langkai Island, depth 1–15 m (*Verheij 0189, 0213, 0214, 0236, 0241, 0265, 0271 & 0277* 13/16-iv-1989; *Verheij 0843 & 0862*, 28/29-xi-1989; *Verheij 1011, 1018, 1042 & 1043*, 8/10-v-1990; *Verheij 1135 & 1145*, 03/04-vii-1990; *Verheij 1204 & 1205*, 13-vii-1990; *Verheij 1262*, 12-ix-1990), Bone Tambung Island, depth 2–35 m (*Verheij 0640*, 12-x-1989; *Verheij 0690 & 0720*, 26-x-1989; *Verheij 0781 & 0791*, 16-xi-1989), Lanyukang Island, depth 5 m (*Verheij 1037*, 10-v-1990) all from the Spermonde Archipelago, SW Sulawesi, Indonesia; Bira, South Sulawesi, Indonesia, depth 2 m (*Verheij 0047*, 17-xii-1988); La Perouse, French Frigate (*Child*, viii-1971, USNC: 71-78-20), Hilo Bay, Hawaii Island (*Child*, iii-1971, USNC: 71-58-47), South Island, Midway Islands (*Child*, viii-1971, USNC: 71-82-42), Waikiki, Oahu Island (*Child*, iii, USNC: 71-50-4), all from the Hawaiian Archipelago.

Description – Plants encrusting, with protuberances or branches; branches cylindrical; plants attached to the substratum or completely free-living. Crustose parts up to several cm thick. Thallus pseudoparenchymatous; cells of adjacent filaments connected laterally by cell fusions connections.

Crustose parts of thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized in a coaxial or non-coaxial manner (cells 8–20 µm in diameter and 15–40 µm long); dorsal region composed of portions of filaments curving outwardly from the ventral region towards the surface (cells 5–10 µm in diameter and 5–20 µm long). Branched parts radial and monomerous; central core composed of filaments arising from the ventral region, organized in a coaxial manner (cells 5–15 µm in diameter and 5–25 µm long); peripheral region (cells 5–10 µm in diameter and 5–15 µm long) composed of portions of filament curving outwardly from the central core towards the surface.

Trichocytes (cells 30–40 µm in diameter and 20–50 µm long) common, occurring solitary, in horizontal fields, or vertical rows at the thallus surface, sometimes becoming buried.

Filaments each terminated by a single, rounded epithallial cell (cells 5–10 µm in diameter and 3–6 µm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly. The epithallial cell layer shedded regularly. Visible in the field as a thin, white sheet detaching from the thallus surface.

Tetrasporangial conceptacle development on the crustose parts or terminally on the branches. Conceptacles 500–850 µm internal diameter and 350–800 µm internal height. Conceptacle roof 15–35 cells thick, formed by filaments surrounding the tetrasporangial disc and raised above the surrounding thallus surface. Cells, surrounding the pore canal, more or less parallel to the thallus surface orientated and protruding into pore canal. Conceptacle floor 25–90 cells below thallus surface. onceptacles 25–90% elevated above thallus surface. Old and empty conceptacles buried. A central columella absent.

Gametangial plants monoecious. Male conceptacles (300–350 µm internal diameter and 300–400 µm internal height) raised above thallus surface. Conceptacle roof 10–25 cells thick. Simple spermatangia occurring on the roof as well as the floor of

the male conceptacle. Female conceptacles (250–450 µm internal diameter and 200–250 µm internal height) raised above thallus surface. Conceptacle roof 10–25 cells thick.

Carposporangial conceptacles 400–700 µm internal diameter and 450–650 µm internal height. Conceptacle roof 30–50 cells thick. Only old carposporangial conceptacles observed.

Remarks – Woelkerling et al. (1993) give an analysis of the type material of *Neogoniolithon brassica-floridum* (as *N. brassica-florida*). Penrose (1990, 1992a) gives a complete analysis of the type material and other critical specimens of *N. fosliei*, a younger, heterotypic synonym of *Neogoniolithon brassica-floridum*. She added an additional set of characters to the species concept after a critical study of numerous collections from southern Australia.

During the present study a critical examination of the type material of *Goniolithon frutescens* Foslie, 1900d, of *G. frutescens* f. *subtilis* Foslie, 1904, *G. laccadivicum* (Foslie) Foslie, 1904, and of the numerous collections in L referred to these taxa has been carried out. The present author agrees with the conclusions of Penrose (1990 & 1992a; as *Neogoniolithon fosliei*) and Woelkerling et al. (1993), and considers that *G. frutescens*, *G. frutescens* f. *subtilis*, and *G. laccadivicum* are heterotypic synonyms of *N. brassica-floridum*.

The specimens from the Spermonde Archipelago and the specimens present in L agree fully with the descriptions given by Penrose (1992a; as *Neogoniolithon fosliei*) and by Woelkerling et al. (1993).

On reefs of the Spermonde Archipelago many different growth forms are represented, which were kept separate by Foslie (1904), as *Goniolithon fosliei*, *G. frutescens*, and *G. laccadivicum*. For ecological field work it would be useful to recognize and name these growth forms, as ecads. Coppejans & Prud'homme van Reine (1992) and Verheij & Prud'homme van Reine (1993) also did not recognize forms and varieties of the green algal species, *Caulerpa racemosa*. However, they recognize 8 ecads, which can be found in separate thalli but also within the same thallus and intermediary growth forms may also occur. The following 3 ecads can be recognized within the species *Neogoniolithon brassica-floridum*. However, intermediate forms or thalli belonging to more than one ecad also can be found.

*Neogoniolithon brassica-floridum* ecad *fosliei*

This ecad includes those specimens of *N. brassica-floridum* which are encrusting, growing attached to the substratum, but sometimes become free-living as a rhodolith.

*Neogoniolithon brassica-floridum* ecad *frutescens*

This ecad includes those specimens of *N. brassica-floridum* which are branched and free-living as rhodoliths.

*Neogoniolithon brassica-floridum* ecad *laccadivicum*

This ecad includes those specimens of *N. brassica-floridum* which are warty, growing attached to the substra-tum or forming rhodoliths.

**Spongites** Kützing, 1841: 30

Remarks – The generic concept follows Penrose (1992a). However, one taxon referred to *Spongites*, *Spongites* spec., is partly in conflict with the circumscription of *Spongites* by Penrose, for further discussion see below. Penrose (1991) emended the generic description of *Spongites* after a critical study of the generic type and other critical collections and she discussed the affinities with closely related genera.

**11. Spongites sulawesiensis** Verheij, *spec. nov.* — Figs. 66–71

*Spongites sulawesiensis* characteribus generis *Spongites*. *Spongites sulawesiensis* a speciebus aliis generis *Spongites* differt corona circa pores tetrasporangiales absente, columella in centro conceptaculae tetrasporangialis presente, et tectum tetrasporangiale plus quam 15 strata cellularum crassum. — Holotypus: *Verheij 1184* (deposited in L, sh. 992.185-200), Kudingareng Keke Island, SW Sulawesi, Indonesia, depth 25 m, 16-vii-1990.

Specimens examined: holotype; Barang Lompo Island, depth 2–20 m (*Verheij 0041*, 13-xii-1988; *Verheij 0078*, 22-i-1989; *Verheij 0083*, 22-i-1989; *Verheij 0458*, 24-vi-1989; *Verheij 0687*, 18-x-1989), Bone Tambung Island, depth 20 m (*Verheij 1010*, 23-v-1990), Kudingareng Keke Island, depth 5–25 m (*Verheij 0409*, 15-viii-1989; *Verheij 0508*, 28-viii-1989; *Verheij 0554*, 22-ix-1989), Samalona Island, depth 5 m (*Verheij 0518*, 31-viii-1989), all from the Spermonde Archipelago, SW Sulawesi, Indonesia.

Description – Plants encrusting or encrusting with branches. Crustose parts up to 10 mm thick. Thallus pseudoparenchymatous; cells of adjacent filaments connected laterally by cell fusions connections.

Crustose parts and sheet-like parts of thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized mostly in a noncoaxial manner (cells 6–12 µm in diameter and 15–20 µm long); dorsal region composed of portions of filaments curving outwardly from the ventral region towards the surface (cells 5–8 µm in diameter and 8–12 µm long).

Trichocytes (cells 8–13 µm in diameter and 15–20 µm long) present, usually occurring solitary, in vertical rows, or in small horizontal fields at the thallus surface, sometimes becoming buried.

Filaments each terminated by a single, rounded epithallial cell (cells 5–8 µm in diameter and 3–5 µm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Tetrasporangial conceptacles 650–800 µm internal diameter and 175–225 µm internal height, raised above the surrounding thallus surface. Tetrasporangial conceptacle roof 15–25 cells thick, formed by filaments surrounding the tetrasporangial disc. Cells, surrounding the pore canal, more or less parallel to the thallus surface orientated and protruding into pore canal. Old tetrasporangial conceptacles filled up and becoming overgrown. A large, central columella present.

Male conceptacles and female conceptacles not observed.

Carposporangial conceptacles (600–700 µm internal diameter and 175–225 µm internal height) raising above thallus surface.

Diagnostic features – *Spongites sulawesiensis* is distinguished from other species of *Spongites* examined in having the following combination of features:

— Trichocytes solitary, in vertical rows or horizontal fields.
— Tetrasporangial conceptacle dimensions (650–800 µm internal diameter, 175–225 µm internal height); roof 15–25 cell layers thick.
— Large, central columella present.
— Carposporangial conceptacle dimensions (600–700 µm internal diameter, 175–225 µm internal height).
— Gonimoblast filaments confined to the periphery of the fusion cell.

