

***Lithophaga* (Bivalvia, Mytilidae), including a new species, boring into mushroom corals (Scleractinia, Fungiidae) off South Sulawesi, Indonesia**

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Bivalve species of the mytilid genus *Lithophaga*, including a new one, are recorded from Indonesian mushroom corals (Scleractinia, Fungiidae). True associations with live hosts include *L. laevigata*, *L. lessepsiana*, *L. lima*, *L. punctata* spec. nov., and *L. simplex*, while specimens of *L. malaccana* and *L. mucronata* have been found in bore holes in encrusted or dead parts of infested corals.

Key words: Bivalvia, Mytilidae, *Lithophaga*, Scleractinia, Fungiidae, Indonesia, South Sulawesi, endoparasitism

## INTRODUCTION

In the mytilid bivalve genus *Lithophaga* Röding, 1798, species are known either to bore into various calcareous substrates, including coral surfaces not covered by live tissue, or, as associates, into living scleractinian hosts (Kleemann, 1995, 1996 and references therein). The Caribbean *L. bisulcata* (d'Orbigny, 1842) is the only known species found in live as well as dead substrates (Scott, 1988). Associations between corals and certain *Lithophaga* species have occurred at least since the late Cretaceous (Kleemann, 1994a, 1994b).

With regard to free-living (unattached) corals, Arnaud & Thomassin (1976) were the first to report an association with *Lithophaga*. They found *L. lessepsiana* (Vaillant, 1865) in the mobile dendrophylliid coral *Heteropsammia michelini* Edwards & Haime, 1848 [= *H. cochlea* (Spengler, 1781) vide Veron & Pichon, 1980, Hoeksema & Best, 1991]. Zibrowius & Arnaud (1995) recorded *L. lima* Lamy, 1919, from a Philippine specimen of *Trachyphyllia geoffroyi* (Audouin, 1826), a semi-buried, unattached scleractinian coral species (Hoeksema, 1993).

Mushroom corals (Scleractinia: Fungiidae) containing specimens of the mytilid genera *Fungiacava* and *Lithophaga*, were collected by the second author in Indonesia, SW Sulawesi, Spermonde Archipelago. In order to find these bivalves, fungiid corals were systematically searched for their symbionts in belt transects (50 m long, 1 m wide) at 3 m depth intervals. Most of the host corals concerned free-living species, whereas a few remain attached (see revision by Hoeksema, 1989). Apart from a note by Hoeksema & Achituv (1993, citing a letter of Dr. C. Massin, Brussels), this is the first documented record of *Lithophaga* in this coral family with mainly free-living species. In comparison, the first record of the related genus *Fungiacava* Goreau et al., 1968, was about 25 years

earlier (Hoeksema & Achituv, 1993 and references therein) from *Fungia* at Eilat, northern Red Sea.

The present mushroom coral material is of special interest as it proved to contain more than one species of truly associated *Lithophaga*, including *L. punctata* Kleemann & Hoeksema, spec. nov. and others settling on dead parts of the "hosts" or on encrustations, e.g., serpulid tubes, of the coral specimens. The other newly recorded endosymbionts of living Fungiidae are *L. laevigata* (Quoy & Gaimard, 1835), *L. lessepsiana*, *L. lima*, and *L. simplex* Iredale, 1939.

#### KEY TO *LITHOPHAGA* SPECIES IN MUSHROOM CORALS FROM INDONESIA

- 1a Specimen a true associate of the host (in most cases seen by the position of the bore hole opening completely surrounded by live tissue, generally on the upper surface of the coral) ..... 2
- 1b Specimen a dead substrate borer (may be difficult to decide, when the position of the bore hole opening is not clearly within a dead part of a live coral but was secondarily surrounded by live coral tissue after larval settlement, e.g., on a scar or the tube of encrusting polychaete worm) ..... 4
- 2a Specimen showing (almost) no adhesive encrustation on the posterior part of the valves, covered by very pale, yellowish periostracum ..... *L. simplex*
- 2b Specimen showing (almost) no adhesive encrustation on the posterior part of the valves, covered by usually bi-coloured periostracum, carrying minute elevated dots antero-laterally to postero-ventrally ..... *L. punctata*
- 2c Specimen with adhesive encrustation on the posterior part of the valves ..... 3
- 3a Posterior encrustation formed by fine ridges, divaricating in a chevron pattern, protruding very little beyond the somewhat attenuated shell rim ..... *L. laevigata*
- 3b Posterior encrustation formed by coarser granules or ridges, interrupted to reticulated, protruding as little teeth beyond the somewhat inflated shell rim ..... *L. lima*
- 3c Posterior encrustation rather weak, formed by fine grained, short ridges in dorsal-ventral direction, protruding very little beyond the shell rim ..... *L. lessepsiana*
- 4a Posterior encrustation formed by relatively strong, smooth looking, pointed elongation of the small, truncated shell ..... *L. mucronata*
- 4b Posterior encrustation formed by fine ridges in a reticulated pattern (may be obscured), protruding (considerably) the elongated shell ..... *L. malaccana*

#### SYSTEMATICS

Family Mytilidae  
 Subfamily Lithophaginae  
 Genus *Lithophaga* Röding, 1798  
 Subgenus *Leiosolenus* Carpenter, 1856

*Lithophaga punctata* spec. nov. (figs 1-5, 12)

Material. – Holotype, RMNH 10132 (figs 1-2). Host species *Sandalolitha robusta* (Quelch, 1886); SE of Samalona I. (7.5 km W of Makassar), 5°07'S 119° 0'E (28.iv.1994). Size 13.5x5.0x4.7 mm, the largest of the

available specimens, elevated lateral dots on the periostracum above the antero-ventral encrustation (not present in other specimens with dots), bi-colouration similar to that of *Lithophaga nasuta* (Philippi, 1846).

