

**Epitoniid parasites (Gastropoda, Caenogastropoda, Epitoniidae)
and their host sea anemones (Cnidaria, Actiniaria, Ceriantharia)
in the Spermonde archipelago, Sulawesi, Indonesia**

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Associations between wentletraps (Gastropoda, Epitoniidae) and sea anemones (Cnidaria, Actiniaria) or tube anemones (Cnidaria, Ceriantharia) that were observed in the Spermonde archipelago, South Sulawesi, Indonesia, are reported. Shells of the various epitoniid species that were recorded are described and figured. Whenever possible, their identification was verified by comparison with type specimens, some of which are also figured. Pending further research, ten more species that could not be identified are additionally mentioned and figured. Photographs of the host anemones are also provided.

Key words: Gastropoda, Caenogastropoda, Epitoniidae, *Epitonium*, *Cirsotrema*, *Sagamiscala*, *Globiscala*, Actiniaria, Ceriantharia, Indonesia, ectoparasites.

INTRODUCTION

The relation between a wentletrap and a sea anemone species was first described by Ankel (1937), who found zooxanthellae and tissues of sea anemone in the stomach of some specimens of *Epitonium clathrus* (L., 1758) from the Mediterranean Sea. Thorson (1957: 58) suggested that the entire family Epitoniidae Berry, 1910, is "more or less adapted to a parasitic mode of life". He based this suggestion on his own observations of *Epitonium tinctum* (Carpenter, 1865) and *Opalia crenimarginata* (Dall, 1917) (= *O. funiculata* Carpenter, 1857). An increasing number of associations between wentletraps (Gastropoda, Caenogastropoda, Epitoniidae) and Cnidarians (Cnidaria, Scleractinia, Actiniaria, Ceriantharia) has been reported since.

Several epitoniid species have been found associated with both corals (Scleractinia) (Bell, 1985; Bosch, 1965; Bratcher, 1982; Dushane, 1988a-c; Gittenberger, 2006; Gittenberger et al., 2000; Hadfield, 1976; Hoeksema, 1988, 1989; Kay, 1979; Loch, 1982; Loo & Chou, 1988; Mienis, 1994; Oliverio et al., 1997; Page & Willan, 1988; Robertson, 1963, 1970; Sabelli & Taviani, 1984; Yamashiro, 1990) and sea anemones (Actiniaria and Ceriantharia) (Albergoni et al., 1970; Fretter & Graham, 1962; Habe, 1943; Hartog, 1987; Hartog et al., 1997; Hochberg, 1971; Hori & Yanagi, 2002; Kay, 1979; Kilburn & Rippey, 1982; Mienis, 1994; Nakayama, 1991; Oliverio, 1986; Perron, 1978; Peterson & Black, 1986; Robertson, 1963, 1981, 1983a-b, 1993; Salo, 1977; Shimek, 1986; Woodward, 1987).

Ankel (1937) suggested that wentletraps are predators that eat small (juvenile) anemones and swallow these entirely. Field observation and laboratory experiments showed that this mode of foraging indeed occurs (Thorson, 1957, Habe, 1943), but that

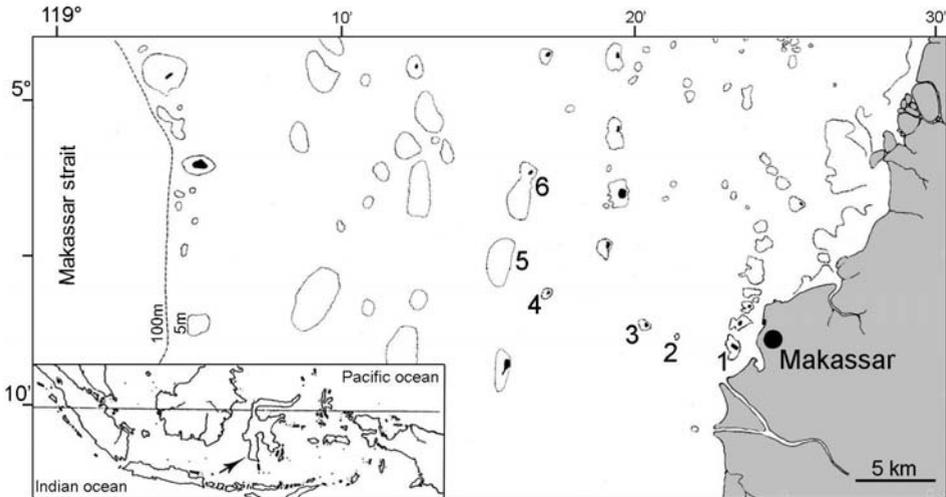


Fig. 1. Localities visited in September and October 2001 at Spermonde archipelago, Sulawesi, Indonesia. 1, Lae Lae island. 2, Bone Baku reef. 3, Samalona island. 4, Kudingareng Keke island. 5, Kapodasang reef. 6, Bone Tambung island.