Remarks – There are two previous accounts of *Spongites sulawesiensis* (Verheij, 1993b: 237 and Verheij, 1993c: 56), but neither includes valid publication of the species. One (Verheij, 1993b) lacks a figure or illustration, or reference to a previously published illustration (thus contravening ICBN Art. 39.1), while the other (Verheij, 1993c) lacks a Latin description or diagnosis (thus contravening ICBN Art. 36.2).

Penrose (1990) referred in an unpublished PhD thesis eleven species to the genus *Spongites*. Ten of these species are new combinations. However, these new combinations were not validly published (contravening ICBN Art. 29.1). This thesis however, contains important information on anatomical characters of representatives of the *Spongites-Neogoniolithon* group. During a visit to LTB, the present author had excess to this valuable thesis and therefore its contents is used in this paper. Penrose (1992b) and Penrose & Woelkerling (1992) referred three of these species to the reappraised genus *Hydrolithon*, i.e. *H. cymodocea*, *H. onkodes*, and *H. reinboldii*. The remaining seven new combinations have not yet been validated (pers. comm. Dr D. Penrose) and therefore are below referred by their basionyms. Three of the species, *Melobesia amplexifrons*, *M. caulerpae*, and *M. coronatus*, are characterized by a corona around the tetrasporangial conceptacle pore. This character does not occur in *Spongites sulawesiensis*. Four of the species, *Lithophyllum antillarum*, *Melobesia caulerpae*, *Melobesia coronatus*, and *Lithophyllum rupestre*, are lacking the central columella which is characterizing the tetrasporangial conceptacles of *Spongites sulawesiensis*. None of the remaining three species, *Spongites fruticulosus*, *Lithophyllum hyperellus*, and *Lithophyllum munitum*, are characterized by tetrasporangial conceptacles with a roof of more than 15 cells thick. The above set of characters makes *Spongites sulawesiensis* unique within the genus *Spongites*.

Penrose (1991) presented an account to *Spongites fruticulosus*. *Spongites fruticulosus* differs from *Spongites sulawesiensis* in: 1) presence of a sieve-like plug in immature tetrasporangial conceptacles, 2) thickness of the tetrasporangial conceptacle roof (8–12 versus 15–25 cells), and 3) diameter of the tetrasporangial conceptacles (350–595 µm versus 650–800 µm). Chamberlain (1993) referred two species to the genus *Spongites*, i.e. *S. yendoi* and *S. decipiens*. Both species differ from *Spongites sulawesiensis* in: 1) the diameter of the tetrasporangial conceptacles (< 500 µm), 2) the diameter of the carposporangial conceptacles (< 500 µm), and 3) thickness of the conceptacle roof (< 10 cells).

*Spongites sulawesiensis* is in appearance difficult to distinguish from *Neogoniolithon brassica-floridum*; however, anatomically this is much easier.

Etymology – The proposed epithet *sulawesiensis* refers to the Indonesian island Sulawesi, where the species was found for the first time.

## 12. *Spongites* spec. — Figs. 58–65

Representative specimens examined: Barang Lompo Island, Spermonde Archipelago, SW Sulawesi, Indonesia, depth 15 m (*Verheij 0065*, 11-i-1989; *Verheij 0319*, 10-v-1989).

Description – Plants encrusting, attached to the substratum by cell cohesion. Crustose parts up to several mm thick. Thallus pseudoparenchymatous; cells of adjacent filaments connected laterally by cell fusions connections.

Crustose parts of thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized in a coaxial or non-coaxial manner (cells 10–18 µm in diameter and 12–25 µm long); dorsal region composed of portions of filaments curving outwardly from the ventral region towards the surface (cells 5–10 µm in diameter and 5–12 µm long).

Trichocytes not found.

Filaments each terminated by a single, rounded epithallial cell (cells 5–8 µm in diameter and 3–5 µm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Tetrasporangial conceptacles not observed.

Gametangial plants monoecious. Male conceptacles (750–950 µm internal diameter and 150–300 µm internal height) slightly raised above thallus surface. Conceptacle roof 20–35 cells thick. Simple spermatangia occurring only the floor of the male conceptacle. Female conceptacles (900–1100 µm internal diameter and 150–250 µm internal height) raised above thallus surface. Conceptacle roof 10–25 cells thick.

Carposporangial conceptacles 1000–1250 µm internal diameter and 450–700 µm internal height. Conceptacle roof 20–40 cells thick.

Diagnostic features – *Spongites* spec. is distinguished from other species of *Spongites* examined in having the following combination of features:

- — Trichocytes apparently absent.
- — Female conceptacles usually large (900–1100 µm internal diameter, 150–250 µm internal height); roof 15–25 cell layers thick.
- — Carposporangial conceptacle dimensions (1000–1250 µm internal diameter, 450–700 µm internal height); roof 20–40 cell layers thick.
- — Gonimoblast filaments all over dorsal side of the fusion cell.
- — Male conceptacle dimensions (750–950 µm internal diameter, 150–300 µm internal height); roof 20–35 cell layers thick.
- — Spermatangia restricted to floor of male conceptacle.

Remarks – Simple spermatangia restricted to the floor of the conceptacle chamber, together with the occurrence of cell fusions, suggested that the thalli are mastophoroid, not *Neogoniolithon*. However, Adey et al. (1982: 58) report spermatangia restricted to the floor in the melobesioid genus *Mesophyllum*. However, this is the only report and needs to be further investigated. The carposporophytes are similar to those reported for *Spongites* (Penrose 1991), *Pneophyllum* (Penrose & Woelkerling, 1985), and *Hydrolithon* (Penrose & Woelkerling, 1992; Penrose, 1992b). These three mastophoroid genera are separated on basis of tetrasporngial conceptacle related characters. Unfortunately, tetrasporangial conceptacles were not found.

The collections are referred to *Spongites* although they are partly in conflict with the circumscription of this genus. The collections are not referred to *Pneophyllum* because of the thickness of the collected thalli (up to several mm's) whereas the maximum reported thickness of *Pneophyllum* is 500 µm (Penrose & Woelkerling, 1991). They are not referred to *Hydrolithon* because of the large dimensions of the carposporangial conceptacles.

Critical studies of tetrasporangial plants of this taxon is needed to elucidate its taxonomic position.

**Subfamily Melobesioideae** Bizzozero, 1885: 109 (as 'Melobesieae')

Remarks – The subfamily concept follows Woelkerling (1988: 158). Woelkerling & Harvey (1992) showed that the presence or absence of a coaxial basal region can not be used as a sole diagnostic character at generic level in the Melobesioideae, as suggested by Lemoine (1928). They regard differences in spermatangial ontogeny and morphology as more reliable diagnostic characters at generic level. Unfortunately, during the present study of the Corallinaceae from the Spermonde Archipelago, most melobesioid taxa were only represented by tetrasporangial plants. Only two species are represented by spermatangial plants as well, i.e. *Lithothamnion prolifer* and *Mesophyllum erubescens*. The spermatangial ontogeny and morphology of this species fully agree with the criteria indicated by Woelkerling & Harvey (1992: 396), and support its placement in *Mesophyllum*.

**Lithothamnion** Heydrich, 1897b: 412

Remarks – Generic concept following Woelkerling (1988: 169–180). This is the only genus of the Corallinaceae with flattened and eared epithallial cells.

**13. Lithothamnion prolifer** Foslie — Figs. 72–82

Basionym: *Lithothamnion prolifer* Foslie, 1904: 18, pl. 1 figs. 17–20.

Homotypic synonym: *Mesophyllum prolifer* (Foslie) Adey, 1970: 25; Adey et al., 1982: 61.

Type collections: lectotype L 943.7-40 (Siboga Expedition collection 146), fragment present in TRH; see also Verheij & Woelkerling (1992: 282) and Woelkerling (1993: 176–178); isolectotype L 943.7-40 (Siboga Expedition collection 139); fragment present in TRH; see also Verheij & Woelkerling (1992: 282) and Woelkerling (1993: 176–178).

Type locality: Lumu Lumu Shoal, Borneo Bank, Indonesia.

Distribution: Indonesia, Papua New Guinea.

Representative specimens examined: lectotype, SE station 78, Lumu Lumu Shoal, Borneo Bank, Indonesia, depth 34 m (SE collections 139 & 146, 10/11-vi-1899, L 943.7-40, fragments present in TRH, no number); Barang Lompo Island, depth 1–5 m (*Verheij 0032*, 12-xii-1988; *Verheij 0058*, 11-i-1989; *Verheij 0559*, 20-ix-1989), Bone Tambung Island, depth 2 m, 16-xi-1989 (*Verheij 0720*), Langkai Island, depth 10 m (*Verheij 0850*, 27-xi-1989; *Verheij 1012*, 08-v-1990; *Verheij 1132*, 04-vii-1990; *Verheij 1182*, 16-vii-1990; *Verheij 1285*, 11-ix-1990), all from the Spermonde Archipelago, SW Sulawesi, Indonesia; Bira, south Sulawesi, Indonesia, depth 3 m (*Verheij 0842*, 16-xii-1988).

Description – Plants encrusting to lumpy, young stages attached older stages becoming detached from substratum. Crustose parts 0.5–2.0 mm thick. Thallus pseudoparenchymatous; the cells of adjacent filaments connected laterally by cell fusions.