Paratype, RMNH 10072. Host species *Fungia (Pleuractis) paumotensis* Stutchbury, 1833; W of Bone Baku reef (5 km W of Makassar), 5°08'S 119°21'E (17.vi.1994). A single specimen, 5 mm in length, the minute latero-ventral dots very densely scattered, no darker stripe visible under a fine posterior-dorsal encrustation. Bore hole opening round, c.1 mm wide, in underside of coral, 10 mm from the periphery. Two fitting fragments, c. 5 cm in length, from one side of an elongated coral; centre and other side of coral missing.

Paratype, RMNH 10076 (figs 3-4). Host species *Fungia (Pleuractis) paumotensis* Stutchbury, 1833; SE of Barang Caddi I. (11 km NW of Makassar), 5°05'S 119°19'E (4.v.1994). Host also contained specimens of a *Leptocochnus* species (Coralliophilidae), a boring gastropod. Size 9.9x4.3x3.6 mm, bi-coloured, lateral dots vary in density, being denser antero-dorsally and scarce ventrally, somewhat dash-like elongated posteriorly (host coral not collected). Specimen with a relatively distinct dorsal elevation and rather stout outline compare with the other paratypes.

Paratype, RMNH 10082 (fig. 5). Host species *Fungia (Verrillofungia) repanda* (Dana, 1846); W of Barang Lompo I. (13 km NW of Makassar), 5°03'S 119°19'E (10.vi.1994). Lateral dots rather evenly distributed, bi-colouration light, antero-lateral encrustation), 2 specimens, 8.6x3.0x2.7 mm and 3.8x1.7x1.5 mm. No coral fragment.

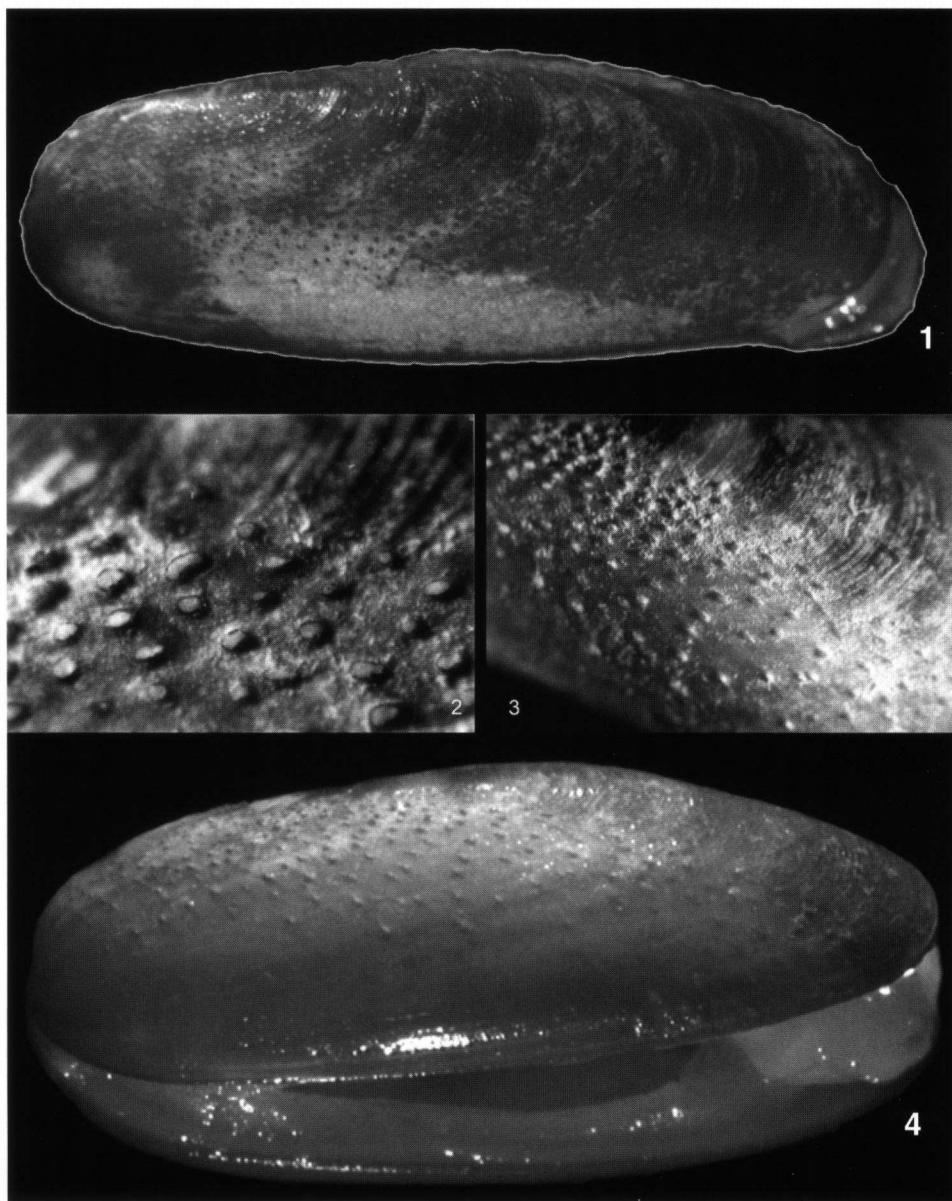
Paratype, RMNH 10094. Host species *Lithophyllon mokai* Hoeksema, 1989; NW of Kudingareng Keke I. (14 km WNW of Makassar), 5°06'S 119°17'E. (15.ix.1994). Length 9.8 mm, broken, no (obvious) dots developed, bi-coloured by darker stripe from umbones to posterior ventral end. No coral fragment collected.

