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Also in: The Nautilus 114(1): 1-13 [2000].

The Nautilus, 114(1) 1-13 (2000)

# *Epitonium* (Gastropoda: Epitoniidae) associated with mushroom corals (Scleractinia: Fungiidae) from Sulawesi, Indonesia, with the description of four new species

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Key words: parasitic snails; coral reefs; coral/mollusc associations; egg-capsules; Indo-Pacific

## Abstract

At least six species of the genus *Epitonium sensu lato* are found associated with mushroom corals (Fungiidae) off Ujung Pandang, Sulawesi, Indonesia. Revised descriptions of *E. costulatum* (Kiener, 1838) and *E. ulu* Pilsbry, 1921 based on type specimens and additional material are given. Four new species are described: *E. hoeksemai*, *E. ingridae*, *E. lochi*, and *E. twilae*. The true identity of *E. bullatum* (Sowerby, 1844), a species not associated with corals and not found in Sulawesi and nearby areas, is clarified. Examination of type specimens made possible the characterization of nominal species that appear to be either identical with or closely related to the fungiid-associated epitoniids found off Sulawesi.

## Contents



## Introduction

Several epitoniid species are known to live in association with sea anemones (phylum Cnidaria, order Actiniaria) (Robertson, 1963; 1983a, b; 1993; Vecchio, 1964; Salo, 1977; Perron, 1978; Kay, 1979; Schimek, 1986; Hartog, 1987; Dushane, 1988a-c; Yamashiro, 1990; Nakayama, 1991; Mienis, 1994). Less commonly, epitoniids are found associated with stony corals (phylum Cnidaria, order Scleractinia), in particular with species of the free-living Fungiidae or mushroom corals (Robertson, 1963, 1970; Bosch, 1965; Hadfield, 1976; Kay, 1979; Bratcher, 1982; Loch, 1982; Sabelli and Taviani, 1984; Bell, 1985; Dushane, 1988a-c; Loo and Chou, 1988; Page and Willan, 1988; Hoeksema, 1988, 1989; Yamashiro, 1990; Mienis, 1994; Oliverio et al., 1997). Only three *Epitonium* species are usually mentioned in the literature in association with fungiids; in one case (Loch, 1982) a fourth species is reported but not named. This paper deals mainly with the taxonomy of the surprisingly high number of species of *Epitonium* found associated with mushroom corals during a survey in a relatively restricted area in Indonesia, off Ujung Pandang (Sulawesi). Four of these species proved to be new to science, although at least one of them had frequently been cited and illustrated under an incorrect name. The shells of these species are very fragile, which might explain why they are mostly poorly represented or not represented at all in most institutional collections. These species are only known from live-collected specimens: it is very unlikely that empty shells will be found washed ashore without being seriously damaged or unrecognizable. A more elaborate analysis of the ecological data collected during the project is being prepared (Gittenberger, A., unpublished data).

The systematic and evolutionary importance of variable characters such as egg-capsules (Figures 36-38), eggs (Figure 41) and mucous threads (Figures

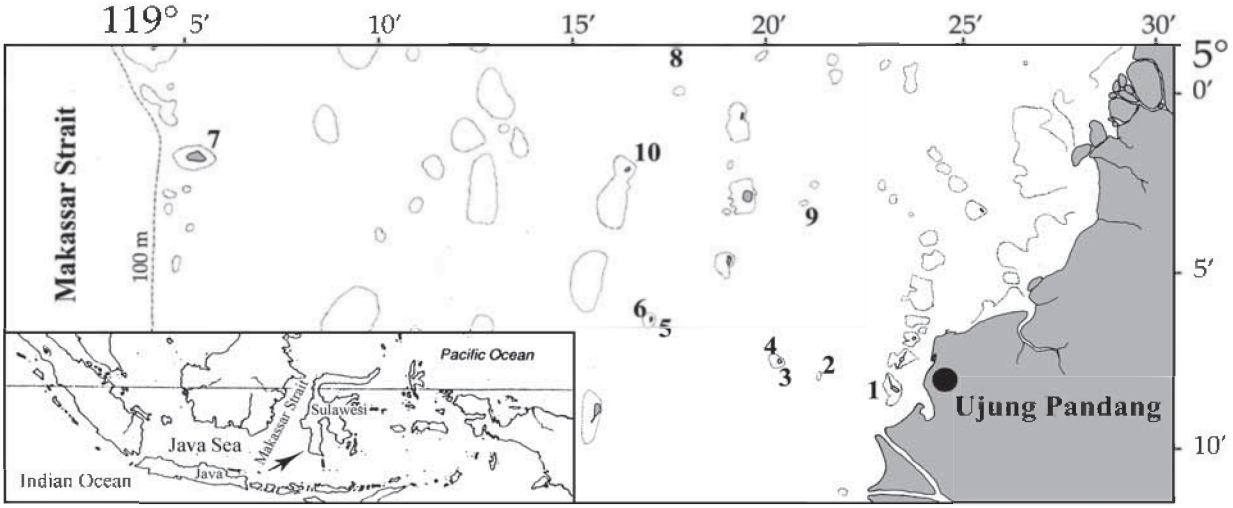



*Figure 1.* Surveyed area off Ujung Pandang, S. Sulawesi, Indonesia. The coral reefs investigated in particular are: 1, W. (Pulau) Lae-Lae; 2, W. Bone Baku; 3, E. (Pulau) Samalona; 4, W. (Pulau) Samalona; 5, E. and ESE (Pulau) Kudingareng Keke; 6, W. (Pulau) Kudingareng Keke; 7, NW Lan[g]kai; 8, Pulau Badi; 9, Bone Lola; 10, (Pulau) Bone Tambung.

43-47), which can be either straight or twisted, is still poorly known. We observed, however, that populations of the different species may differ in these characters. With exception of one article by Oliverio *et al.* (1997), the literature is scanty in respect to these characters. Oliverio et al., while discussing the coral-associated epitoniid *Epitonium billeeanum* Dushane and Bratcher, 1965, figured the egg-capsules, eggs, mucous threads (of the twisted type) and shells of veliger larvae. We did not observe a difference in sculpture or well-defined transition between the protoconch 1, formed by the shell gland of the larva inside the egg-capsule, and protoconch 2, secreted by the velum of the swimming veliger between hatching and settling. The protoconchs (Figures 16, 25-29, 42, 48) turned out to be very uniform among the various species studied here, all of which apparently have planktotrophic development. Sclerites of at least one species of soft coral, probably of the genus *Sinularia* May, 1898 (subclass Octocorallia, order Alcyonacea, family Alcyoniidae) (L. P. van Ofwegen, NNM) were found associated with the egg-capsules of some species (Figures 39-40).

In a monograph on Epitoniidae from southern Africa and Mozambique, Kilburn (1985: 240) stated that "epitoniid taxonomy remains in a chaotic state, particularly above the species level." Kilburn observed that the classification of the genus *Epitonium* is (p. 280) "very tentative and is aimed solely at grouping together similar species for convenience sake." Clench and Turner (1951) and Bouchet and Warén (1986) followed a similar approach in their revision of eastern Atlantic Epitoniidae. Because we could not unequivocally classify all Indonesian species within one or more of the 19 subgenera used by Kilburn (1985) or the 39 subgenera listed by Wenz (1940) under "*Scala*" (= *Epitonium*), we decided to refrain from following any subgeneric classification. The epitoniid species described in this study live associated with mushroom corals and at least some of them are so similar that they seem to be closely related phylogenetically. They point to possible adaptive radiation within a single clade. Adequate phylogenetic analyses including other species of *Epitonium* co-occurring with different hosts in the same general area could help clarify whether these species found in association with fungiid corals form a monophyletic group.