Crustose parts of thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized in a noncoaxial manner (cells 9–15 μm in diameter and 9–26 μm long); dorsal region composed of portions of filaments curving outwardly from the ventral region towards the surface (cells 6–12 μm in diameter and 3–10 μm long). Lumpy or protuberant parts radial and monomerous; central core composed of filaments arising from the ventral region, organized in a noncoaxial manner (cells 6–12 μm in diameter and 10–25 μm long); peripheral region (cells 5–10 μm in diameter and 5–12 μm long) composed of portions of filament curving outwardly from the central core towards the surface.

Trichocytes not found.

Filaments each terminated by a single, more or less flattened and flared epithallial cell (cells 7–11 μm in diameter and 2–5 μm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Tetrasporangial conceptacles 800–1200 μm internal diameter and 300–400 μm internal height. Tetrasporangial conceptacle roof 5–6 cells thick, multiporate (75–150 pores), arising from filaments interspersing the developing tetrasporangia. Old and empty tetrasporangial conceptacles buried and infilled by filaments of large cells, 3–8 cells long, arising from the stalk cell.

Dendroid or simple spermatangia occurring on the roof as well as the floor of the male conceptacle (800–1000 μm internal diameter and 200–400 μm internal height). Female conceptacles not seen.

Carposporangial conceptacles (1000–1200 μm internal diameter, 400–600 μm internal height).

Male and female/carposporangial conceptacles occurring on the same plant.

Diagnostic features – *Lithothamnion prolifer* is distinguished from other species of *Lithothamnion* examined in having the following combination of features:

- — Trichocytes apparenty absent.
- — Epithallial cells flattened and flared.
- — Tetrasporangial conceptacles usually large (800–1200 μm internal diameter, 300–400 μm internal height); roof 5–6 cell layers thick.
- — Male conceptacles usually large (800–1000 μm internal diameter, 200–400 μm internal height).
- — Spermatangia simple and dendroid, occurring on conceptacle roof and floor.
- — Carposporangial conceptacles usually large (1000–1200 μm internal diameter, 400–600 μm internal height).

Remarks – Based on the presence of a noncoaxial ventral region, or locally irregular coaxial, Adey (1970: 25) and Adey et al. (1982: 61) referred this taxon to *Mesophyllum*. However, both did not mention the shape of the epithallial cells, which is characteristic for *Lithothamnion*. Woelkerling & Harvey (1992: 395) concluded

that a noncoaxial ventral region could not be accepted as the sole character to delimit *Mesophyllum*, and that a set of characters is needed. A critical examination of the type collection of *Lithothamnion prolifer* showed that 1) the epithallial cells are flattened and eared cells, and i2) the ventral region predominantly noncoaxial. This, in combination with the observed dendroid spermatangia on the floor and roof of the male conceptacle, agrees only with *Lithothamnion*.

**Mesophyllum** Lemoine, 1928: 251–254

Remarks – The generic concept follows Woelkerling & Harvey (1992: 395).

### 14. **Mesophyllum erubescens** (Foslie) Lemoine — Figs. 83–89

Basionym: *Lithothamnion erubescens* Foslie, 1900d: 9; Foslie, 1901a: 3; Foslie, 1901b: 4; Foslie, 1901e: 3; Foslie, 1904: 31.

Homotypic synonym: *Mesophyllum erubescens* (Foslie) Lemoine, 1928: 252.

Heterotypic synonyms: *Lithothamnion erubescens* f. *madagascarensis* Foslie, 1901e: 3; Yendo, 1902: 187; Masaki, 1968: 13. — *Lithothamnion madagascarensis* Foslie, 1906: 19. — *Mesophyllum madagascarensis* (Foslie) Adey, 1970: 25; Adey et al., 1982: 58 (as *M. madagascariensis*).

Type collections: holotype *Lithothamnion erubescens* f. *madagascarensis* TRH, no number; see also Woelkerling (1993: 142); see also Woelkerling (1993: 85 & 86).

Type locality: *Lithothamnion erubescens*: Brazil. — *Lithothamnion erubescens* f. *madagascarensis*: Madagascar.

Distribution: Pantropical.

Representative specimens examined: holotype *Lithothamnion erubescens*, TRH, no number; holotype *L. erubescens* f. *madagascarensis*, TRH, no number; Barang Lompo Island, depth 5–25 m (*Verheij 0038*, 12-xii-1988; *Verheij 0362*, 25-v-1989; *Verheij 0686*, 18-x-1989; *Verheij 0748*, 8-xi-1989; *Verheij 0779*, 15-xi-1989; *Verheij 0986*, 10-iv-1990), Kudingareng Lompo Island, depth 25–35 m (*Verheij 0297*, 2-v-1989; *Verheij 0439*, 24-viii-1989; *Verheij 0628*, 10-x-1989), Samalona Island, depth 20–30 m (*Verheij 0459, 0460 & 0462*, 31-viii-1989; *Verheij 0520*, 1-iv-1989; *Verheij 0698*, 12–x-1989; *Verheij 0956*, 5-iv-1990; *Verheij 1207*, 28-viii-1990), all from the Spermonde Archipelago, SW Sulawesi, Indonesia; Lombok Island, Indonesia, depth 1 m (*Verheij 0943*, 27-xii-1989); Kawaihae, Hawaii Island (*Child*, iii-1971, USNC: 71-57-17), Honaunau, Oahu Island (*Child*, iii-1971, USNC: 71-53-21), Kaneohe Island (*Child*, viii-1971, USNC: 71-81-9, 71-81-31, 71-81-35), all from the Hawaiian Archipelago.

Description – Plants initially encrusting but soon becoming protuberant or lumpy, young stages attached older stages becoming detached from substratum and forming rhodoliths. Crustose parts < 1.0 mm thick. Thallus pseudoparenchymatous; cells of adjacent filaments connected laterally by cell fusions.

Young, crustose parts of thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized in a more or less coaxial manner (cells 5–12 μm in diameter and 13–21 μm long); dorsal region composed of portions of filaments curving outwardly from the ventral region towards the surface (cells 5–11 μm in diameter and 5–10 μm long).

Protuberant or branched parts radial and monomerous; central core composed of filaments arising from the ventral region, organized in a coaxial manner (cells 5–12 μm in diameter and 13–20 μm long); peripheral region (cells 5–10 μm in diameter

and 5–11 µm long) composed of portions of filament curving outwardly from the central core towards the surface.

Filaments each terminated by a single, rounded epithallial cell (cells 6–10 µm in diameter and 3–5 µm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Trichocytes rare (cells 10–15 µm in diameter, 7–12 µm long) occurring solitary.

Tetrasporangial conceptacles 350–475 µm internal diameter and 75–200 µm internal height. Tetrasporangial conceptacle roof 4–6 cells thick, multiporate (50–75 pores), arising from filaments interspersing the developing tetrasporangia. Intersporangial, non calcified filaments 3–4 cells long. Elongated basal cell of the filaments aligning tetrasporangial pores present. Old and empty tetrasporangial conceptacles buried and infilled by filaments of large cells, 3–8 cells long, arising from the stalk cell.

Simple spermatangia occurring on the roof and floor of the male conceptacle (200 µm internal diameter, 50–100 µm internal height). Female conceptacles not found. Carposporangial conceptacles (450–550 µm internal diameter, 250–350 µm internal height). Male and female/carposporangial conceptacles occurring on the same plant.

Diagnostic features – *Mesophyllum erubescens* is distinguished from other species of *Mesophyllum* examined in having the following combination of features:

— Trichocytes rare.
— Tetrasporangial conceptacle roof 4–6 cell layers thick.
— More than 50 pores in tetrasporangial conceptacle roof.
— Elongated basal pore cell present.
— Noncalcified, intersporangial filaments 3–4 cells long.

Remarks – *Mesophyllum erubescens* can be easily distinguished from the other *Mesophyllum* species on basis of the elongated cells at the base of the pores of tetrasporangial conceptacles. It is also the sole *Mesophyllum* species in which trichocytes were observed.

### 15. **Mesophyllum funafutiense** (Foslie) Verheij — Figs. 90–94

Basionym: *Lithothamnion philippii* Foslie f. *funafutiensis* Foslie, 1899: 3.

Homotypic synonym: *Mesophyllum funafutiense* (Foslie) Verheij, 1993b: 238. — *Lithothamnion funafutiense* (Foslie) Foslie, 1901b: 17.

Heterotypic synonyms: *Lithothamnion funafutiense* Foslie f. *purpurascens* Foslie, 1901b: 18. — *Lithothamnion purpurascens* (Foslie) Foslie, 1907c: 182; Lemoine, 1917; Papenfuss, 1968. — *Mesophyllum purpurascens* (Foslie) Adey, 1970: 26.

Type collections: lectotype *Lithothamnion philippii* f. *funafutiensis*, TRH no number; see also Woelkerling (1993: 100 & 101); holotype *Lithothamnion funafutiense* f. *purpurascens* TRH no number, 7-iii-1900; see also Woelkerling (1993: 184 & 185).

Type localities: *Lithothamnion philippii* f. *funafutiensis*: Tutange, Funafuti, Tuvalu. — *L. funafutiense* f. *purpurascens*: north side of Koh Chang, Gulf of Thailand, Thailand, 7-iii-1900.