Paratype, RMNH 10122. Host species *Fungia (Verrillofungia) repanda* Dana, 1846; N of Samalona I. (7.5 km W of Makassar), 5°07'S 119°20'E (21.v.1994). Size 10.3x3.7x3.5 mm, dots very obvious, but antero-ventral commissure without dots; umbos eroded. The bore hole, 11.5x4 mm, had its orifice 18 mm away from the edge and > 50 mm from the centre on the corals upper side.

Paratype, RMNH 10128. Host species *Halomitra pileus* (Linnaeus, 1758); S of Samalona I. (7.5 km W of Makassar), 5°07'S 119°20'E (31.v.1994). Length 8 mm, dots visible, no apparent encrustation.

**Diagnosis.** – Valves with minute, elevated dots antero-laterally to postero-ventrally, periostracum darker above that area.

**Description.** – Shell small, thin, very fragile, umbos sub-terminal and inconspicuous, anterior end almost hemispherical, posterior end in dorsal or ventral view more wedge-shaped, with a evenly rounded, not truncated edge, and lacking calcareous prolongations or solid deposits on the shell. Shell outline is usually slender elliptical, rarely somewhat stout, ventral margin slightly convex, dorsal margin in most cases with a longer anterior than posterior part, measured from the usually indistinct dorsal angle. The posterior slope of the dorsal edge descends in a slightly curved line, while its anterior slope is straight. Minute, elevated dots characterize the outer shell surface in front and below a thought line, which descends from the umbones to the lower posterior edge. The surface past that line is smooth, except for the normal concentric growth increments, if not covered by unconsolidated, probably detrital deposits, and usually shows a distinctly darker pigmented periostracum than the fair coloured antero-ventral part of the shell. Sometimes the darker pigmented part is restricted to a wedge-shaped area or stripe, starting with its pointed end at the umbones and running towards the posterior end. The elevated dots are circular to kidney-shaped, but mostly oval in outline. Their density varies very much between specimens, from hardly any dots to very many, and in their distribution on individual shells (figs 1-5). They may be aggregated antero-laterally and sparse near the ventral and anterior commissure. Sometimes dots appear to be rather evenly distributed or partly arranged in rows of varying direction. Except in very young spe-



Figs 1-4. *Lithophaga punctata* spec. nov. 1, holotype in left lateral view (RMNH 10132), length 13.5 mm; 2, surface close-up of holotype; 3, surface close-up of paratype (RMNH 10076); 4, paratype (RMNH 10076), length 9.9 mm.

cimens, up to 5 mm in length, dots seem eroded as sometimes parts of the lateral surface or the umbos. Deposits on the shells are usually sparse and indistinct, with no prolongations of the valves.

See Material for data on individual specimens.

Comparison with other species. – The clearly visible elevated dots on part of the shell surface are a unique feature in the genus (probably even in bivalves) and separate the new species from other coral-associated *Lithophaga* species (see Discussion). The bi-coloration also separates it from the pale (and usually much bigger) specimens of *L. simplex*, lacking distinct deposits on its shell as in *L. punctata* spec. nov. The other coral-associated species known from the area, *L. laevigata* (fig. 6), *L. lima* (fig. 7) and *L. lessepsiana* (fig. 8), usually have adhesive calcareous deposits developed on the posterior extremities at least in larger specimens, which can be used for determination (see below).

### *Lithophaga simplex* Iredale, 1939

Material. – RMNH 10092. Host species *Astreopora myriophthalma* (Lamarck, 1816), Acroporidae; NW of Kudingareng Keke I., 5°06'S 119°17'E (25.v.1994). (?) RMNH 10125. Identity uncertain. Host species *Fungia* (*Wellsofungia*) *granulosa* Klunzinger, 1879; S of Samalona I., 5°07'S 119°20'E (1994). (?) RMNH 10086. Identity uncertain. Host species *Sandalolitha robusta* (Quelch, 1886); W of Barang Lompo I. (= 13 km NW of Makassar).

*Astreopora* is a well know host genus of this species (Kleemann, 1980, 1995, Mokady et al., 1992, 1993).