## Material and methods

Samples were collected off the coast of Ujung Pandang, Sulawesi, Indonesia. The fungiid fauna of the area (Figure 1) is relatively well known; see Hoeksema (1989) for details. During the period April-June, 1997, 9 coral reefs were inspected, to a depth of 18 m (rarely 24 m). Approximately $10^4$ mushroom corals,

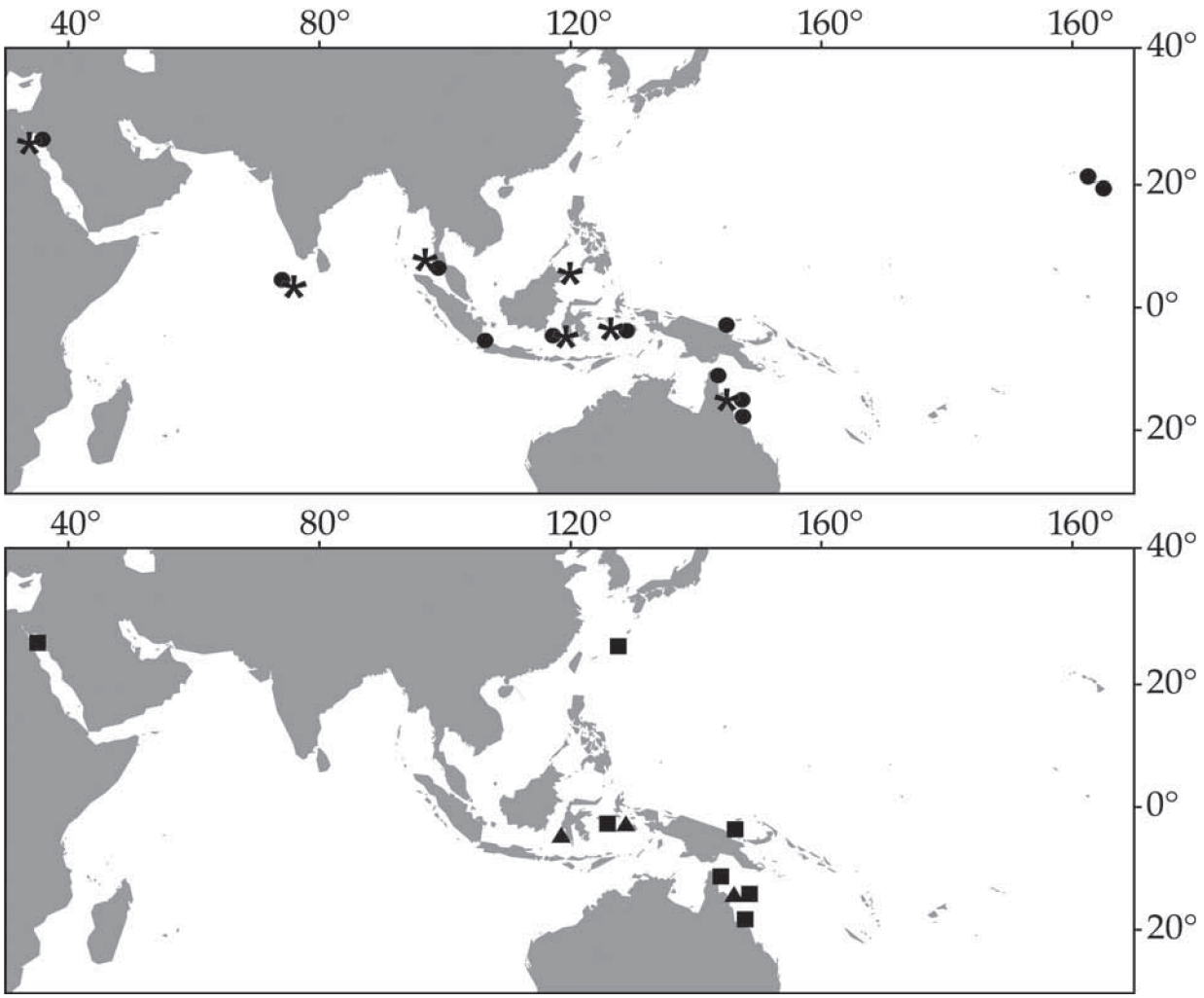
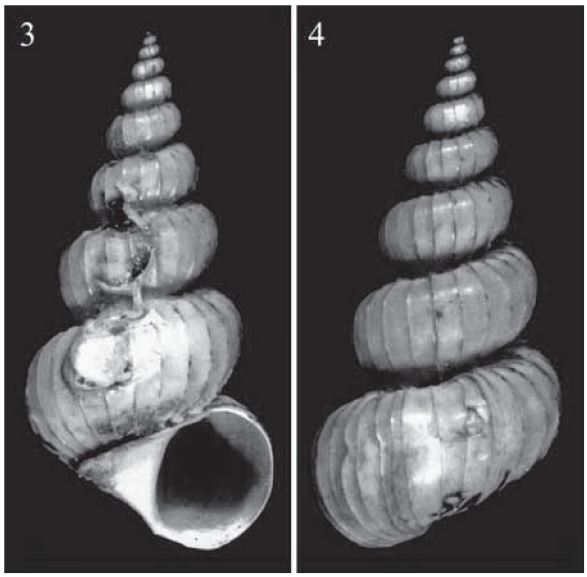



*Figure 2.* Maps of the Indo-Pacific Region, from the Red Sea to the Hawaiian Archipelago, showing records of the *Epitonium* species in this study known from more than two localities: *Epitonium costulatum* (Kiener, 1838) (stars), *E. ingridae* new species (triangles), *E. twilae* new species (squares) and *E. ulu* Pilsbry, 1921 (circles).

belonging to about 30 species of free-living Fungiidae, were searched for epitoniids and their eggs. Beneath these corals, about $10^3$ specimens of *Epitonium*, some of which with egg-capsules, were collected. The identifications of the coral species were made or at least checked by Dr. B. W. Hoeksema. The snails were classified into morphological categories according to characters of shell, egg-capsules, and proboscis. Secondarily, the species thus distinguished were analysed ecologically for preferential depths, hosts, and substrates. The ecological data will be discussed in a future article (Gittenberger & Hoeksema, chapter 9).

The various *Epitonium* species recorded during the survey were identified by review of the literature, consultation with specialists, and by comparison with material deposited in several collections; this includes comparison with type specimens of conchologically similar taxa. These types are mentioned in the systematic treatment of each species.

From the about $10^3$ specimens collected, only shells with more than 4 mm length were measured. The number of specimens (n) measured in the calculation of mean values is mentioned at the beginning of the descriptions. Means are indicated between the extremes (minimum-mean-maximum). To allow for




*Figures 3-4. Epitonium costulatum* (Kiener 1838), holotype (MHNG 1152/16). Shell length 3.3 cm.

better comparisons, shell sculpture is described for both the fifth teleoconch whorl and where the teleoconch is 5 mm in width, a part of the spire that is in part independent of the actual whorl number. The term protoconch refers to the protoconchs 1 + 2. The maximum diameter of protoconch 1 was measured in two shells for each species (except for *E. lochi* because of insufficient material), using SEM photographs of specimens prepared from egg- capsules (Figures 30-31); because very similar values were consistently found, no more measurements were taken. Shells of *Epitonium* species cannot be recognized as fully grown or not. Comparative informal observations indicate that when the snails start laying eggs they have not yet reached maximum size. No minimum values are included in the descriptions but only the largest specimen and the largest number of whorls. After removal from 70% ethanol, egg-capsules without embedded sand quickly collapsed; these could not be photographed. Unless stated otherwise, all descriptions refer to material from off Ujung Pandang.

The following institutional abbreviations are used: AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, The Natural History Museum, London; LACM, Natural History Museum of Los Angeles County, Los Angeles; MHNG, Muséum d'Histoire Naturelle, Genève; MNHN, Muséum national d'Histoire naturelle, Paris; MZB, Museum Zoologicum Bogoriense, Bogor, Indonesia; NNM, National Museum of Natural History, Leiden. Numbers following a slash after collection numbers refer to number of shells in relevant lots.

## Systematics

Family Epitoniidae Berry, 1910
Genus *Epitonium* Röding, 1798

*Epitonium costulatum* (Kiener, 1838)
(Figures 2-6, 22, 25, 38-41, 47)

*Scalaria costulatum* Kiener, 1838: pl. 2, fig. 4; 1838: 5.
*Epitonium costulatum* Robertson, 1963: 57, pl. 5, fig. 4; 1970: 45; Loch, 1982: 4, 1 fig.; Dushane, 1988a: 30, figs. 1, 2.