Representative specimens examined: lectotype *Lithothamnion philippii* f. *funafutiensis*, TRH no number; holotype *L. funafutiense* f. *purpurascens*, TRH no number, 7-iii-1900; Kudingareng Keke Island, depth 15–35 m (*Verheij B15*, 25-vi-1985; *Verheij 0298*, 02-v-1989), Barang Lompo Island, depth 5 m (*Verheij 0085*, 22-i-1989), Samalona Island, depth 5 m (*Verheij 0424*, 22-viii-1989), all from the Spermonde Archipelago, Indonesia.

Description – Plants encrusting to slightly lumpy, attached to substratum. Thallus several mm thick. Thallus pseudoparenchymatous; cells of adjacent filaments connected laterally by cell fusions.

Crustose parts of thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized in a coaxial manner (cells 5–15 µm in diameter and 15–20 µm long); dorsal region composed of portions of filaments curving outwardly from the ventral region towards the surface (cells 5–10 µm in diameter and 5–10 µm long).

Trichocytes not found.

Filaments each terminated by a single epithallial cell (cells 5–10 µm in diameter and 3–6 µm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Tetrasporangial conceptacles 450–600 µm internal diameter and 150–225 µm internal height. Tetrasporangial conceptacle roof 8–10 cells thick, multiporate (35–70 pores), arising from filaments interspersing the developing tetrasporangia. Intersporangial, non calcified filaments not observed. An elongated basal cell of the filament aligning absent. Old and empty tetrasporangial conceptacles become buried and infilled by filaments of large cells, 3–8 cells long, arising from the stalk cell.

Gametangial and carposporangial plants were not observed.

Diagnostic features – *Mesophyllum funafutiense* is distinguished from other species of *Mesophyllum* examined in having the following combination of features:

— Trichocytes absent.
— Tetrasporangial conceptacle roof 8–10 cell layers thick.
— 35–70 pores in tetrasporangial conceptacle roof.
— Elongated basal pore cell absent.

Remarks – During the present study the lectotype collection of this species was examined. Contrary to Adey (1970) it was found that the type material does not have flared epithallial cells or other characteristics considered diagnostic of *Lithothamnion*. All characters shown in the type and in the other specimens examined are consistent with placing the species in *Mesophyllum*. Up to now male plants are unknown and therefore the placement of *funafutiense* in *Mesophyllum* needs to be reassessed when details of spermatangial ontogeny have been elucidated because patterns of spermatangial ontogeny have been used by Woelkerling & Harvey (1992) to help delimit *Mesophyllum* from several other genera of Melobesioideae.

### 16. **Mesophyllum syrphetodes** Adey et al. — Figs. 95, 96

Basionym: *Mesophyllum syrphetodes* Adey et al., 1982: 63.
Type collection: holotype USNC 71-72-2, leg. Child.
Type locality: 20 m, SW Molokai Island, Hawaiian Archipelago.
Distribution: Tropical Indo-Pacific.
Representative specimens examined: holotype, Molokai Island, Hawaiian Archipelago, 20 m (*Child*, viii-1971, USNC: 71-72-2); Kudingareng Keke Island, 30–35 m (*Verheij B155*, 16/17-vii-1985; *Verheij 0296*, 2-v-1989), Bone Tambung Island, depth 35 m (*Verheij 0641*, 12-x-1989), all from

the Spermonde Archipelago, SW Sulawesi, Indonesia; Maui Island (*Child*, viii-1971, USNC: 71-71-1), Molokai Island (*Child*, viii-1971, USNC: 71-65-1 & 71-73-6), Midway, South Island (*Child*, viii-1971, USNC: 71-82-20), Kaneohe, Oahu Island (*Child*, viii-1971, USNC: 71-81-15) all from the Hawaiian Archipelago.

Description – Plants crustose with small protuberances, sometimes enclosing substratum and forming rhodoliths. Crustose parts thin < 1.0 mm thick. Thallus pseudoparenchymatous; cells of adjacent filaments connected laterally by cell fusions.

Crustose parts of thalli dorsiventral and monomerous; ventral region composed of filaments more or less paralleling the substratum and organized in a more or less coaxial manner (cells 3–10 µm in diameter and 13–20 µm long); dorsal region composed of portions of filaments curving outwardly from the ventral region towards the surface (cells 7–9 µm in diameter and 6–13 µm long).

Protuberances radial and monomerous; central core composed of filaments arising from the ventral region, organized in a coaxial manner (cells 5–10 µm in diameter and 10–20 µm long); peripheral region (cells 5–9 µm in diameter and 5–15 µm long) composed of portions of filament curving outwardly from the central core towards the surface.

Trichocytes not found.

Filaments each terminated by a single, rounded epithallial cell (cells 5–9 µm in diameter and 2–4 µm long) and one subepithallial meristematic cell producing new epithallial cells outwardly or additional vegetative cells inwardly.

Tetrasporangial conceptacles 250–350 µm internal diameter and 100–150 µm internal height. Tetrasporangial conceptacle roof multiporate (20–40 pores), 4–6 cells thick, arising from filaments interspersing the developing tetrasporangia. Intersporangial, non calcified filaments 1 cell long. An elongated basal cell of the filament aligning absent. Old and empty tetrasporangial conceptacles become buried and filled in with filaments of large cells, 3–5 cells long, arising from the stalk cell.

Gametangial conceptacles not observed.

Diagnostic features – *Mesophyllum syrphetodes* is distinguished from other species of *Mesophyllum* examined in having the following combination of features:

— Trichocytes apparently absent.
— Tetrasporangial conceptacle roof 4–6 cell layers thick.
— 20–40 pores in tetrasporangial conceptacle roof.
— Elongated basal pore cell absent.
— Noncalcified, intersporangial filaments 1 cell long.

Remarks – The external morphology of this species is highly variable. The type collections in USNC are mainly crustose, while the collections from the Spermonde Archipelago are mainly protuberant or branched.

## CONCLUDING REMARKS

Foslie (1904) reported 32 species of nongeniculate Corallinales from Indonesia, collected during the Siboga Expedition (1899–1900). Four of these were recently referred to the Sporolithaceae (Verheij, 1993a). Additionally, Weber-van Bosse

(1926) reported one new species, *Sporolithon lemoinei*, from the Kei Islands, Indonesia. Since 1926 the nongeniculate Corallinaceae from Indonesia have not been studied.

In the present paper 16 species of nongeniculate Corallinaceae are reported from the Spermonde Archipelago. Nine of these species were also collected during the Siboga Expedition, and reported by Foslie. Twelve of Foslie's 32 nongeniculate Corallinaceae species from the Siboga Expedition, are included in these 9 species.

Foslie's species concept was mainly based on external appearance and on vegetative characters. These characters are presently regarded as highly unstable (e.g. Woelkerling, 1988; Woelkerling & Campbell, 1992). Present-day species delimitation is mainly based on characters related to reproductive structures, tetrasporangial and/or gametangial conceptacles, and not to vegetative structures. This often results in 1) lumping of taxa and in 2) species with a highly variable external morphology (see Figs. 53–55). There are still 16 names, published by Foslie (1904) for Siboga Expedition Corallinales, which have not been studied in detail. Thus it is not yet possible to indicate how many 'modern' species these remaining 16 nongeniculate Corallinaceae species represent. This is outside the scope of the present study and needs critical examination of numerous type collections as well as of the relevant Siboga collections.

During the Siboga Expedition Weber-van Bosse collected, according to modern species concepts, only two nongeniculate coralline species in the Spermonde Archipelago: *Hydrolithon reinboldii* and *Neogoniolithon brassica-floridum* (as *Goniolithon fosliei*). Both species were also found during the present study. The 'rich' present-day coralline flora of the Spermonde Archipelago is probably not a result of an improvement of the environment, but a result of the methods and time span of sampling. The two years of fieldwork during the present study have to be compared to only four weeks for the Siboga Expedition, and for sampling methods, SCUBA diving as opposed to dredging and surface sampling have to be considered.

It might be emphasized that the number of species increases towards the edge of the shelf of the Spermonde Archipelago, where the clearest water is found. Only a few species where found around Lae Lae Island, close to the river outlet of the Jeneberang river. In general, the substratum coverage also increases towards the edge of the shelf (Erftemeijer, pers. comm.; Verheij & Povel in Verheij, 1993c). It seems that turbidity and grazing are the two most important controlling factors for the coralline algal flora in the Spermonde Archipelago (Verheij & Povel in Verheij, 1993c).