there are other ways in which wentletraps may feed. *Epitonium echinaticostum* (Orbigny, 1842) for example feeds on the tentacles of sea anemones by enclosing the tip of a tentacle with its proboscis and then eating it (Robertson, 1983a). The same behaviour has been observed in *E. albidum* (d'Orbigny, 1842) (see Robertson, 1983d) and in *E. tinctum* (Carpenter, 1864) and *E. indianorum* (Carpenter, 1864) (see Salo, 1977). Wentletraps have also been observed while inserting their proboscis into the stem of the anemone and sucking up body fluids (Perron, 1978; Robertson, 1962). We have not made any observation on the feeding of the snails.

Reports on associations between wentletraps and sea anemones in the Indo-Pacific are scarce (table 1), considering the numerous epitoniid species that have been described from that region (Weil et al., 1999; Nakayama, 2003). The present, preliminary study deals with the associations between wentletraps and sea anemones found in the Spermonde archipelago off the coast of Makassar (Sulawesi, Indonesia). Several wentletraps were collected as live animals, but in some cases only empty shells were found. The majority of those, relatively fragile shells, were found in good shape. Therefore, we assume that those snails died not long before collecting and regarded the ecological data as for living animals. Shells of all the presumed epitoniid species are figured. Most species could not be identified unequivocally however, because in several cases only one or a few, often damaged shells (for example without protoconch whorls) were available for study. Apart from that, the intraspecific variation is insufficiently known for many epitoniid species, which may have large geographical ranges. The type series have not always been described in sufficient detail to enable the recognition of similar or sibling species, which are not uncommon among the Epitoniidae (Gittenberger, 2006). Photographs of representative specimens of the anemone species are also provided.

Next to two generally accepted, relatively easily diagnosable genera, we have used the generic name *Epitonium* Röding, 1798, in a very conservative sense and without any

subgeneric subdivisions. This so-called genus badly needs to be thoroughly revised, since very many species with similar shells have been lumped together here. Recently, molecular and ecological data and details of the jaw and the radula in particular indicate that this has resulted in a subjective, artificial classification (Gittenberger, 2006). As long as only the shells of most type species of the many epitoniid nominal taxa are known, their classification can be based on highly subjective interpretations only. In some cases, subgeneric names can be used then for the sake of convenience and easier species recognition as was argued by Kilburn (1982). However, there is no consensus about the interpretation of most 'subgenera', as becomes evident by comparing for example the classifications by Kilburn (1985), Weil et al. (1999) and Nakayama (2003). Therefore, we have omitted subgeneric names altogether.

MATERIAL AND METHODS

The major part of the research material was collected by skin- and scuba-diving at seven reefs in the Spermonde archipelago (fig. 1) during September and October 2001.

GPS locality data were plotted in Google Earth (<http://earth.google.com>). A KML file is available for download at www.baskokshoorn.nl/KML/EpitoniidaeSpermonde.kml. Some material was already available in the collection of the National Museum of Natural History *Naturalis* in Leiden. For the latter material no ecological data were available. First of all, the surface of the sea anemones and the surrounding substratum were searched for epitoniids. Often egg capsules were found on top of the substratum around the anemone, indicating the presence of a snail. After this, sand was collected from underneath and directly around the anemone, not more than a hand length from the stem. The sand was sieved to make collecting easier. The snails were preserved in ethanol 96%. Empty shells are kept in the dry collection of the National Museum of Natural History *Naturalis*, Leiden. To ensure proper identification of the research material, several specimens from type series in The Natural History Museum, London, were studied for comparison.

The location, the depth and the kind of substratum where the sea anemone was found, were registered. Four categories of substrate were recognized, i.e. (1) sand, (2) sand/rubble, (3) rubble and (4) coral (table 1, below).

All sea anemone forms were photographed (figs 35-55). On the basis of both these pictures and notes made during the dives, the species were eventually identified (Fautin & Allen, 1982; Dunn, 1981). Inspected individual sea anemones were marked with coloured

Substratum type	Definition
Sand	75-100% of substratum consists of fragments smaller than or equal to 10 mm.
Sand / Rubble	mixture of fragments larger than 10 mm and fragments smaller than or equal to 10 mm is between 25-75%
Rubble	75-100% of substratum consists of fragments larger than 10 mm.
Coral	none or very little loose particles between living corals

Table 1. Definitions of the substratum types as used in this paper.

aquarium gravel to prevent them from being examined a second time.