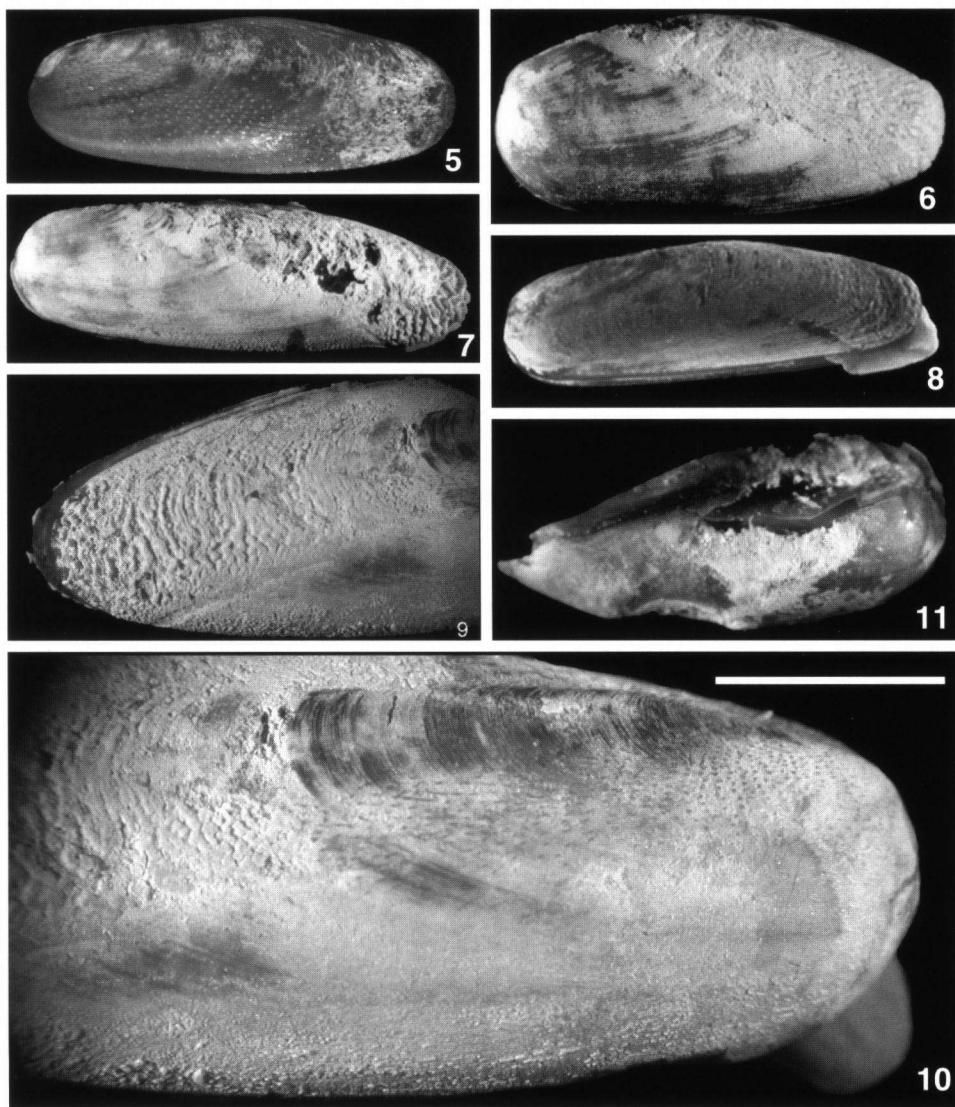
Two small, probably juvenile bivalves, extracted from fungiid hosts may also represent *Lithophaga simplex*. One 4.5 mm long specimen penetrated a disc-shaped *Fungia granulosa*, 40 mm wide, through the upper side, in a distance of 8.5 mm from the central fossa. The other, 3.5 mm long bivalve, bored also from above in a *Sandalolitha robusta* coral. The bore hole was next to an insured area with several borings from polychaete worms, probably belonging to the genus *Pherusa* (family Flabelligeridae) (two species), and one *Gastrochaena* sp. bore hole. Both *Lithophaga* specimens are lacking a distinctive shell encrustation and show a very uniform pale yellow and smooth periostracum without elevated dots and quite likely represent *L. simplex*.

### *Lithophaga laevigata* (Quoy & Gaimard, 1835) (fig. 6)

Material. – RMNH 10117 (fig. 6). Host species *Fungia* (*Verrillofungia*) *scabra*, Döderlein, 1901; S of Panikiang I., 4°22'S 119°35'E (30.viii.1994). RMNH 10118 (one specimen). Host species *F. (V.) spinifer* Clareboudt & Hoeksema 1987; W of Badi I., 4°57'S 119°17'E (2.vi.1994).

The specimen in a *Fungia scabra* coral, S of Panikiang I., 12.5x5.8x5.3 mm (fig. 6), had its ~2 mm wide bore hole orifice on the upper side of the coral. The other specimen, 15x5.6x5 mm, belongs to a fragment of *F. spinifer* collected W of Badi I. The latter sample, also includes a specimen of *Lithophaga mucronata*?, 12x4.4x4.3 mm, with posterior shell encrustations projecting far beyond the shell rims.

The diagnostic feature in *Lithophaga laevigata* is the adhesive posterior shell encrustation, consisting of fine, somewhat wavy and horizontal ridges, divaricating in a chevron pattern and protruding only little over the shell edge (fig. 6; Kleemann, 1977: fig. 6).



Figs 5-11. Indonesian *Lithophaga* specimens from fungiid corals. 5, paratype of *L. punctata* (RMNH 10082), 8.6 mm; 6, *L. laevigata* (RMNH 10117), 12.5 mm; 7, *L. lima* (RMNH 10073), 19.7 mm; 8, *L. lessepsiana* (RMNH 78861) (pars), 25.0 mm; 9-10, *L. lima* (hybrid?) (RMNH 10091), 23.1 mm (total length); 9, posterior shell encrustation; 10, note elevated dots, a feature of *L. punctata*, scale bar 5 mm; 11, *L. mucronata* (RMNH 78860), 11.1 mm, dorsal view, note etch mark (depression) in right valve caused by the occurrence of a conspecific individual in the same host.

*Lithophaga lessepsiana* (Vaillant, 1865) (fig. 8)

Material. – RMNH 10093. Host species *Halomitra pileus* (Linnaeus, 1758); NW of Kudingareng Keke I., 5°06'S 119°17'E (15.ix.1994). RMNH 78861. Host species *Lithophyllon undulatum* Rehberg, 1892; W of Bone Tambung I., 5°02'S 119°16'E (14.v.1994). RMNH 10130 (fig. 8). Host species *Fungia* (*Danafungia*) *horrida* Dana, 1846; S of Samalona I., 5°07'S 119°20'E (31.v.1994). (?) RMNH 10124. Identity uncertain. Host species *Herpolitha limax* (Esper, 1797); N of Samalona I., 5°07'S 119°20'E (21.v.1994).

A specimen, 10 mm in length, from a *Halomitra pileus* coral, NW of Kudingareng Keke I. Two further bivalves, one 10.7x4.7x4.4 mm, from *Lithophyllon undulatum*, and the other 25x8x8 mm (fig. 8), from a *Fungia horrida* coral, both S of Samalona I., likely represent *Lithophaga lessepsiana*, but show indistinct posterior shell encrustations. A broken specimen, 27.7x10x9 mm, from a *Herpolitha limax* coral, with dark and laterally quite eroded periostracum, a weak posterior encrustation of probably accumulated detritus rather than calcareous deposit, might belong to *L. lessepsiana*.