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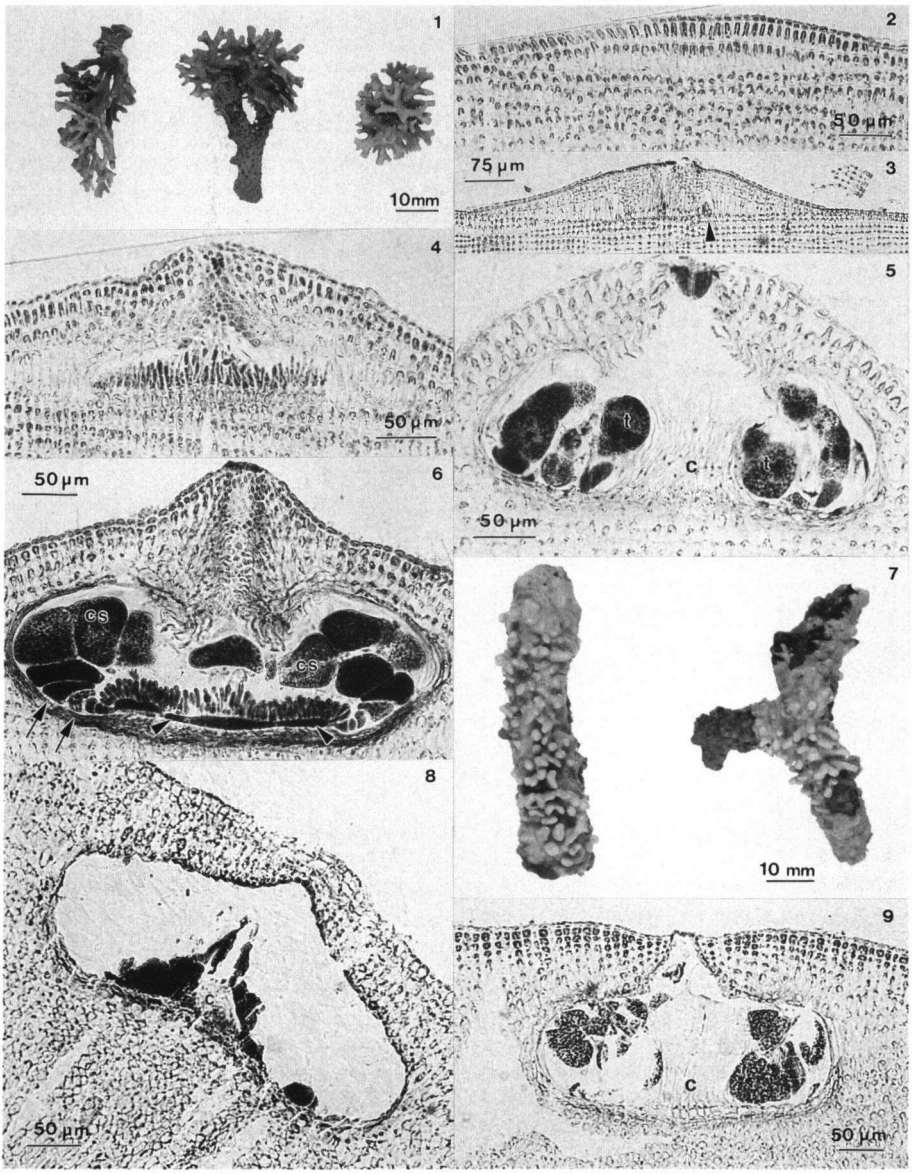
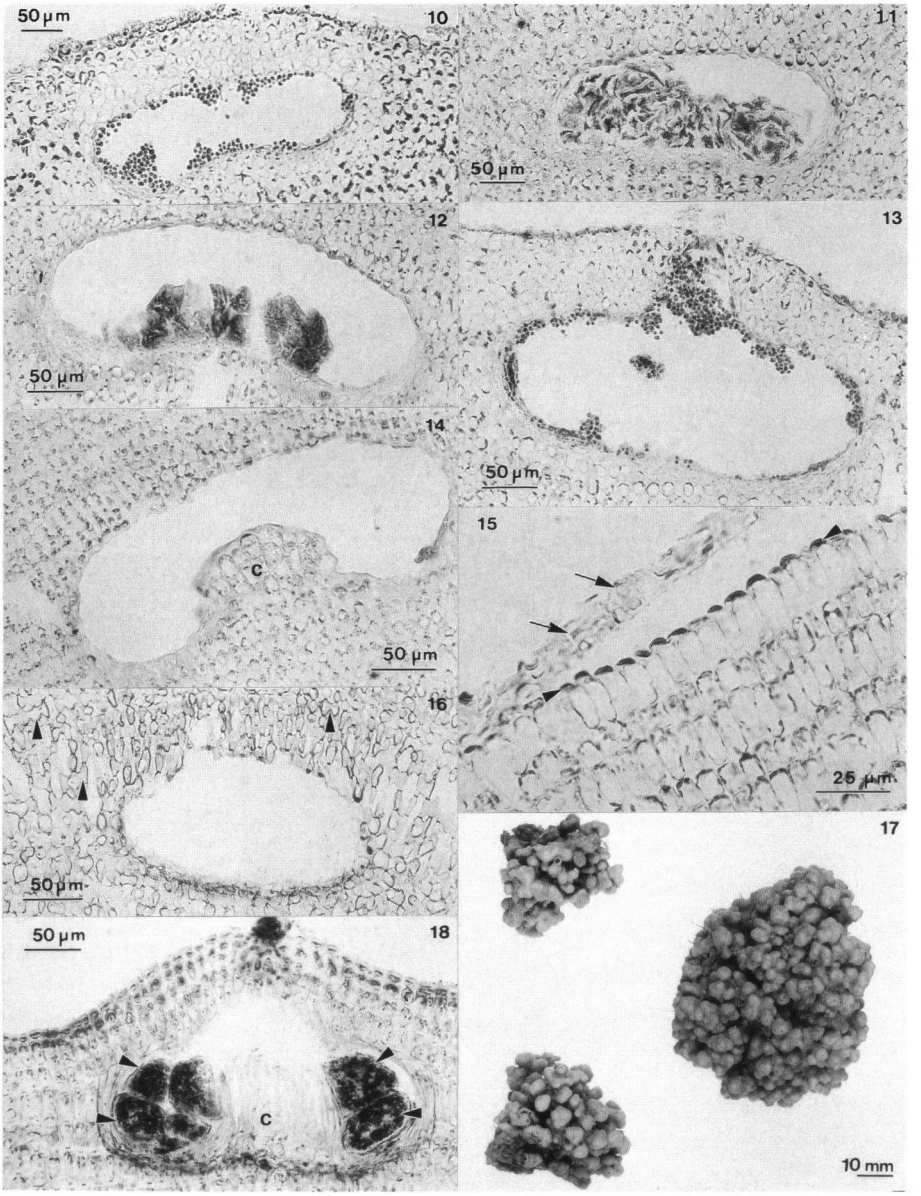
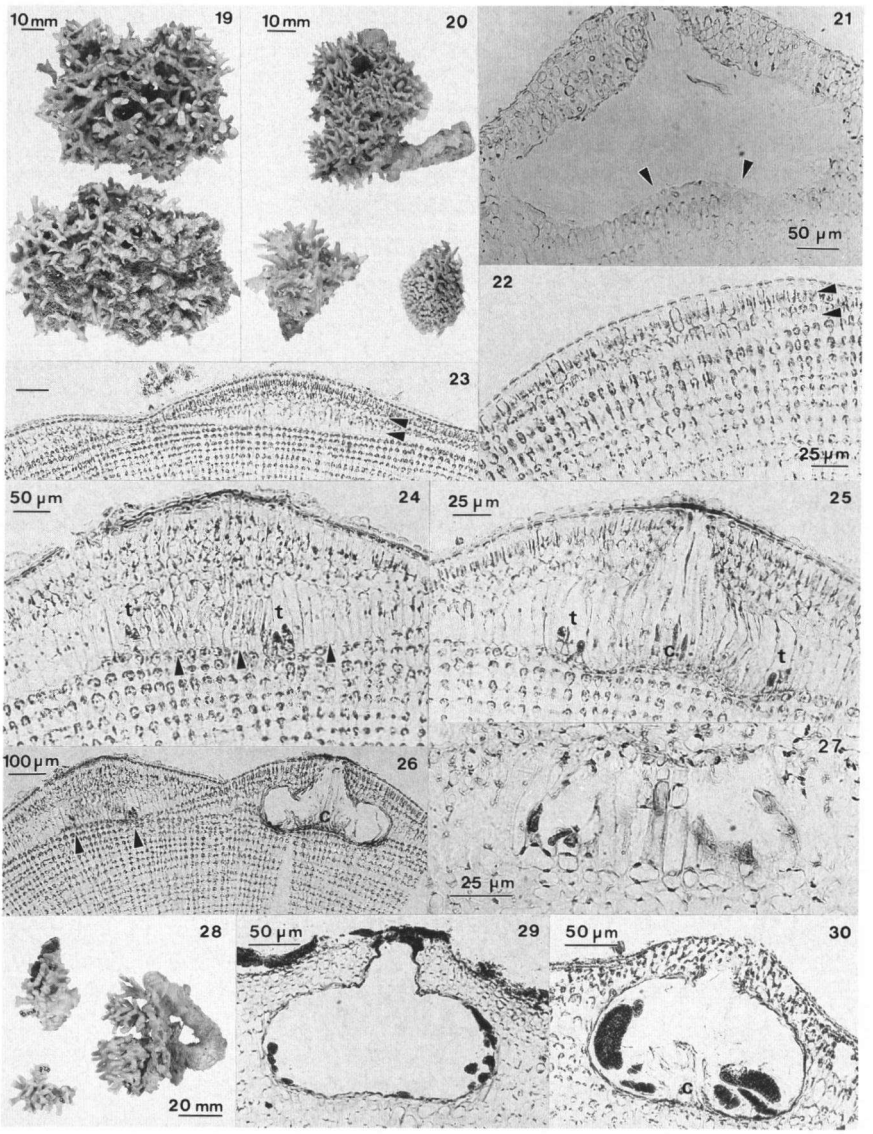