Description:

Shell (Figures 3-6, 22, 25.) (n = 7): Fragile (large specimens) to very fragile, moderately elongate-conical, creamy white, reaching 32 mm in length, with at least 1 damaged specimen (from Ambon) measuring 41.2 mm. Length/width ratio 1.6-1.9-2.2. Protoconch whorls 3 3/8; maximum protoconch 1 diameter 0.14 mm (n = 2). Protoconch with numerous fine, incised, axial lines. Teleoconch with up to 10 whorls, separated by very deep (fenestrated) suture. Successive whorls are almost detached. Teleoconch with evenly spaced, orthocline, thin costae, damaged in all examined specimens. Over most of their length, the costae appear to be curved abaperturally at the outer margin. Costae adapically relatively high and erect, not coronate, becoming short towards columella. Costae mostly continuous, but touching only slightly those of adjoining whorls. Very weak spiral lines present. Fifth teleoconch whorl (width 4.9 mm) with 16-18.4-26 costae. Five mm width whorl (whorl 4, 5, or 6) with 16-17.4-20 costae. Aperture subcircular. Apertural length/shell length ratio 0.3. Umbilicus moderately wide.

Egg-capsules (Figures 38, 39, 40, 47): Embedded with sand and closely connected along a straight,

longitudinally striated, mucous thread (Figure 47). Capsules asymmetrical, somewhat conical with a circular widest part. Capsules 3.0-3.3-3.5 mm in length and 1.5-1.6-2.0 mm in width (n = 8). One egg-capsule contains 70-175-335 eggs (n = 5).

Proboscis: With some irregularly interrupted, longitudinal, white zones, which are as wide as the transparent interspaces.

Type material (Figures 3-4): Holotype MHNG 1152/16.

Type locality: Unknown.

Other material examined: NNM, Indonesia, Ambon, Hitu, outer part of Ambon Bay, E. and W. sides of Laha, A. Fortuin and J. C. den Hartog leg.; LACM 124505, Thailand, Phuket Island.

Records in the literature: Australia: Queensland, Thetford Reef off Cairns (Loch, 1982: 4). Philippines: Bongao Channel, Sanga Sanga (Robertson, 1963: 57-58, pl. 5, fig. 4). Thailand: Raya Island (Dushane, 1988a: 32). Maldives, Little Hiva (Dushane, 1988a: 32). Red Sea: Straits of Than (Dushane, 1988a: 30-31); Sinai, Thomas Reef, 27°59`N, 34°27`E (Dushane, 1988a: 32).

Distribution (Figure 2): Australia (Queensland), Indonesia (Sulawesi), Philippines, Thailand, and Egypt (Red Sea).

Habitat: Snails were recorded at 6-12 m depth. Coral hosts were *Ctenactis echinata* (Pallas, 1766), and *Herpolitha limax* (Esper, 1797). Groups of one to four snails were found in the sand (sometimes buried) under a single coral with sometimes close to a few hundreds egg-capsules.

Remarks: The data provided by Sherborn and Woodward (1901) are insufficient to indicate the exact year of publication of the new taxa in Kiener`s monograph on the `Genre Scalaire`. We follow Troschel (1839), who listed Kiener`s undated work, with the new species in it, in his `Report on the achievements in zoology during the year 1838. V. Mollusca` [in German]. The names are printed both on the plates and in the main text of Kiener`s work.

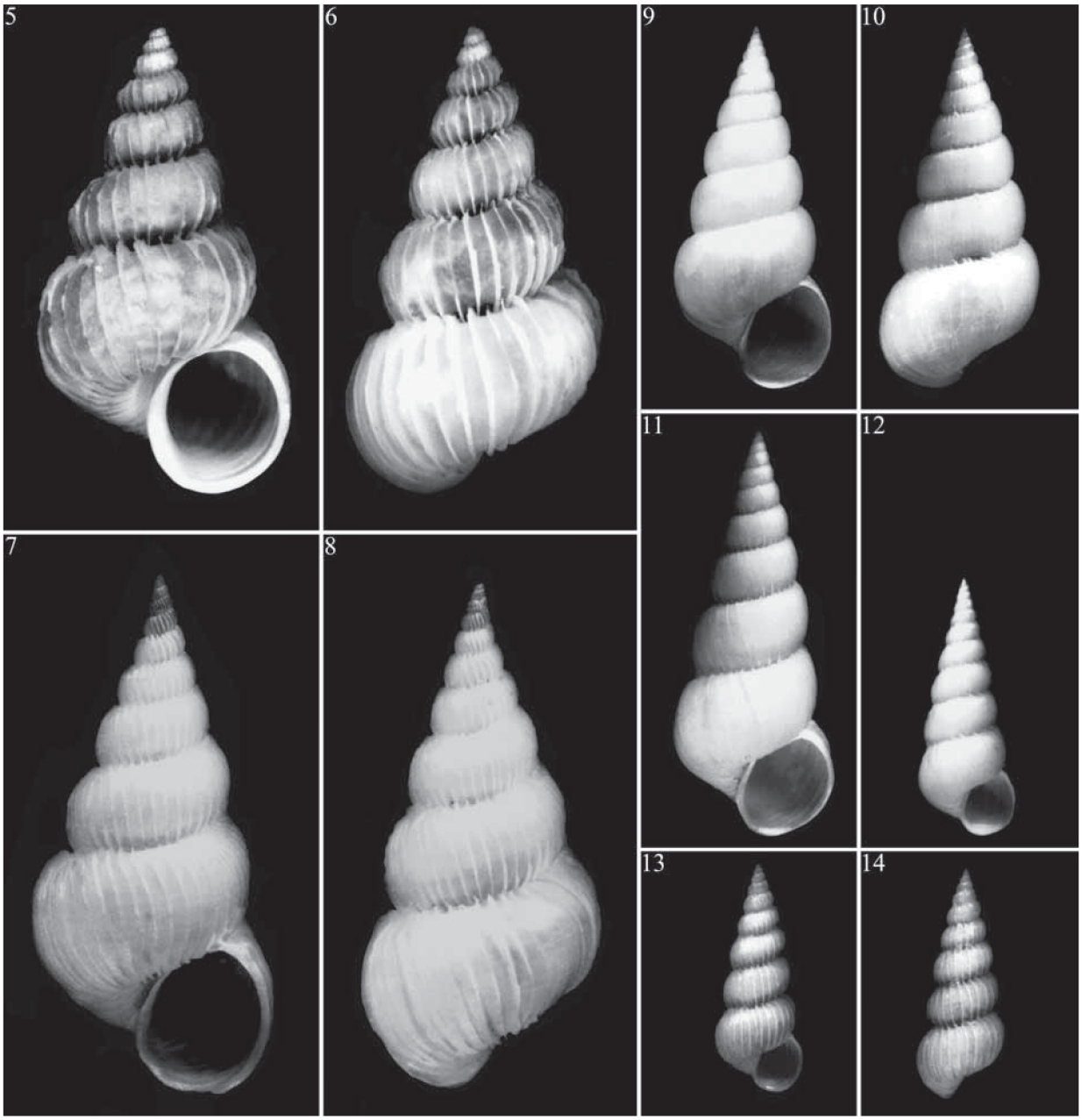
The severely damaged holotype of this species (Figures 3-4) is a relatively elongate shell. Shells of this species are most similar to those of *Epitonium pallasii* (Kiener, 1838), a species originally described from an unknown locality, but now known from the Indo-West Pacific (Kaicher, 1980: 2382; Eisenberg, 1981: pl. 37, fig. 9; Wilson, 1993: 278, pl. 44, fig. 6a-b). According to Kiener (1838) and in agreement with Wilson`s description ("about ten costae on the last whorl") and the figures in the literature, *E. pallasii* differs from *E. costulatum* by the stronger shells with thicker costae, which are more widely spaced. Dushane (1988a: 30, fig. 2) figured very similar egg-capsules of this species, reporting two connecting threads for material from the Red Sea.

*Epitonium hoeksemai* A. Gittenberger and Goud new species
(Figures 9-10, 18, 20, 26, 43)

Description:

Shell (Figures 9-10, 18, 20, 26) (n=9): Very fragile, elongate-conical, creamy white, reaching 19 mm in length. Length/width ratio 1.6-1.9-2.4. Protoconch whorls 3. Maximum protoconch 1 diameter 0.13 mm (n = 2). Protoconch with numerous very fine, incised, axial lines. Teleoconch whorls up to 9 1/8, separated by a moderately deep suture. Teleoconch sculpture (Figures 18, 20) of somewhat unevenly spaced, orthocline, relatively low costae, and low spiral threads that become conspicuously more numerous and variable on the abapical whorls. Costae on entire teleoconch more prominent than spiral sculpture. Third teleoconch whorl has ca. 12 spiral threads, fifth ca. 25. Costae not always continuous, touching the adjoining whorls, where they are curved adaperturally. Fifth teleoconch whorl (width 2.1 mm) with 24-27-29 costae. Five mm width whorl (whorl 8, 9 or 10) with 32-35-38 costae. Aperture subcircular. Apertural length/shell length ratio 0.28-0.29-0.30. Umbilicus very narrow.