*Lithophaga lima* Lamy, 1919 (figs 7, 9-10, 13-14)

Material. – RMNH 10073. Host species *Fungia* (*Verrillofungia*) *scabra* Döderlein, 1901; W of Bone Baku reef, 5°08'S 119°21'E (17.vi.1994). RMNH 10091. Host species *Fungia* (*Pleuraetis*) *moluccensis* Van der Horst, 1919; W of Gusung I., 5°07.5'S 119°23'E (2.v.1994). RMNH 10074. Host species *Lithophyllon undulatum* Rehberg, 1892; S of Barang Caddi I., 5°05'S 119°19'E (23.v.1994).

One specimen, 19.7x6.8x6.1 mm (fig. 7), from a *Fungia scabra* coral, W of Bone Baku reef, plus a shell fragment still in situ. The bivalve had lived with the ventral side up. The boring opening lies about 25 mm off the host's centre, between septa, and the bore hole terminates below the coral fossa. Several layers of calcareous deposits, lining the wall near the opening, shifted it a little towards the centre. The latter coral sample included two specimens of *Lithophaga mucronata* (see there). One specimen, 23.1x8.0x7 mm (fig. 9), in a *F. moluccensis* coral, W of Gusung I. The shell has latero-posteriorly the characteristic, rippled encrustation, thickening somewhat towards the edges and protruding them very little in a serrated pattern. Surprisingly, also elevated dots can be observed (fig. 10), missing in conspecifics, and regarded the typical feature of *Lithophaga punctata* spec. nov. The bivalve bored from the side of the elevated central part of the coral downwards in a steep angle towards center.

Another specimen, 21.0x7.7x6.8 mm, with a posterior encrustation similar to *Lithophaga lima*, bored in a *Lithophyllon undulatum* coral, S of Barang Caddi I. The shell has a thin, darker pigmented stripe running laterally from the umbos to the posterior end. No coral fragment was collected with the bivalve.

*Lithophaga malaccana* (Reeve, 1857)

Material. – RMNH 10077. Host species *Podabacia crustacea* (Pallas, 1766); W of Barang Caddi I., 5°05'S 119°19'E (10.vi.1994). RMNH 10119. Host species *Fungia* (*Cycloseris*) *sinensis* Milne Edwards & Haime, 1851; W of Badi I., 4°57'S 119°17'E (2.vi.1994). RMNH 10088. Host species *Lithophyllon undulatum* Rehberg, 1892; W of Bone Tambung I., 5°02'S 119°16'E (14.v.1994).

One free, broken specimen, 12.9x4.2x4 mm, from dead part of a *Podabacia crustacea* coral, W of Barang Caddi I., which included a second specimen and polychaete worms.



Fig. 12. A specimen of *Lithophaga punctata* spec. nov. boring in the upper side of a *Fungia (Verrillofungia) spinifer* coral that has been broken open (Kudingareng Keke I.).

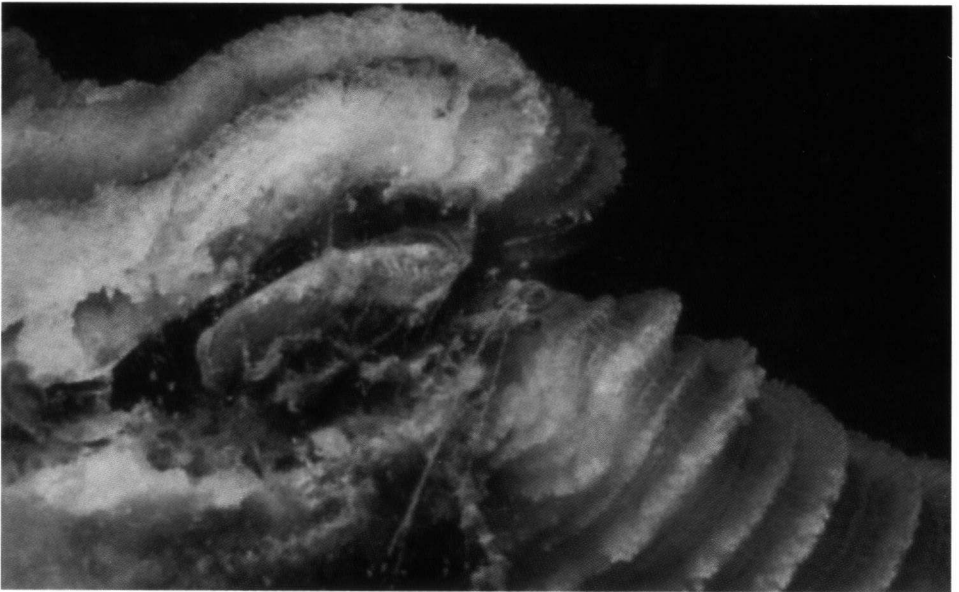


Fig. 13. A specimen of *Lithophaga lima* boring in the upper periphery of a *Fungia (Pleuractis) moluccensis* coral that has been broken open (Lae-Lae I., RMNH 84615).