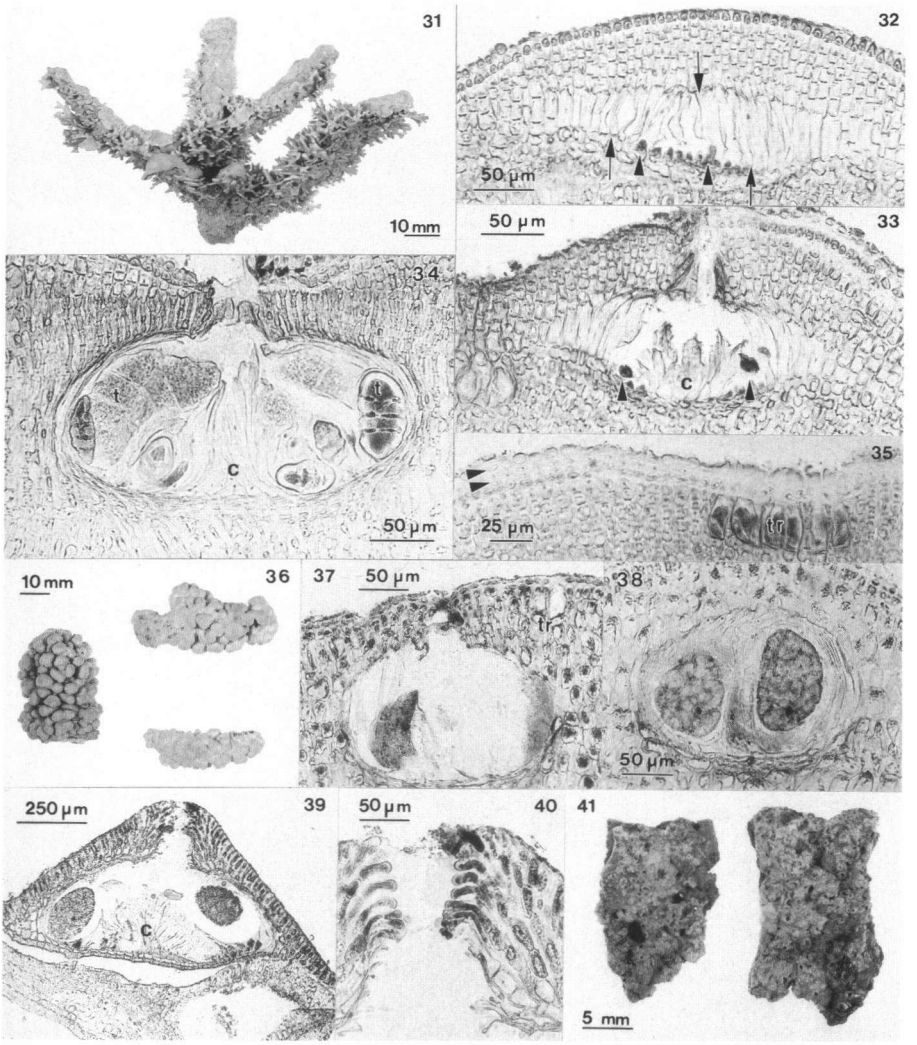

Figs. 1–9. Habits and reproductive structures (in vertical section). — *Lithophyllum bamberi:* **1:** Habit (L 986.106-630). **2:** Early stage in tetrasporangial conceptacle development (*Verheij 0101*). **3:** Older stage in tetrasporangial conceptacle development. Note tetrasporangial initials (arrow heads) (*Verheij 0192*). **4:** Female conceptacle (*Verheij 0101*). **5:** Mature tetrasporangial conceptacle with sporangia. Note columella (c) and tetrasporangia (t) (*Verheij 0101*). **6:** Conceptacle with carposporophytes. Note large fusion cell (arrow heads), carpospores (cs), and gonimoblast filaments (arrows) (*Verheij 0020*). — *Lithophyllum kotschyanum:* **7:** Habit (*Verheij 1133*). **8:** Old tetrasporangial conceptacle. Note remains of a columella (c) (holotype TRH, no number). **9:** Mature tetrasporangial conceptacle. Note central columella (c) (*Verheij 1133*).



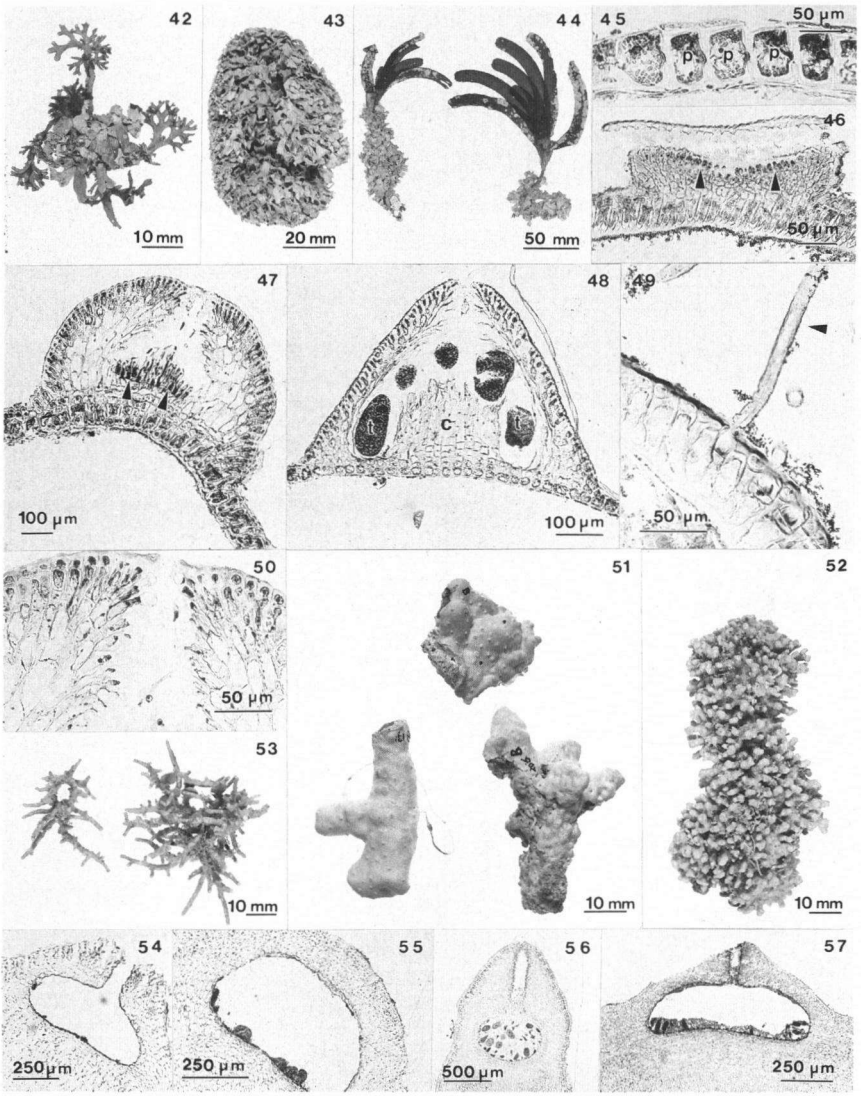

Figs. 10–18. *Lithophyllum okamurai*: habit and reproductive structures (in vertical section). — **10:** Old, buried male conceptacle (lectotype f. *okamurai*). **11:** Old, buried conceptacle with the remains of carposporophytes (same lectotype). **12:** Old, buried conceptacle with the remains of carposporophytes (lectotype f. *trincomaliense*). **13:** Old, buried male conceptacle (lectotype f. *valida*). **14:** Old, buried tetrasporangial conceptacle with the remains of a columella showing some secondary meristematic activity (c) (lectotype f. *trincomaliense*). **15:** Shedding of outer layers of cells. Note shedded cell layers (arrows) and new epithallium cells (arrow heads) (lectotype f. *valida*). **16:** Old, buried conceptacle. Note cell fusions (arrow heads) (lectotype f. *ptychoides*). **17:** Habit (*Verheij 0217*). **18:** Bisporangial conceptacle. Note columella (c) and bispores (arrow heads) (*Verheij 0217*).