Egg-capsules (Figure 43): Sub-spherical, white, transparent, with protuberances but no embedded sand. Capsules closely connected to each other along a twisted mucous thread.




*Figures 5-14.* Species of *Epitonium* associated with mushroom corals off Ujung Pandang. 5-6, *E. costulatum* (Kiener, 1838), length 2.8 cm; 7-8, *E. ingridae* new species, holotype, NNM 59088, length 2.0 cm; 9-10 *E. hoeksemai* new species, holotype, NNM 59074, length 1.3 cm; 11-12. *E. ulu* Pilsbry, 1921, length 1.6 cm and 1.0 cm, respectively; 13-14. *E. lochi* new species, holotype, NNM 59094, length 0.9 cm.

Habitat: This species was recorded at 5-15 m depth. Coral hosts were *Heliofungia actiniformis* (Quoy and Gaimard, 1833) and *Fungia fungites* (Linnaeus, 1758). One to 5 specimens were found attached by mucous threads to the underside of a coral near a few hundreds egg-capsules.

Type material: Holotype NNM 59074, from type locality. Paratypes: NNM 59081/1, Indonesia, Sulawesi, off Ujung Pandang, W. Lae-Lae, 9

m; NNM 59079/1, MZB/1, W. Bone Baku, 6 m; NNM 59080/1, 59082/1, 9 m; NNM 59086/2, type locality; NNM 59076/1, 6 m; NNM 59077/5, 12 m; NNM 59083/1, E. Kudingareng Keke, 3 m; W. Kudingareng Keke, 12 m; NNM 59075/1, 14 m; NNM 59084/1, NW Lankai, 6 m; NNM 59087/2, Bone Lola, 15 m; NNM 59085/1, Bone Tambung, 6 m.

Type locality: Indonesia, Sulawesi, off Ujung Pandang, W. Samalona, 5 m depth.

Distribution: Only known from Indonesia, off Sulawesi

Etymology: This species is named after Dr. B. W. Hoeksema, who supervised the field portion of this project.

Remarks: Shells of this species resemble those of *Epitonium ulu*, but differ by a length/width ratio of ca. 1.9 instead of ca. 2.6. Because most examined specimens are damaged, the fine structure of the costae could not be observed. The teleoconch sculpture appears always obsolete to the naked eye. The number of spiral threads increases more conspicuously in *E. hoeksemai*, with ca. 13 spiral threads added between the third and the fifth whorl. In *E. lochi* new species (see below), on the other hand, there is a more clearly reticulate sculpture on the early teleoconch whorls.

*Epitonium ingridae* A. Gittenberger and Goud new species
(Figures 2, 7-8 23-24, 27, 30, 36, 46)

Description:

Shell (Figures 7-8, 23-24, 27, 30) (n = 5): Very fragile, moderately slender conical, creamy white; reaching 20.8 mm in length. Length/width ratio 2.0-2.2-2.3. Protoconch whorls ca. 3. Protoconch with three whorls; with numerous fine, incised, axial lines. Maximum diameter of protoconch 1, 0.14-0.15 mm (n = 2) (Figure 30). Teleoconch whorls up to 10, separated by deep suture. Teleoconch sculpture of evenly spaced, orthocline, thin, lamellate costae, and numerous very fine spiral threads (>100 on the 9th whorl), superimposed on somewhat coarser spiral cordlets (ca. 15 on fifth teleoconch whorl). Initial whorls with multiple, lamellate costae, fused together to form thicker ones (Figures 23, 24). Coarser spiral cordlets are most prominent on initial teleoconch whorls, where they are superimposed on costae (Figure 24); coarser cordlets become obsolete on most abapical whorls. Costae are more or less damaged in all specimens; better preserved costae coronate. Particularly below the periphery, costae somewhat curved abaperturally at their free margins, whereas adapically more erect and slightly curved abaperturally or adaperturally near suture, depending on position of costa on adjoining whorl. Costae mostly continuous, but hardly touching each other. Fifth teleoconch whorl (width 3.8 mm) with 20-24-31 costae. Five mm width whorl (whorl 6 or 7) with 23-30-33 costae. Aperture subcircular. Apertural length/shell length ratio 0.3. Umbilicus very narrow.

Egg capules (Figures 36, 46) (n = 8): Oval (Figure 36), embedded with sand and closely connected along straight, longitudinally striated, mucous thread (Figure 46). Capsules 3.0-3.3-3.5 mm in length and 1.5-1.6-2.0 mm in width. Capsules contain 93-120-173 white eggs.

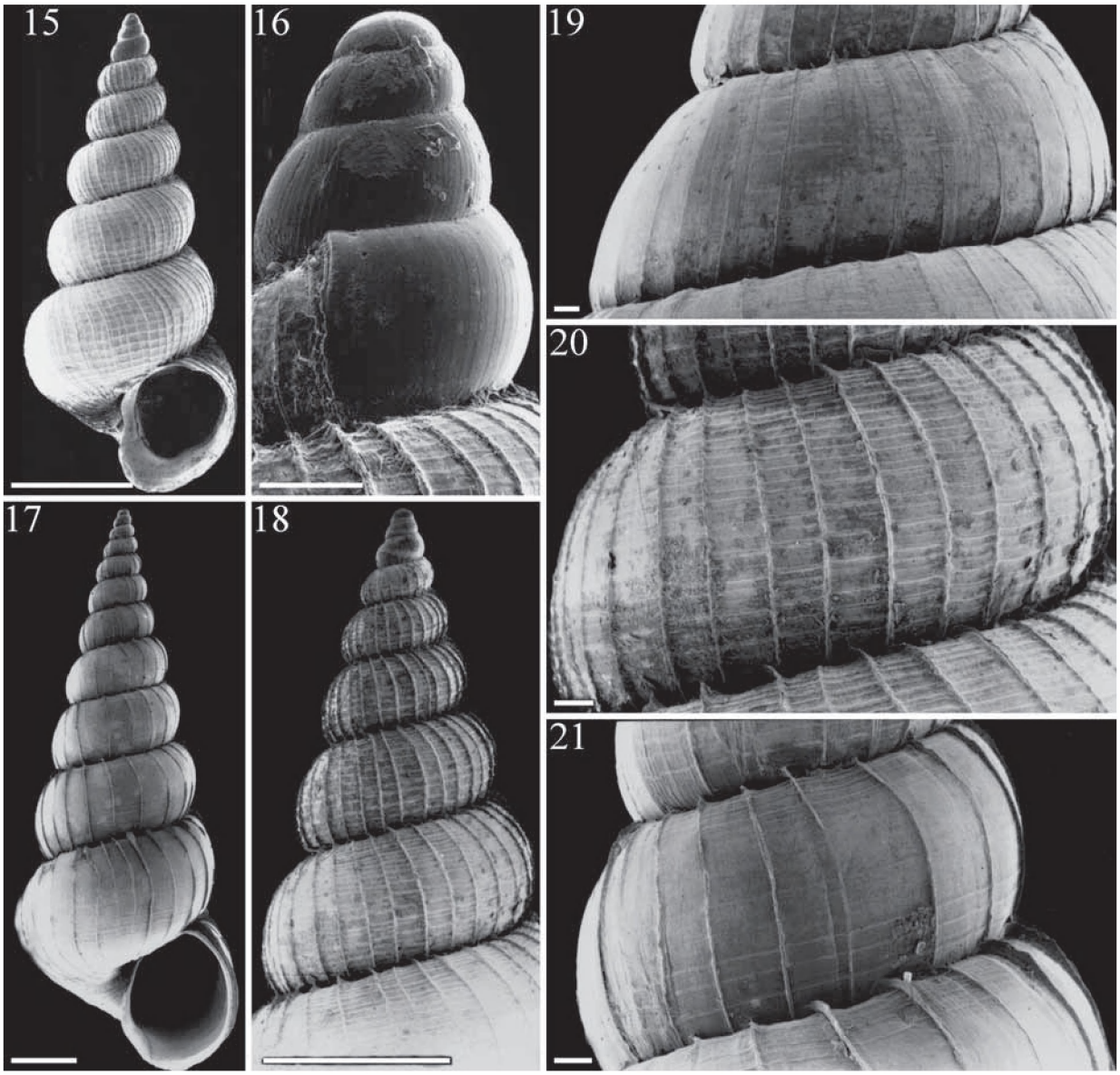
Proboscis: Whitish.