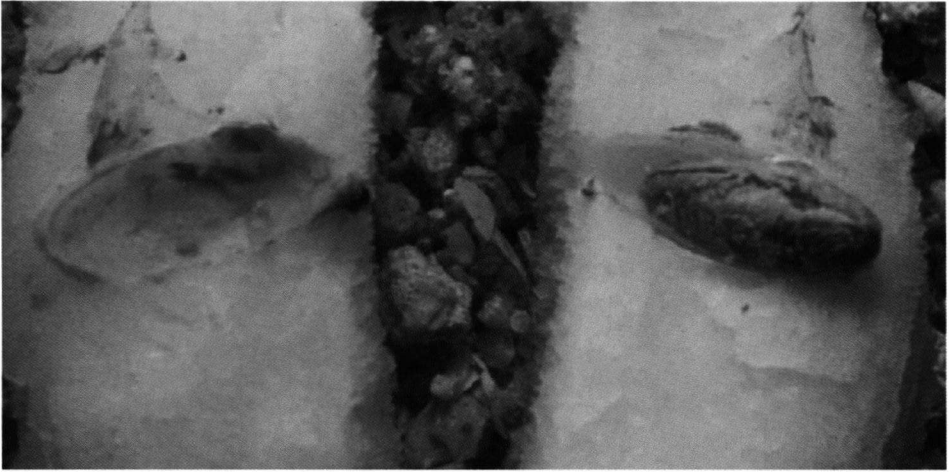


Fig. 14. A specimen of *Lithophaga lima* boring in the lower side of a *Fungia* (*Verrillofungia*) *scabra* coral that has been split into two parts (Samalona I., RMNH 84614).

The live coral fragments included several individuals of *Fungiacava*. A small specimen, 7.2x2.5x2.4 mm, from a *Lithophyllon undulatum* coral resembles *Lithophaga malaccana*. Another specimen, 11.5x4.0x3.3 mm, from a *Fungia sinensis* specimen (fragments small but looking very different, with one empty *Leptoconchus* shell), W of Badi I., resembles more elongated *L. malaccana* than truncated *L. mucronata*.

*Lithophaga mucronata* (Philippi, 1846) (fig. 11)

Material. – RMNH 10111. Host species *Heliofungia actiniformis* Quoy & Gaimard, 1833; E of Lae-Lae I., 5°08'S 119°23'E (30.iv.1994). RMNH 78860 (fig. 11). Host species *Fungia* (*Verrillofungia*) *scabra*, Döderlein, 1901; W of Bone Baku reef, 5°08'S 119°21'E (17.vi.1994). RMNH 10134. Host species *Fungia* (*Pleuractis*) *mohuccensis* Van der Horst, 1919; W of Samalona I., 5°07'S 119°20'E (28.iv.1994).

Several specimens bored in a *Heliofungia actiniformis* coral, W of Lae Lae I., from the lower side where the coral surface was insured and partly covered by epiphytes. Two complete bivalves, 6.9x4.6x3.4 mm and 5.4x2.8x2.8 mm, and 4 pairs of smaller, empty shells. Two specimens from a *Fungia scabra* coral, one free and measuring 11.1x4.5x4.7 mm (fig. 11), the other still enclosed in the coral skeleton. The bore hole opening of both lie in serpulid tubes on the central underside of the coral, which may have enabled the settling of the veligers on dead surface. Associated *Lithophaga lessepsiana* bored from the upper surface of the same coral specimen (see there).

Five small specimens close together in a dead part of a *Fungia mohuccensis* coral, W of Samalona I. Three of these, ~5 mm in length, are still in a fragment of the coral and one of them obviously took over an old bore hole in which shell remains can be seen. The other two specimens measured 5.4x2.1x2.0 mm and 5.2x2.4x2.3 mm respectively.

Shells very small, fragile and stunted at the posterior end but camouflaged by compact and smooth looking posterior encrustation. The usually pointed appendages, reaching distinctly beyond the shell edges, are sometimes only developed on one side (fig. 11). The

figured specimen shows an etch-mark as a depression in the right valve, which was caused by a neighbouring bivalve.

### CROSS-SHELF DISTRIBUTION AND HOST SPECIFICITY

The present results (27 records in table 1) suggest that the *Lithophaga* species recorded from mushroom corals at the Spermonde Shelf, South Sulawesi, predominantly occur on nearshore reefs (fig. 15). This is most clearly shown by *L. lima* (2-11 km offshore) and *L. mucronata* (2-6 km). The new species *L. punctata* appears to be the most common boring *Lithophaga* in fungiids and has also been found rather nearshore (4-13 km). *L. laevigata* (1-22 km) and *L. lessepsiana* (6-18 km) show the widest ranges, whereas *L. malaccana* (11-22 km) appears to show the most offshore distribution of all. Another boring mytilid, *Fungiacava eilatensis*, shows a wider offshore distribution range, 2-36 km (Hoeksema & Kleemann, 2002). The *Lithophaga* ranges are based on very few records. More observations are needed to find clear interspecific differences in cross-shelf distribution patterns.

It is obvious that there is no clear host-specificity in the associations of *Lithophaga* and mushroom coral species. This is also seen in the bivalve-coral relationships of *Fungiacava eilatensis* with fungiids (Hoeksema & Kleemann, 2002). If the cross-shelf ranges of the host species at South Sulawesi (Hoeksema 1990) are considered, it appears that none of the present *Lithophaga* ranges are restricted by the availability of suitable host species.

### DISCUSSION

The distinction of *Lithophaga* species is largely based on different patterns of adhesive calcareous deposits, particularly on the posterior shell surface. Those on ventral parts and anterior end are usually too similar, if present, to distinguish between species. Additionally, accumulated detritus in secreted mucus may lie loosely on any part of the shell, sometimes obscuring an otherwise typical posterior encrustation, but covers mainly antero-dorsal parts.

The consistence of this antero-dorsal cover is primarily soft but may be consolidated in calcareous bore hole lining. In coral associated bivalves, keeping pace with growth of their host, this may yield to "false floors" in the bore holes, precipitated from mucus secretion.