The following descriptions and notes are primarily based on the material collected during this project. Only when more than a single specimen is present, the number is added after the registration number. The host sea anemone species are listed under habitat with - for each species - the number of epitoniids found with representatives of the host species.

Abbreviations: BM, The Natural History Museum, London; RMNH, National Museum of Natural History *Naturalis*, Leiden.

SYSTEMATICS

Epitoniidae, Epitoniinae Berry, 1910

Cirsotrema Mörch, 1852.

Type species: *Scalaria varicosa* Lamarck, 1822.

The shells are robust, chalk-white, not glossy, with a very characteristic sculpture of regularly undulating prominent radial ribs and some varices. The ribs differ strikingly from the straight costae in most epitoniid species; they are more or less clearly composed of multiple layers and wherever the undulations of adjoining ribs contact each other, the shell surface is typically 'multiperforate'. There are also spiral elements in the sculpture. A microsculpture of spiral and radial lines may also be discernible. The apertural lip is formed by a solid, broad varix.

Cirsotrema multiperforata (Sowerby [II], 1874) (figs 2, 3)

Scalaria multiperforata Sowerby [II], 1874: pl. XVI, species 125 ("Black River Bay, Mauritius"). Syntype: BMNH 198144/1 (fig. 2).

Cirsotrema multiperforata; Kaicher, 1980: Epitoniidae I: 2321.

Material studied. — W. side of Kapodasang reef, 5°5'35" S 119°15'20" E (RMNH 87758, 88491); E side of Samalona Isl., 5°7'28" S 119°20'38" E (RMNH 87751, -752, -755, -756, -757, -791, -792, -793, -798, -799, -800, -814, -815, -816); SW. side of Samalona Isl., 5°7'42" S 119°20'31" E (RMNH 87779); W. side of Kudingareng Keke Isl., 5°6'9" S 119°17'9" E (RMNH 87767); SW. side of Kudingareng Keke Isl., 5°6'21" S 119°17'3" E (RMNH 87775); NW. side of Bone Tambung Isl., 5°2'5" S 119°16'16" E (RMNH 87784, -786, -787).

Description (n = 22; data on the holotype are added between brackets). — Shell very robust, slender conical, sand-coloured, reaching 21.2 mm [16.3 mm] in height. Height/width ratio 1.8-3.3-3.7 [3.5]. In our material the protoconchs are damaged or absent; remaining protoconch whorls creamy white or yellowish, smooth. Teleoconch whorls up to 10? (in a 19 mm high specimen) [8]; suture shallow. Teleoconch with broad costae with undulating edges that are irregularly fused. Costae not in line on adjoining whorls; their numbers increasing on the younger whorls. Costae often coronate; few peaks merged with costae on preceding whorl. Some costae thickened to varices, 1-2 [2] per whorl. Where visible, interspaces with dense axial and spiral sculpture. Third teleo-

conch whorl with 10-16 [17] costae; fifth with 16-21[18] costae. Last whorl with thick spiral ridge. Apertural height/shell height 0.2-0.3-0.4 [0.3]. Umbilicus absent.

Habitat. — The snails were found at 3-30 m on sand (17×) and sand/rubble (3×) (two specimens are from an unknown depth and substratum). They were collected from underneath the host anemones *Actinodendron plumosum* (5), *Actinodendron arboreum* (2), *Ceriantharia spec.* (3), *Stichodactyla haddoni* (3), *Stichodactyla spec.* (1), *Macroductyla doreensis* (1), *Heteractis crispa* (1) and six unidentified hosts.

Remarks. — *Cirsotrema multiperforata* has been synonymized with *C. varicosum* (Lamarck, 1822) by Weil et al. (1998: 198). However, no arguments were presented to support this and no reason was found here to accept that view. There are distinct differences between the two species. In *C. varicosum* the number of costae usually remains constant over the whorls, while in *C. multiperforata* the number increases abapically. In *C. varicosum* the number of costae on the third teleoconch whorl ranges from 16-19, whereas in *C. multiperforata* the number ranges from 10-16. Kaicher's (1980-1983) view that the number of varices on the whorls is diagnostic, could not be confirmed in our material.

Cirsotrema varicosum (Lamarck, 1822) (figs 4-6)

Scalaria varicosa Lamarck, 1822: 227 (type locality not indicated). Mermod & Binder, 1963: 162, 163, fig. 228 (lectotype).