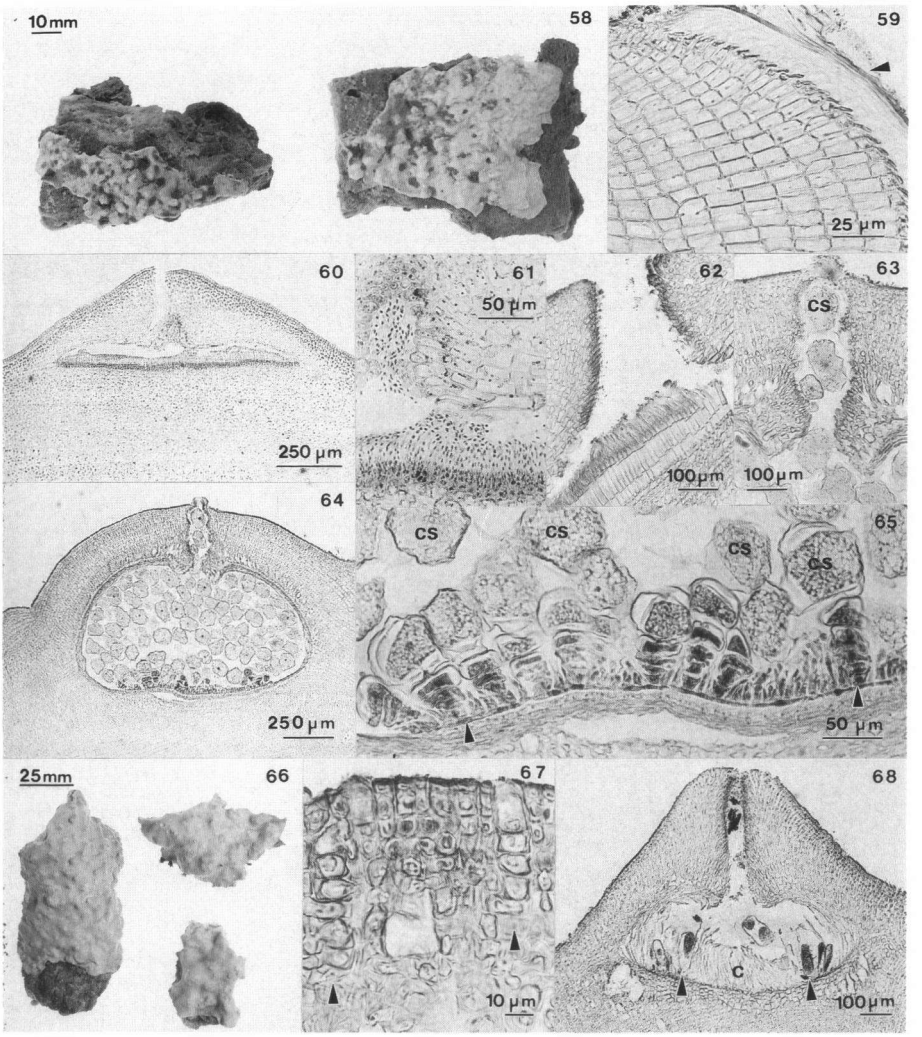

Figs. 19–30. Habits and reproductive structures (in vertical section). — *Lithophyllum tamiense:* **19:** Habit (lectotype PC). **20:** Habit (*Verheij B38, B98, B125*). **21:** Old tetrasporangial conceptacle. Note remains of columella (arrow heads) (lectotype PC). **22–26:** Developmental stages of tetrasporangial conceptacles (*Verheij 0718*). **22:** Youngest stage, local cell elongation (arrow heads). **23:** Older stage, several additional elongated cell layers are formed (arrow heads). **24:** Older stage. Note tetrasporangial initials (t) and filaments forming the conceptacle roof (arrow heads). **25:** Older stage. Note tetrasporangial initials (t), developing columella (c) and cell layer closing conceptacle pore (arrow heads). **26:** Empty conceptacle, partly overgrown by a young conceptacle. Note columella (c) and tetrasporangial initials (arrow heads). — *Hydrolithon gardineri:* **27:** Buried, not completely developed tetrasporangial conceptacle. Note filaments forming conceptacle roof (lectotype TRH). **28:** Habit (*Verheij B228*). **29:** Empty tetrasporangial conceptacle (lectotype TRH). **30:** Mature tetrasporangial conceptacle. Note slightly developed columella (c) (*Verheij B228*).



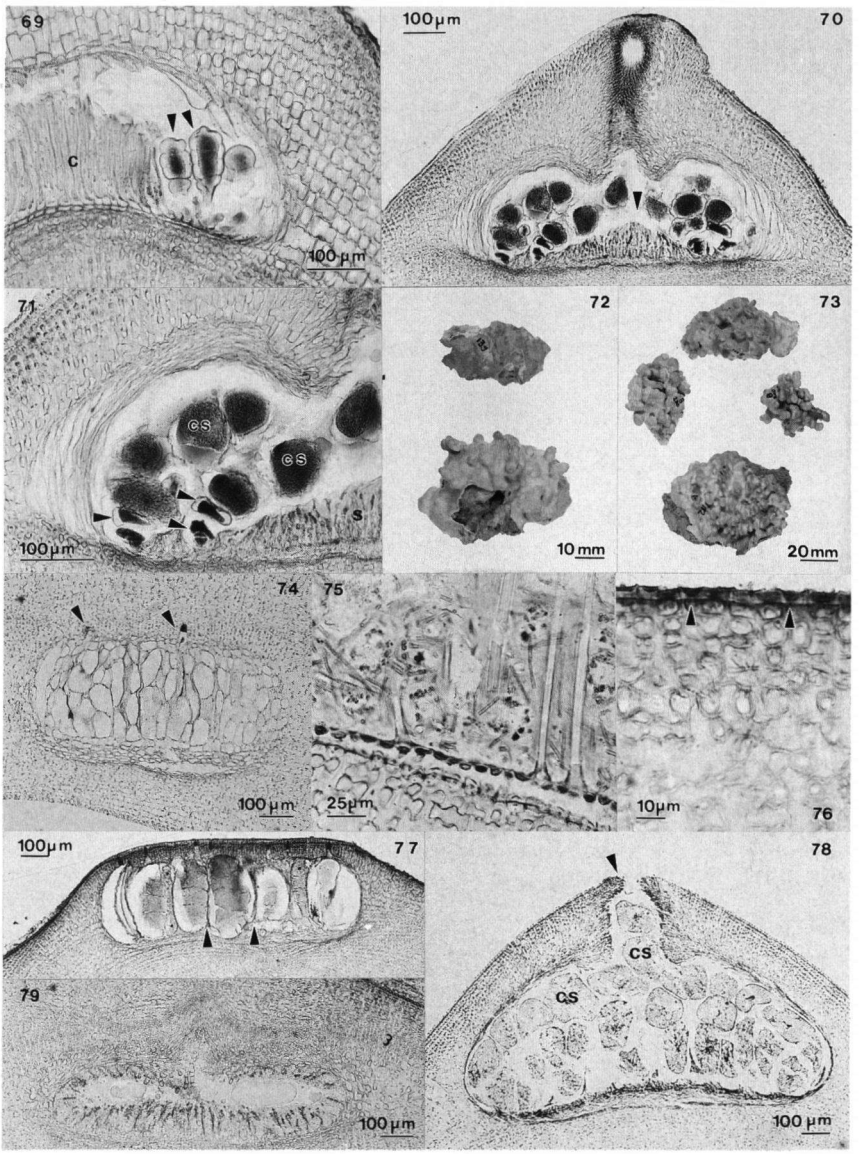

Figs. 31–41.Habits and reproductive structures (in vertical section). — *Hydrolithon onkodes:* **31:** Habit (*Verheij B261*). **32–34:** Developmental stages of tetrasporangial conceptacles (*Verheij 0056*). **32:** Youngest stage. Note tetrasporangial initials (arrow heads) and filaments forming the roof (arrows). **33:** Older stage. Note tetrasporangial initials (arrow heads) and columella (c). **34:** Mature stage. Note tetrasporangia (t) and columella (c). **35:** Horizontal field of trichocytes (tr). Note multilayered epithallium (arrow heads). — *Hydrolithon reinboldii:* **36:** Habit (*Verheij B40, B165, B204*). **37:** Old tetrasporangial conceptacle. Note trichocyte (tr) (*Verheij 0273*). **38:** Mature tetrasporangial conceptacle (*Verheij 0274*). — *Mastophora pacifica:* **39:** Mature tetrasporangial conceptacle. Note columella (c) (*Verheij 0020*). **40:** Detail of tetrasporangial pore. Note terminal cells of roof filaments, with swollen apical tip protruding into the pore canal (*Verheij 0020*). **41:** Habit (*Verheij 0020*).