In *Lithophaga punctata* spec. nov., a variable shell encrustation, ventral in the holotype (fig. 1), postero-dorsal in paratype RMNH 10072, may be present or missing as in some of the paratypes (RMNH 10076, figs 3-4). Thus, it is regarded a facultative and indistinct feature. The elevated dots, however, variable in density, seem to be a distinctive species-specific character (figs 1-5), although found once in a specimen, RMNH 10091 (figs 9-10), considered to represent *L. lima*, according to the posterior encrustation pattern. The possibility of a hybrid seems plausible (see below). This enigmatic shell sculpture, probably unique within bivalvia, needs to be investigated in detail. The bi-coloration of the periostracum is not restricted to the new species. It is also present in others, e.g., in beach-rock and dead coral boring *L. nasuta*.

*Lithophaga simplex*, is also lacking a distinct encrustation pattern, while the other here considered species, particularly in older specimens, can usually be distinguished by this feature (see key above). Thus, the two, very small specimens probably representing *L. simplex*, RMNH 10125 and another specimen, could be misidentified due to not yet

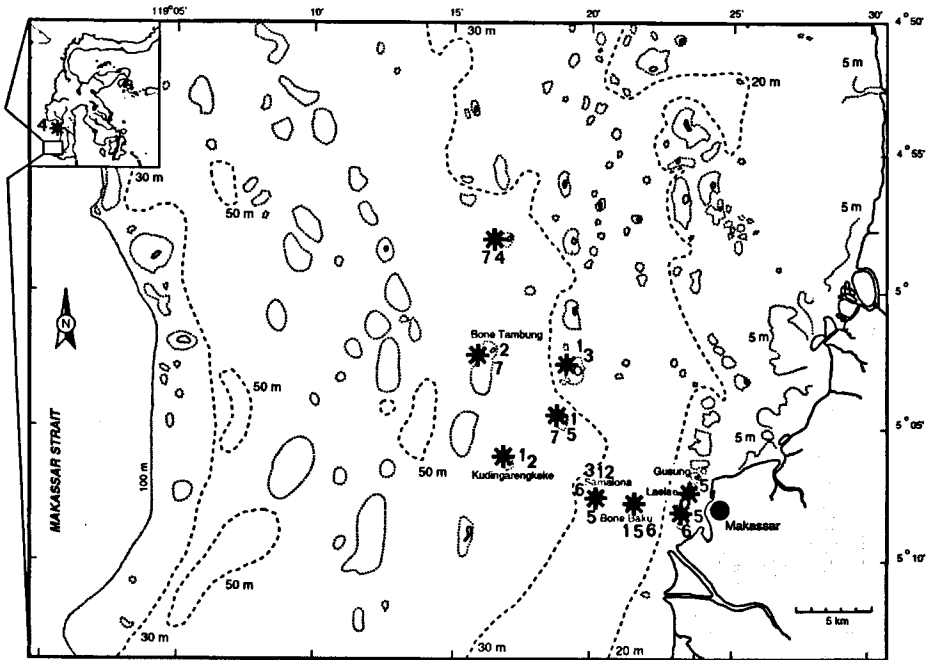


Fig. 15. Localities of seven *Lithophaga* species at South Sulawesi (see table 1). Panikiang I. is about 100 km to the north of Makassar (inset): 1, *L. punctata*; 2, *L. lessepsiana*; 3, *L. simplex* (?); 4, *L. laevigata*, 5, *L. lima*; 6, *L. mucronata*; 7, *L. malaccana*.

developed features of other species. Sometimes, even quite big specimens are difficult to determine when they show indistinct or mixed features, possibly caused by hybridisation (see above). For these reasons, associations, marked by (?) in table 1 have to be considered with caution.

The known associations of *Lithophaga* with corals (Mokady et al. 1994, Kleemann 1995, 1996, and references cited by these authors) are sometimes widespread, taxonomically as well as geographically. Previously, only *Fungiacava* was known to inhabit fungiid hosts.

There are some contradictory statements concerning host-specificity in various *Lithophaga* species, e.g., *L. lessepsiana*. Pocilloporid *Stylophora pistillata* (Esper, 1797), from the Gulf of Suez, is the host coral of the syntypes of *L. lessepsiana* (Kleemann, 1980). Arnaud & Thomassin (1976) and Kleemann (1980) reported it from free-living dendrophylliid *Heteropsammia michelini* (= *H. cochlea*), SW of Madagascar respectively Lizard Island, Great Barrier Reef. In the Gulf of Eilat, Red Sea, Mokady et al. (1991) stated this species to occur only in *S. pistillata*, while Kleemann (1995) reported it from five *Stylophora* and one *Pocillopora* species from Safaga, northern Red Sea, and *Heteropsammia*, *Pocillopora* and *Stylophora* from the Great Barrier Reef.

The spectrum of host corals is often astonishingly wide, as *L. laevigata* and *L. purpurea* use hosts out of at least four and *L. lima* of five scleractinian families. Rarely the spectrum is narrow as in *L. kuehneli* Kleemann, 1977, being restricted to the subgenus *Acropora* (*Isopora*) Studer, 1878 (see Kleemann, 1995: table 1). The host range of *L. punctata* spec. nov., probably restricted to (some) genera of family Fungiidae, appears intermediate.

Table 1. Overview of *Lithophaga* specimens in 15 fungiid host species (Scleractinia: Fungiidae) recorded at the Spermonde Archipelago, South Sulawesi, Indonesia.