Type material: Holotype NNM 59088, from type locality. Paratypes: NNM 59089/1, Indonesia, Sulawesi, off Ujung Pandang, W. Kudingareng Keke, 12 m; NNM 59090/2, 59092/1, E. Samalona, 9 m; NNM 59091/1, 24 m; NNM 59093/1, Bone Tambung, 7 m.

Type locality: Indonesia, Sulawesi, off Ujung Pandang, ESE. Kudingareng Keke, 15 m.

Other material examined: AMS 329657, Australia, Queensland, off Macgillivray Bay, Lizard island, 14°39`S, 145°29`E, 10 m, I. Loch leg.; NNM unnumbered, 1 shell, Indonesia, Ambon, Hitu, outer part of Ambon Bay, eastern Laha, J. C. den Hartog leg.

Distribution (Figure 2): Australia, Queensland; Indonesia, Ambon, and Sulawesi.




*Figures 15-21.* SEM micrographs of species of *Epitonium* associated with mushroom corals off Ujung Pandang. 15-16, *E. lochi* new species; 15, Shell. Scale line = 1 mm. 16, Protoconch. Scale line = 0.1 mm. 17, *E. ulu* Pilsbry, 1921, shell. Scale line = 1 mm. 18, *E. hoeksemai* new species, apical whorls. Scale line = 1 mm. 19, *E. twilae* new species, teleoconch whorl sculpture. Scale line = 0.1 mm. 20, *E. hoeksemai* new species, teleoconch sculpture. Scale line = 0.1 mm. 21, *E. ulu* Pilsbry, 1921, teleoconch whorl sculpture. Scale line = 0.1 mm.

Habitat: Specimens of this species were found at 7-24 m depth. Coral hosts were *Fungia concinna* Verrill, 1864, *F. fungites*, *Heliofungia actiniformis*, *Herpolitha limax* and *Polyphyllia talpina* (Lamarck, 1801). Specimens were found attached by mucous threads to the underside of a coral: one or two specimens were found associated with up to a few hundreds egg-capsules.

Etymology: This species is named after Ms. Ingrid van der Loo, Leiden.

Remarks: Conchologically this species resembles the 'probable holotype' (Kaicher, 1951: 3036) of *Epitonium dubium* Sowerby, 1844 (BMNH 1981234) from the Philippines, which is an imperfect shell with a broken aperture and several

apical whorls missing. Its length could have been ca. 20 mm. Costae of adjacent whorls are continuous, slightly curved toward aperture adapically and away from aperture abapically, not projecting over suture. The holotype of *Epitonium dubium* most clearly differs from *E. ingridae* by its less prominent teleoconch sculpture and thicker, not lamellate costae. The specimen figured by De Boury (1912: pl. 7, fig. 4, *Scala dubia*), which might represent *E. dubium* (*cf.* Kilburn, 1985: 327) has more oblique costae. The identity of *Scalaria grayi* Nyst, 1871, (*nomen novum* for *Scalaria striata* Gray, 1847, not Defrance, 1827) is unclear; Tryon (1887: 60, as *S. striata*) and De Boury (1912: 95, as *S. striata* and *S. grayi*) considered this nominal taxon a synonym of *S. dubia.* Kilburn (1985: 327) questioned this synonymy. The shell of *S. grayi* figured by Tryon (1887: pl. 12, fig. 68, as *S. striata*) has a more shallow suture and relatively larger aperture when compared to *E. ingridae*. The new species also resembles *Epitonium friabilis* (Sowerby, 1844) from Western Australia, Swan River. The hototype (BMNH 1966653), figured by Kaicher (1980: 2329), is 16 mm in length and 7 mm in width, with ten whorls. It differs most conspicuously from *E. ingridae* by its closed umbilicus and absence of spiral threads. The species described and illustrated from Sydney Harbour as *Foliaceiscala barissa* by Iredale (1936: 300, pl. 22, fig. 15) seems to be similar in shape and size, but the costae are described as "of different strength, some fine, others large and recurved, while still others approach varices in size."

*Epitonium lochi* A. Gittenberger and Goud new species
(Figures 13-16, 37, 45)
?*Epitonium* species 4: Loch, 1982: 4-5. 1 fig. (see remarks below).

Description:

Shell (Figures 13-16) (n = 4): Very fragile, elongate-conical, creamy white, reaching 8.5 mm in length. Length/width ratio 2.0.-2.3-2.7. Protoconch whorls 3 1/4. Maximum diameter of protoconch 1, 0.12 mm (n = 1). Protoconch with numerous fine, incised, axial lines. Teleoconch whorls up to 8, separated by a very deep suture. Teleoconch with evenly spaced, orthocline, lamellate costae, crossing low spiral threads that are approximately a half to a fifth as wide as the interspaces (Figure 15). Reticulate pattern present on most adapical whorls, replaced by spiral threads on later whorls. Third whorl with ca. 13 spiral threads, fifth one with ca. 15; spiral threads equally prominent throughout whorl. Costae usually not continuous, lamellar but rather low, barely touching preceding whorl. Due to damage in most specimens, fine structure of costae could not be examined. Fifth teleoconch whorl (width 1.3 mm) with 24-25-26 costae and 12-13-15 spiral threads. Aperture subcircular. Apertural length/shell length ratio 0.22-0.23. Umbilicus absent.

Egg-capsules (Figures 37, 45): The roundish, white, egg-capsules (Figure 37) are mixed with sand, and closely connected to each other along a straight mucous thread without well-defined sculpture (Figure 45).

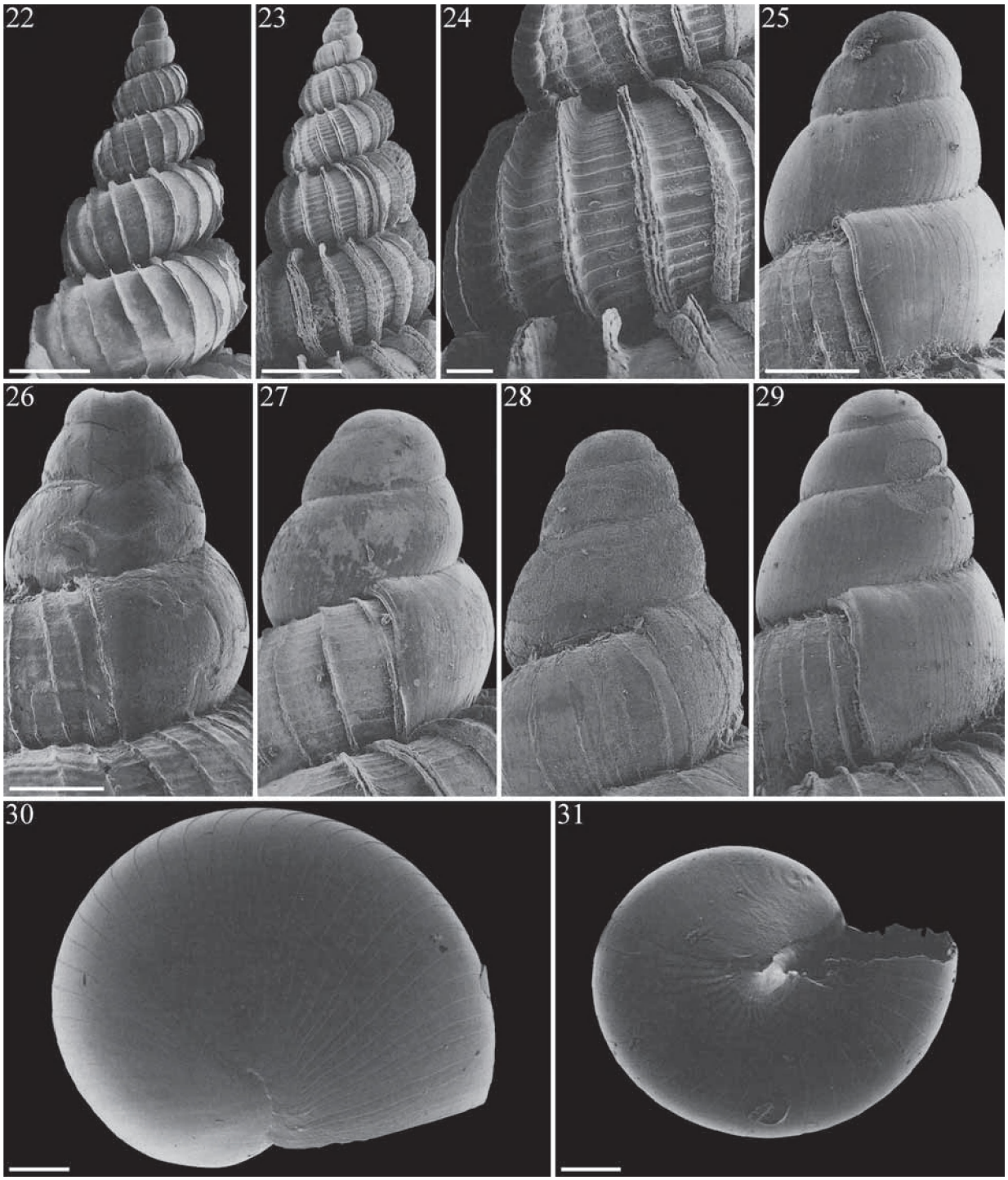
Type material: Holotype NNM 59094, from type locality. Paratypes: NNM 59095/2, 59096/1, Indonesia, Sulawesi, off Ujung Pandang, MZB/1, type locality; 16 m; NNM 59098/1, 18 m; NNM 59099/1, E. Kudingareng Keke, 3 m; 59100/1, 12 m; 59102/1, 18 m; NNM 59101/2, ESE Kudingareng Keke, 15 m; 59103/1, Pulau Badi, 24 m. See also Remarks.