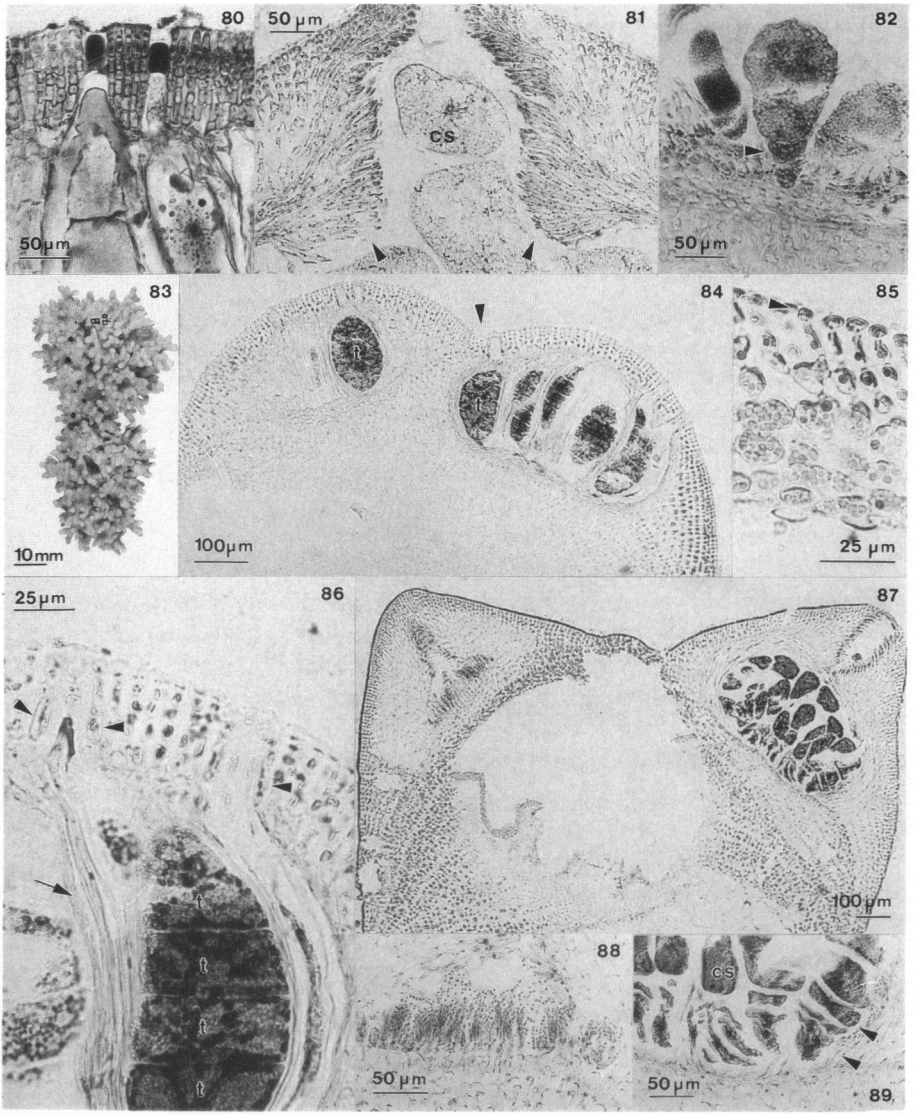

Figs. 42–57. Habits and reproductive structures (in vertical section). — *Mastophora rosea:* **42:** Habit lectotype *M. affinis* (L 943.7-29). **43:** Habit lectotype *M. macrocarpa* f. *condensata* (L 943.10-60). **44:** Habit *M. rosea* (L 992.057-060). **45:** Vegetative part of thallus. Note basal region composed of palisade cells (p) (*Verheij 0008*). **46:** Early developmental stage of female conceptacle. Note carpogonia (arrow heads) and shedding of overlaying epithallial cells (*Verheij 0049*). **47:** Mature female conceptacle. Note carpogonia (arrow heads) (*Verheij 0049*). **48:** Mature tetrasporangial conceptacle. Note columella (c) and tetrasporangia (t) (*Verheij 0008*). **49:** Detail of trichocytes. Note one trichocyte bearing a hair (arrow head) (*Verheij 0049*). **50:** Detail of tetrasporangial pore. Note terminal cells of roof filaments, with swollen apical tip protruding the pore (*Verheij 0049*). — *Neogoniolithon brassica-floridum:* **51:** Habit ecad *fosliei* (L 992.185-250). **52:** Habit ecad *laccadivicum* (*Verheij 0862*). **53:** Habit ecad *frutescens* (*Verheij 0843*). **54:** Empty tetrasporangial conceptacle, lectotype *G. frutescens* f. *frutescens* (TRH no number). **55:** Empty tetrasporangial conceptacle, lectotype *G. laccadivicum* (TRH no number). **56:** Mature tetrasporangial conceptacle ecad *frutescens* (*Verheij 0213*). **57:** Ibid. ecad *fosliei* (*Verheij 0271*).



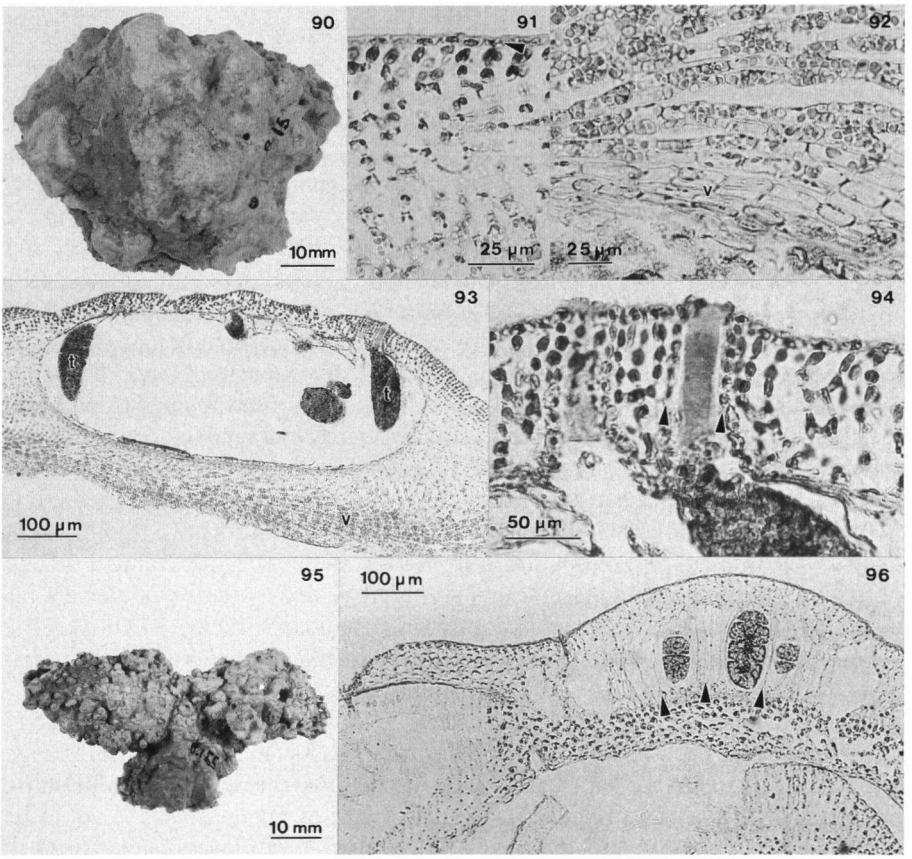

Figs. 58–68. Habits and reproductive structures (in vertical section). — *Spongites* spec. (58 & 60: *Verheij 0319*; 59, 61–65: *Verheij 0065*): **58:** Habit. **59:** Detail of grow margin of thallus. Note muscilenous layer (arrow head). **60:** Male conceptacle. **61:** Detail spermatangia. Note spermatangia restricted to floor. **62:** Detail of broken female conceptacle. **63:** Detail of pore of cystocarpic conceptacle. Note carpospores (cs). **64:** Cystocarpic conceptacle. Note gonimoblast filaments arizing all over the floor (arrow heads) and carpospores throughout the conceptacle chamber. **65:** Detail of cystocarpic conceptacle floor. Note gonimoblast filaments (g) and carpospores (cs). — *Spongites sulawesiensis:* **66:** Habit (*Verheij 1184*). **67:** Detail trichocytes (arrow heads) (*Verheij 0006*). **68:** Tetrasporangial conceptacle. Note columella (c) (*Verheij 0078*).




Figs. 69–79. Habits and reproductive structures (in vertical section). — *Spongites sulawesiensis:* **69:** Detail tetrasporangial conceptacle. Note tetrasporangia (arrow head) and columella (c) (*Verheij 0030*). **70:** Cystocarpic conceptacle. Note sterile center (arrow heads) (*Verheij 0071*). **71:** Detail cystocarpic conceptacle. Note sterile centre (s), carpospores (cs) and gonimoblast filaments (arrow heads) (*Verheij 0071*). — *Lithothamnion prolifer:* **72:** Habit lectotype (L 943.7-40). **73:** Habit (L 986.106-502). **74:** Filled in, overgrown tetrasporangial conceptacle. Note pores (arrow heads) (L 943.7-40). **75:** Epithallium covered with sponge tissue is shedded (*Verheij 0790*). **76:** Detail of epithallium with flatted and eared epithallial cells (arrows) (*Verheij 0058b*). **77:** Tetrasporangial conceptacle. Note non calcified intersporangial filaments (arrow heads) (*Verheij 0058a*). **78:** Carposporangial conceptacle. Note narrow apical part of pore (arrow heads) and carpospores (cs) (*Verheij 1182*). **79:** Old, overgrown male conceptacle. Note dendroid spermatangia (*Verheij 0058b*).




Figs. 80–89. Habits and reproductive structures (in vertical section). — *Lithothamnion prolifer:* **80:** Detail tetrasporangial pores. Note rounded cells lining the pore canal (*Verheij 0058a*). **81:** Detail carposporangial conceptacle pore. Note narrow apical part of pore, paintbrush-like base of the pore (arrows), and carpospores (cs) (*Verheij 1182*). **82:** Detail gonimoblast filament (arrow heads) and obscure fusion cell (arrow) (*Verheij 1182*). — *Mesophyllum erubescens:* **83:** Habit (L 986.106-496). **84:** Mature and almost mature tetrasporangial conceptacles. Note the youngest conceptacles almost overgrow a pore of the older conceptacle (arrow head) and tetraspores (t) (*Verheij 0038*). **85:** Detail of dorsal region. Note rounded epithallium cells (arrow heads) (*Verheij 0956*). **86:** Detail of tetrasporangial pore. Note elongated basal cells of the pore (arrow heads), tetraspores (t), and noncalcified intersporangial filaments (arrow) (*Verheij 0038*). **87:** Male and carposporangial conceptacles on one thallus (*Verheij 0956*). **88:** Detail of male conceptacle (*Verheij 0956*). **89:** Detail of carposporangial conceptacle. Note short gonimoblast filaments (arrow heads) and carpospores (cs) (*Verheij 0956*).




Figs. 90–96. Habits and reproductive structures (in vertical section). — *Mesophyllum funafutiense:* **90:** Habit (L 986.106-507). **91:** Detail of dorsal region. Note rounded epithallium cells (arrow heads) (*Verheij 0298*). **92:** Detail of ventral region. Note noncoaxial arranged filaments (v) (*Verheij 0298*). **93:** Almost empty, old tetrasporangial conceptacle. Note tetrasporangia (t) and an almost coaxial arranged ventral region (v) (*Verheij 0298*). **94:** Detail of tetrasporangial pore. Note rounded cells alining the pore canal (arrow heads) (*Verheij 0298*). — *Mesophyllum syrphetodes:* **95:** Habit (L 986.106-493). **96:** Tetrasporangial conceptacle. Note one cell long intersporangial filaments (arrow heads) (*Verheij 0296*).