<i>Lithophaga</i> species	Fungiid host species	Reef	Distance offshore km	Catalogue no. RMNH
<i>L. punctata</i>	<i>Fungia</i> ( <i>Verrillofungia</i> ) <i>repanda</i> Dana, 1846	Samalona I.	6	10122
<i>L. punctata</i>	idem	Barang Lompo I.	12	10082
<i>L. punctata</i>	<i>F. (V.) spinifer</i> Claereboudt & Hoeksema, 1987	Kudingareng Keke I.	13	photo
<i>L. punctata</i>	<i>F. (Pleuractis) paumotensis</i> Stutchbury, 1833	Bone Baku reef	4	10072
<i>L. punctata</i>	idem	Barang Caddi I.	11	10076
<i>L. punctata</i>	<i>Sandalolitha robusta</i> (Quelch, 1886)	Samalona I.	6	10132
<i>L. punctata</i>	<i>Halomitra pileus</i> (Linnaeus, 1758)	Samalona I.	6	10128
<i>L. punctata</i>	<i>Lithophyllon mokai</i> Hoeksema, 1989	Kudingareng Keke I.	13	10094
<i>L. lessepsiana</i>	<i>Fungia</i> ( <i>Danafungia</i> ) <i>horrida</i> Dana, 1846	Samalona I.	6	10130
<i>L. lessepsiana</i>	<i>Herpolitha limax</i> (Esper, 1797)	Samalona I.	6	10124
<i>L. lessepsiana</i>	<i>Halomitra pileus</i> (Linnaeus, 1758)	Kudingareng Keke I.	13	10093
<i>L. lessepsiana</i>	<i>Lithophyllon undulatum</i> Rehberg, 1892	Bone Tambung I.	18	78861
<i>L. simplex</i> (?)	<i>Fungia</i> ( <i>Wellsofungia</i> ) <i>granulosa</i> Klunzinger, 1879	Samalona I.	6	10125
<i>L. simplex</i> (?)	<i>Sandalolitha robusta</i> (Quelch, 1886)	Barang Lompo I.	12	10086
<i>L. laevigata</i>	<i>Fungia</i> ( <i>Verrillofungia</i> ) <i>scabra</i> Döderlein, 1901	Panikiang I.	1	10117
<i>L. laevigata</i>	<i>F. (V.) spinifer</i> Claereboudt & Hoeksema, 1987	Badi I.	22	10118
<i>L. lima</i>	<i>Fungia</i> ( <i>Verrillofungia</i> ) <i>scabra</i> Döderlein, 1901	Bone Baku reef	4	10073
<i>L. lima</i>	idem	Samalona I.	6	84614
<i>L. lima</i>	<i>Fungia</i> ( <i>Pleuractis</i> ) <i>moluccensis</i> Van der Horst, 1919	Gusung I.	2	10091
<i>L. lima</i>	idem	Lae-Lae I.	2	84615
<i>L. lima</i>	<i>Lithophyllon undulatum</i> Rehberg, 1892	Barang Caddi I.	11	10074
<i>L. mucronata</i>	<i>Fungia</i> ( <i>Verrillofungia</i> ) <i>scabra</i> Döderlein, 1901	Bone Baku reef	4	78860
<i>L. mucronata</i>	<i>F. (Pleuractis) moluccensis</i> Van der Horst, 1919	Samalona I.	6	10134
<i>L. mucronata</i>	<i>Heliofungia actiniformis</i> Quoy & Gaimard, 1833	Lae-Lae I.	2	10111
<i>L. malaccana</i>	<i>F. (Cycloseris) sinensis</i> Milne Edw. & Haime, 1851	Badi I.	22	10119
<i>L. malaccana</i>	<i>Podabacia crustacea</i> (Pallas, 1766)	Barang Caddi I.	11	10077
<i>L. malaccana</i>	<i>Lithophyllon undulatum</i> Rehberg, 1892	Bone Tambung I.	18	10088
<i>L. sp. indet.</i>	<i>Fungia</i> ( <i>Wellsofungia</i> ) <i>granulosa</i> Klunzinger, 1879	Samalona I.	6	10138

Associations can have a wide geographical range, but some occur in one area and not in another, although potential partners are present or even common in both. E.g., *L. simplex* can be found commonly around Lizard Island, Great Barrier Reef, in several species of *Favia*, but not so in the northern Red Sea. This is difficult to interpret as *Gomastrea* and *Astreopora* serve as hosts in both areas (Kleemann, 1995: table 1), with *Astreopora* being the preferred host of *L. simplex* in the Red Sea (Mokady et al., 1992, Kleemann own observation). On the other hand, Mokady et al. (1994) argue for a very high degree of species specificity between *Lithophaga* and their hosts in the Red Sea, and a paraphyletic status

for *L. simplex* from *Astreopora* and *Goniastrea* respectively, without distinguishing between a male and female tree as appropriate in Mytilidae.

The number and species of hosts for a bivalve species can change within its geographical distribution, in some cases drastically, e.g., *L. lima* (Kleemann, 1995: table 1). Locally, the host spectrum varies greatly also in *Fungiacava* (Hoeksema & Kleemann, 2002.) or in the pectinid *Pedum spondyloideum* (Gmelin, 1791) (Kleemann, 2001).

Another difficulty for the understanding of the observed associations is the fact that overlaps do occur in two ways: (1) by occurrence of more than one *Lithophaga* species in a single host coral, although this is relatively rare, and (2) by a coral species serving as host for different bivalves in distinct geographical areas, as e.g. in *Cyphastrea microphthalma* (Lamarck, 1816) (see Kleemann, 1995: table 1).

*Leiosolenus* Carpenter, 1856, is the oldest of available subgenus names for *Lithophaga* and was given generic rank by some authors (e.g. Nielsen, 1986). Here, *Leiosolenus* is used to distinguish all species with some sort of self-established shell encrustation from those without: *Lithophaga* sensu stricto, showing very fine, radiating striae in the antero-ventral periostracum. Probably, it would be more justified to distinguish *Lithophaga* subgenera according to being a coral associate or a dead substrate borer, instead of minor differences in shell encrustation. The latter allow species specific differentiation as the various patterns prove to be maintained in bivalves of respective species, extracted from different substrates and localities.

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