Type locality: Indonesia, Sulawesi, off Ujung Pandang, W. Kudingareng Keke, 12 m.

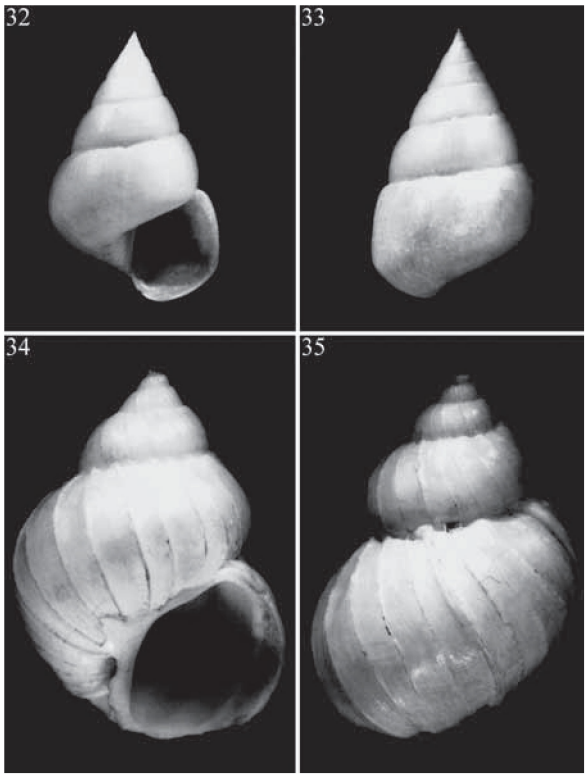
Other material examined: AMS 329687/2, Australia, Queensland, Lizard Island, Watsons Bay, 14°40'S, 145°27'E, 24 m, I. Loch leg.; AMS 329688/1, 329689/1, Granite Bluff, 14°39'S, 145°27'E, 23 m, I. Loch leg. (see Remarks below).

Distribution: Indonesia and probably Australia.

Habitat: The snails were found at 3-24 m depth. *Fungia costulata* Ortmann, 1889, and *F. tenuis* Dana, 1846, were coral hosts. If the Australian record really proves to refer to this species, *Fungia cyclolites* Lamarck, 1816, should be included as an additional host (Loch, 1982: 4). One to 4 specimens were found attached by a straight mucous thread (Figure 45) to the underside of a coral accompanied by up to a few hundreds egg-capsules.




*Figures 22-31.* SEM micrographs of species of *Epitonium* associated with mushroom corals off Ujung Pandang (unless stated otherwise). 22, *E. costulatum* (Kiener, 1838), Indonesia, Ambon, Hitu, outer parts of Ambon Bay, W. Laha, apical whorls. Scale line = 0.5 mm; 23-24, *E. ingridae* new species. 23, Apical whorls. Scale line = 0.5 mm. 24, Teleoconch whorl sculpture. Scale line = 0.1 mm. 25-29, Protoconch; 25, *E. costulatum* (Kiener, 1838) (same shell as figure 22). Scale line = 0.1 mm; 26, *E. hoeksemai* new species; 27, *E. ingridae* new species. 28, *E. twilae* new species. 29, *E. ulu* Pilsbry, 1921. Scale line = 0.1 mm. 30-31, Protoconch 1; 30, *E. ingridae* new species. 31, *E. twilae* new species. Scale line = 0.02 mm.




*Figures 32-35.* Species of *Epitonium* often confused in the literature. 32-33, *E. twilae* new species, holotype, NNM 59104, length 1.5 cm. 34-35, *E. bullatum* (Sowerby, 1844), holotype, BMNH 198136, length 2.0 cm.

Etymology: This species is named after Mr. Ian Loch, who described this or a very similar species from Australia, without naming it.

Remarks: Loch (1982) referred to and figured an unnamed 'species 4' from Australia, distinguishing it from *E. ulu*. We were able to compare that material with the specimens collected off Ujung Pandang. In the Australian specimens, the spiral threads are somewhat more prominent, which could represent some degree of intraspecific variation. The limited amount of material does not allow for conclusions on the identity of the Australian specimens; this prevented their inclusion as paratypes.

Conchologically this species is most similar to *Epitonium zatrephes* Melvill, 1910 (holotype BMNH 191281683), from the Mekran coast. This shell is figured by Kaicher (1980: 2377); it differs by having continuous costae and by the more narrowly spaced spiral threads, which are about as wide as their interspaces.

The holotype of *Epitonium obliqua* (Sowerby, 1844) [*Scalaria*] (BMNH 1981231) also resembles *E. lochi*, but differs in having a clearly open, though narrow, umbilicus, and continuous costae.

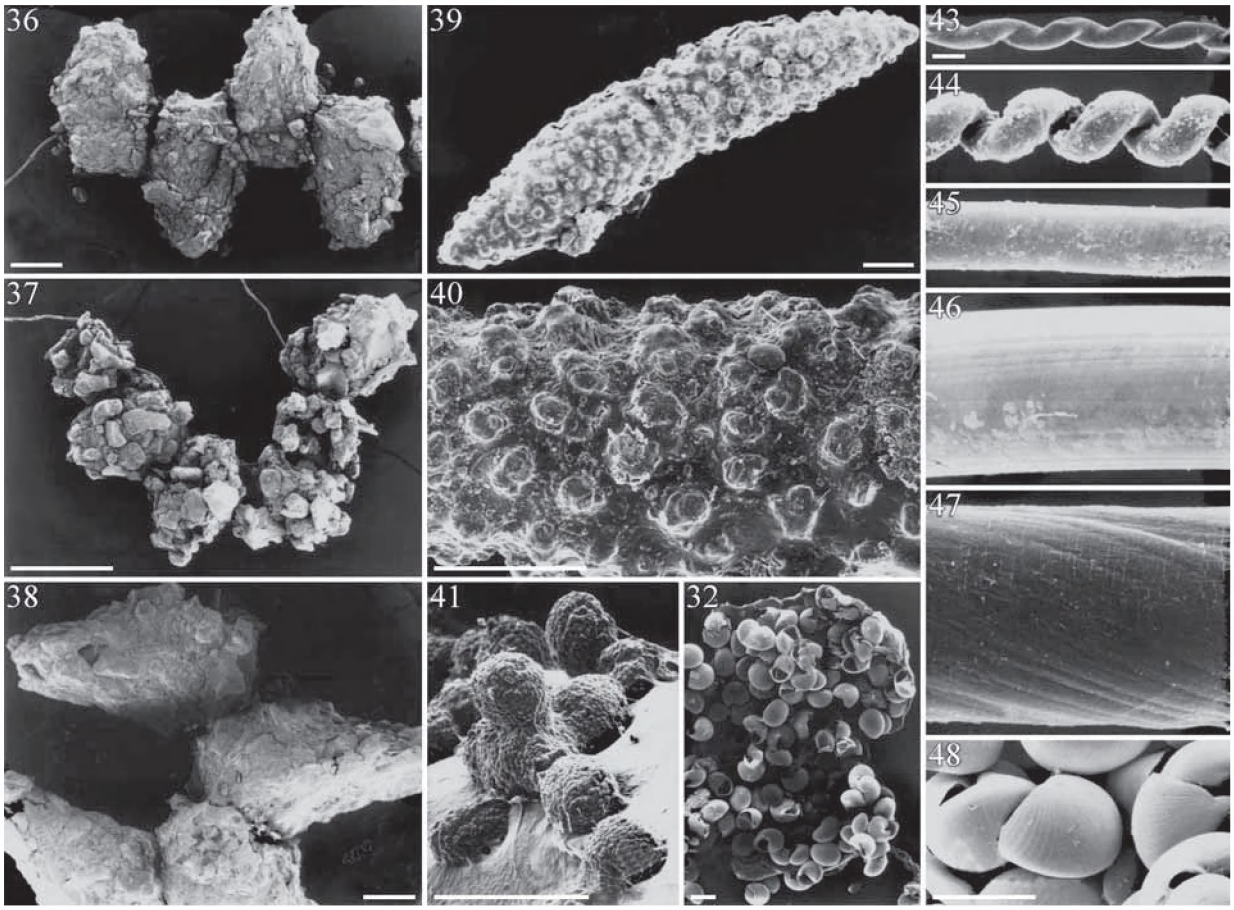
The holotype of *Epitonium deflersi* (Jousseaume, 1911) [*Tenuiscala*] (MNHN De Boury-2706) from Aden, which has a broken aperture and missing apical whorls, can notwithstanding be distinguished from *E. lochi* by the relatively small shell length/width ratio (only ca. 1.9) and the presence of some varices. This holotype is also figured by Kaicher (1981: 3116).

*Epitonium twilae* A. Gittenberger and Goud new species
(Figures 2, 19, 28, 32-33, 48)

*Epitonium bullatum* (Sowerby, 1844): Dushane. 1988: 30, figs. 5, 6. Yamashiro, 1990: 299 figs. 1-6. Not *Scalaria bullatum* Sowerby, 1844.
*Epitonium* species 2: Loch. 1982: 3-4, 1 fig.
*Epitonium* sp.: Bratcher, 1982: 3, fig. 1.

Description:

Shell (Figures 19, 28, 31, 32-33, 48) (n = 20): Very fragile, broad-conical, creamy white, reaching 17 mm in length. Length/width ratio 1.2-1.4-1.6. Protoconch whorls 3. Protoconch with numerous very fine, incised, axial lines. Maximum protoconch 1 diameter 0.12-0.13 mm (n = 2). Teleoconch whorls up to 9, straight-sided, separated by a shallow suture. Teleoconch sculpture (Figure 19) of unevenly spaced, fine, orthocline, more or less obsolete costae, not or only in part lamellate, and numerous low spiral threads that are separated by interspaces that vary from as wide as the spiral threads to three times as wide. Costae not continuous, not curved, barely touching adjacent whorls. Fifth teleoconch whorl (width = 2.5 mm) with 19-24.4-30 costae. Five mm width whorl (whorl 6 or 7) with 24-31-36 costae. Aperture subcircular. Apertural length/shell length ratio 0.37-0.44-0.52. Umbilicus very narrow.




*Figures 36-48.* Species of *Epitonium* associated with mushroom corals off Ujung Pandang. 36-38, Egg-capsules. 36, *E. ingridae*. Scale line = 1 mm. 37, *E. lochi* new species. Scale line = 1 mm. 38, *E. costulatum* (Kiener, 1838). Scale line 1 mm. 39, Sclerite of alcyoniid octocoral found in association with egg-capsules of *E. costulatum*. Scale line = 0.1 mm; 40, Detail of figure 39. Scale line = 0.1 mm. 41, *E. costulatum*, eggs within a capsule. 42, *E. ulu*, egg-capsule with protoconchs 1. Scale line = 0.1 mm. 43-47, Mucous threads. Scale line, with figure 43, = 0.01 mm. 43, *E. hoeksemai*. 44, *E. ulu*. 45, *E. lochi*. 46, *E. ingidae*. 47, *E. costulatum*. 48, *E. twilae*, larval shells (= protoconchs 1). Scale line = 0.1 mm.

Egg-capsules (n = 10): Egg-capsules roundish, white, transparent, with protuberances, without embedded sand, closely connected along straight mucous thread. Egg-capsules 1.2-1.4-1.6 mm diameter, with 342-425-532 white eggs per capsule.

Type material: Holotype NNM 59104, from type locality. Paratypes: NNM 59149/1, Indonesia, Sulawesi, off Ujung Pandang: W. Lae-Lae, 7 m; NNM 59148/2, 9 m; NNM 59145/1, type locality, 3 m; NNM 59105/1, 59138/3, 6 m; NNM 59127/1, 59129/1, 59141/10, 59147/1, 59150/2, 9 m; NNM 59126/1, 59142/1, 59143/1, 12 m; MNM 59146, 15 m; NNM 59139, ESE Samalona, 5 m; NNM 59131/4, 12 m; NNM 59140/5, 13 m; NNM 59116/1, 59117/1, 59132/3, 59133/2, 59134/1, 59135/1, W. Samalona, 9 m; NNM 59121/1, 59122/1, 12 m; NNM 59118/1, 15 m; NNM 59151/1, E. Kudingareng Keke, 9 m; NNM 59106/1, 59107/1, W. Kudingareng Keke, 9 m; NNM 59115/3, 10 m; NNM 59113/1, 59114/1, 12 m; NNM 59108/1, 59109/1, 59110/1, 59111/2, 59112/1, 15 m; NNM 59123/1, 59124/1, 18 m; NNM 59152/1, 59153/1, 24 m; NNM 59137/1, NW Lankai, 12 m; NNM 59159/5, Pulau Badi, 25 m; NNM 59161/2, Bone Lola, 8 m; NNM 59160/1, 9 m; NNM 59154/2, 59155/2, 59156/2, 59163/1, Bone Tambung, 5 m;

NNM 59157/1, 22 m. Only the specimens from off Ujung Pandang are considered the type series (see Distribution below).

Type locality: Indonesia, Sulawesi, off Ujung Pandang, W. Bone Baku, 6 m.

Other material examined: AMS 329653/1, Australia, Queensland (see also Loch, 1982: 3, 4, 1 fig.): No. 5 Sandbank Reef, 13°45'S, 144°16'E, 9 m, I. Loch leg.; AMS 099803/2, 0998041, 099805/1, 098806/1, 100188/14, 329680/1, 329683/2, off Lizard Island, 14°39'-14°42'S, 145°23'-145°28'E, 2-11 m, P. H. Colman, I. Loch and W. F. Ponder leg.; AMS 329672/1, Opal Reef, N. of Cairns, 16°15'S, 145°50'E, 9 m, I. Loch leg.; AMS 096575/2, 101238/2, 147334/2, 329676/4, 329679/3, 329670/1, E-NE of Townsvile, 18°46'-18°57'S, 147°31'-147°44'E, 9-18 m, I. Loch leg. NNM unnumbered, Indonesia, Ambon, Hitu, outer part of Ambon Bay, W. Laha, J. C. den Hartog leg.; NNM unnumbered, Sulawesi, off Ujung Pandang.

Records in the literature: Papua New Guinea, Nagada (16 km N. of Madang) (Bratcher, 1982: 3, 1 fig.). Japan, Sesoko Island, Okinawa (Yamashiro, 1990: 299-305, figs. 1-6). Egypt, Red Sea, Sinai, Thomas Reef, 27°59'N, 34°27'E (Dushane, 1988a: 31, figs. 5, 6).

Distribution (Figure 2): Australia (Queensland), Papua New Guinea, Indonesia, Japan, and Egypt (Red Sea).

Habitat: This species was found from 3 m to the maximum diving depth of 24 m. In the literature that might refer to this species a depth of 45 m was mentioned (Loch, 1982). The following coral host species were recorded: *Ctenactis echinata, Herpolitha limax, Sandalolitha dentata* Quelch, 1884, *S. robusta* (Quelch, 1886) and *Zoopilus echinatus* Dana, 1846. Clung with mucous threads to the underside of a coral, one to fourteen specimens were found accompanied by up to a few hundreds of egg-capsules.

Etymology: This species is named after Mrs. Twila Bratcher, of Los Angeles, California, USA, who first differentiated the new taxon from *E. bullatum*.

Remarks: This species has been misidentified by various authors (Dushane, 1988a; Yamashiro, 1990; Mienis, 1994, conditionally) as *Epitonium bullatum* (Sowerby, 1844), a species associated with sea anemones (Kilburn and Rippey, 1982; Kilburn, 1985; Mienis, 1994). The badly damaged holotype of *E. bullatum* (Figures 34, 35) has a more globular, far less fragile shell with convex whorls, costae occasionally forming a varix, and only about 5 teleoconch whorls at a length of 19 mm (several apical whorls are missing). The specimens illustrated by Jousseaume (1921: pl. 3, fig. 2), Azuma (1962: fig. 2, as *Globiscala kashiwajimensis*), Kilburn and Rippey (1982: pl. 11, fig. 15), Kilburn (1985: 330, figures 160-163) and Wilson (1993: p1. 44, fig. 9) exemplify the variability of *E. bullatum*. Although *E. twilae* differs conspicuously in shape from the other *Epitonium* species in this study, its protoconch (Figures 28, 31, 48) cannot be distinguished from that of these other species.
Yamashiro (1990) published various data on the life history of *E. twilae* (as *E. bullatum*). That author described the egg-capsules as elliptical, 0.88 mm in length and 0.75 mm in width, containing 38-98 eggs each. These data differ from our results. Based on very similar shell morphologies, however, we consider his specimens and the ones examined in this section to be conspecific.
Despite the fact that *E. twilae* differs markedly in shell morphology from *E. ulu*, the protoconchs of these species are very similar.

*Epitonium ulu* Pilsbry, 1921
(Figures 2, 11-12, 17, 21, 29, 44)

*Epitonium ulu* Pilsbry, 1921: 376, fig. 11c; Bosch, 1965: 267, fig. 1; Robertson, 1970: 45; Hadfield, 1976: 135, Table 1; Taylor, 1977: 253, 258, fig. 7; Kay, 1979: 156, fig. 53a, b; Loch, 1982: 3, 1 fig.; Bell, 1985: 159, figs. 1-6; Dushane, 1988a: 31, figs. 3, 4; 1988c: 9, 1 fig.; Wilson, 1993: 273.

Description:

Shell (Figures 11-12, 17, 21, 29) (n = 20): Very fragile, elongate-conical, creamy white; reaching 16 mm in length. Length/width ratio 2.3-2.6-3.6. Protoconch whorls 3. Maximum protoconch 1 diameter 0.13 mm (n = 2). Protoconch with

numerous, very fine, incised, axial lines. Teleoconch whorls up to 12, separated by moderately deep suture. Teleoconch sculpture varying in intensity from well-defined to obsolete. Costae unevenly spaced, orthocline, more or less lamellate or obsolete, not continuous, relatively prominent adapically and clearly encroaching on adjacent whorl, curved in adapertural direction (Figure 21). Spiral threads vary in strength on a single whorl; spiral threads only slightly increasing in number on later whorls. Fifth teleoconch whorl (width 2.0 mm) with 15-23-28 costae and 9-11-15 spiral threads. Five mm width whorl (between whorl 8 and 11) with 19-28-33 costae and 10-14-25 spiral threads. Aperture circular to somewhat oval. Apertural length/shell length ratio 0.20-0.26-0.29. Umbilicus very narrow to closed.

Egg-capsules (Figure 44): Egg-capsules roundish to oval, white, granulated, sometimes embedded with sand. Egg-capsules closely connected along a twisted mucous thread (Figure 44); Dushane (1988a: 32) reported 3 twisted threads. Capsule diameter 0.8-1.3-1.7 mm (n = 5). One capsule contains 67-225-405 eggs. Dushane (1988a: 32) reported 400-600 eggs within a capsule, which she described as papillose, with softly rounded papillae. Kay (1979: fig. 53B) figures the egg-capsules as elliptical, 1.1 mm in width and ca. 1.6 mm in length. See Bell (1982; 1985) and Dushane (1988a) for further data on egg-capsules, life history, and other relevant aspects.

Proboscis: Whitish, with some transversal, transparent bands.

Type material: Holotype ANSP 127818, from type locality.

Type locality: USA, Hawaii, Hilo.

Other material examined: ANSP 127818, USA, Hawaii, Big Island, Hilo; AMS 138321/1, Australia, Queensland (see also Loch, 1982: 3, 1 fig.), Eel Reef, 12°24`S, 143°22`E, 4-8 m, I. Loch leg.; AMS 329660/1, Long Sandy Reef, 12°29`S, 143°46`E, 10 m, I. Loch, leg.; AMS 099801/3, 099802/2, 100821/1, 329656/3, near Lizard Island, 14°40`-14°42`S, 145°23`-145°28`E, 1.5-14 m, P. H. Colman and I. Loch leg.; AMS 138320/1, S. Escape Reef, 15°53`S, 145°49`E, 18 m, I. Loch, leg.; AMS 096573/7, 329649/2, 329650/1, 329651/1, 329652/1, 329655/2, 329658/7, E-NE of Townsville, 18°46`-18°57`S, 147°31`-147°44`E, 6-15 m, I. Loch leg.; NNM unnumbered, Indonesia: Ambon, Hitu, outer part of Ambon Bay, E. and W. Laha, A. Fortuin and J. C. den Hartog leg.; LACM 86-163, Java, off Jakarta, Kepulauan Seribu (= Thousand Islands), Pulau Pelangi and Pulau Putri; AMS 138318/1, Malaysia: Pulau Singa Besar, Pulau Langkawi, 6°14`S, 99°44`E, 1 m, I. Loch, leg.

Records in the literature: USA, Hawaii, Oahu, Kaneoke Bay (Bell, 1985: 159-164, figs. 1-6); Papua New Guinea (Dushane, 1988a: 32); Maldives (Dushane, 1988a: 32); Egypt (Red Sea), Straits of Tiran, Tiran Island and Sinafir Island (Dushane, 1988a: 31, 32, figs. 3, 4); Sinai, Thomas Reef, 27°59`N, 34°27`E (Dushane, 1988a: 31, figs. 5, 6).

Distribution (Figure 2): Hawaii, Australia (Queensland), Indonesia, Malaysia, Maldives, and Egypt (Red Sea).

Habitat: This species was recorded at 3-24 m depth. Coral hosts were *Fungia spinifer* Claereboudt and Hoeksema, 1987, *F. scabra* Döderlein, 1901, *F. concinna*, *F. horrida* Dana, 1846, *F. scruposa* Klunzinger, 1879, *F. fungites*, *F. granulosa* Klunzinger, 1879, *F. scutaria* Lamarck, 1801, *F. moluccensis* Van der Horst, 1919, *F. gravis* Nemenzo, 1955, and *F. paumotensis* Stutchbury, 1833. One to 11 specimens, free or accompanied by up to a few hundreds of egg-capsules, were observed on the individual corals, attached with mucous threads to the underside or on the substrate of these hosts.

Remarks: Shells of this species vary considerably in length/width ratio, intensity of teleoconch sculpture and number of costae. They differ from *E. hoeksemai* by a length/width ratio of ca. 2.6 instead of ca. 1.9 and by the presence of less than 20 spiral threads on the fifth teleoconch whorl. It is the most common epitoniid species associated with Fungiidae in the study area.

## Acknowledgements

We are particularly grateful to Dr. B. W. Hoeksema for his most valuable assistance in collecting and identifying the fungiid corals examined in this article and for contributing his expertise on corals. We thank all who allowed us to examine material in the molluscan collections under their care: Dr. P. Bouchet (MNHN), Mr. I. Loch (AMS), Dr. Y. Finet (MHNG), Dr. J. H. McLean (LACM), Dr. C. Rosenberg (ANSP), and Mrs. K. Way (BMNH). We also thank Mr. A. Weil and Mrs. L. Brown, who contributed expertise on epitoniids, and Dr. L. P. van Ofwegen (NNM), who identified the sclerites associated with some egg-capsules. Some photographs were taken by A 't Hooft (University of Leiden Institute of Evolutionary and Ecological Sciences, Leiden). This project was subsidized by the Royal Dutch Academy of Sciences, the Stichting Jan Joost ter Pelkwijkfonds and the Leiden University Foundation.

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At the time the manuscript was being sent for typesetting, the authors received the following book:

**Weil, A., L. Brown and B. Neville. 1999.** The wentletrap book. Guide to the Recent Epitoniidae of the world. Evolver srl, Roma, 246 pp.

This work apparently does not contain data that could substantially add or change the contents of the present article.