Cirsotrema (Cirsotrema) varicosum; Kilburn, 1985: 253, fig. 21. Weil et al., 1999: 84, figs 247-248. Nakayama, 2003: 23, pl. 3 figs 17-20.

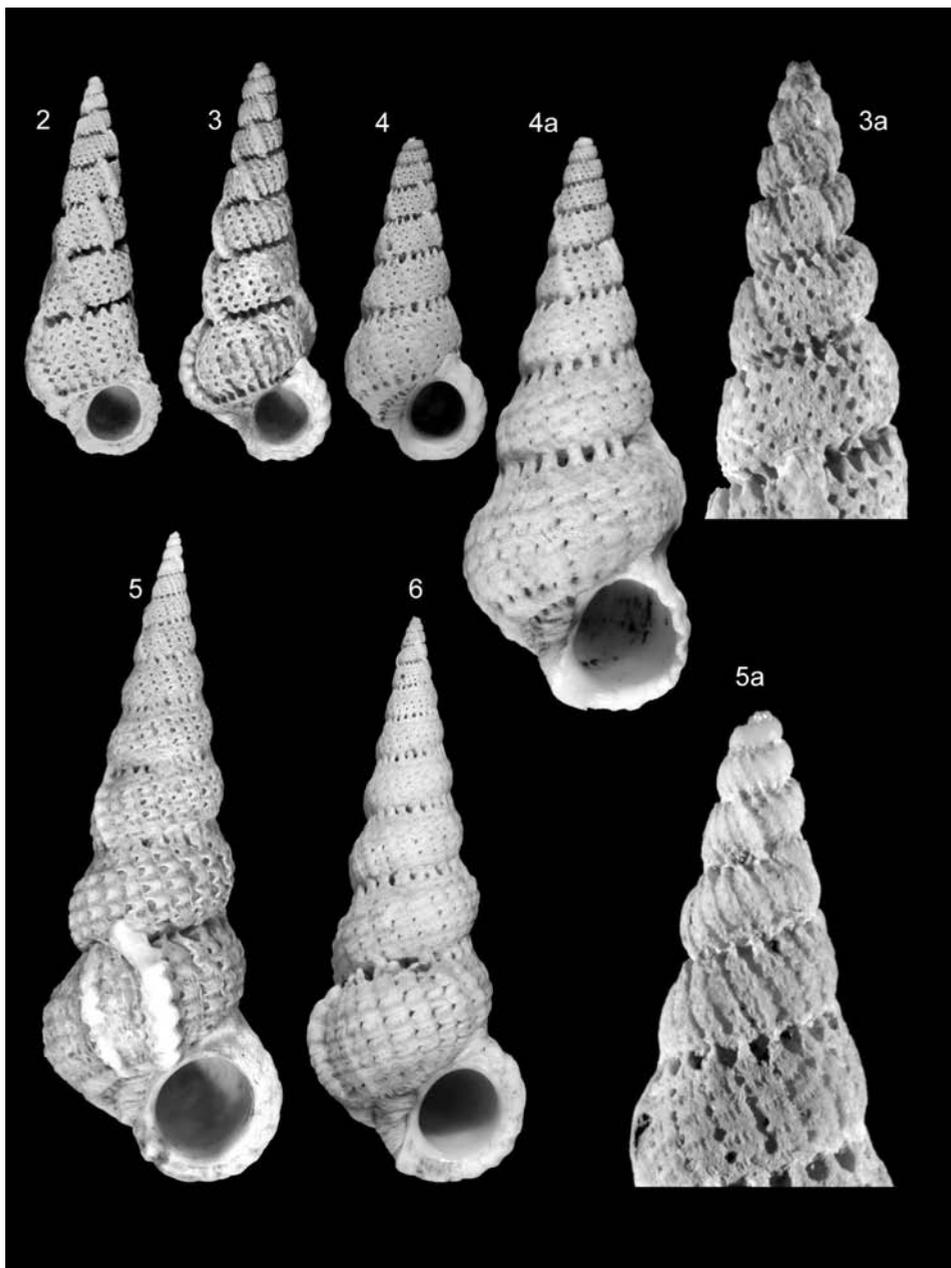
Cirsotrema varicosum; Kaicher, 1981: Epitoniidae II: 3118 (lectotype).

Material studied. — W. side of Kudingareng Keke Isl., 5°6'9"S / 119°17'9"E (RMNH 87771, 87812, 87813, 88489); E. side of Samalona Isl., 5°7'28"S / 119°20'38"E (RMNH 87753, -754, 764); SW. side of Samalona Isl., 5°7'42"S / 119°20'31"E (RMNH 87778).

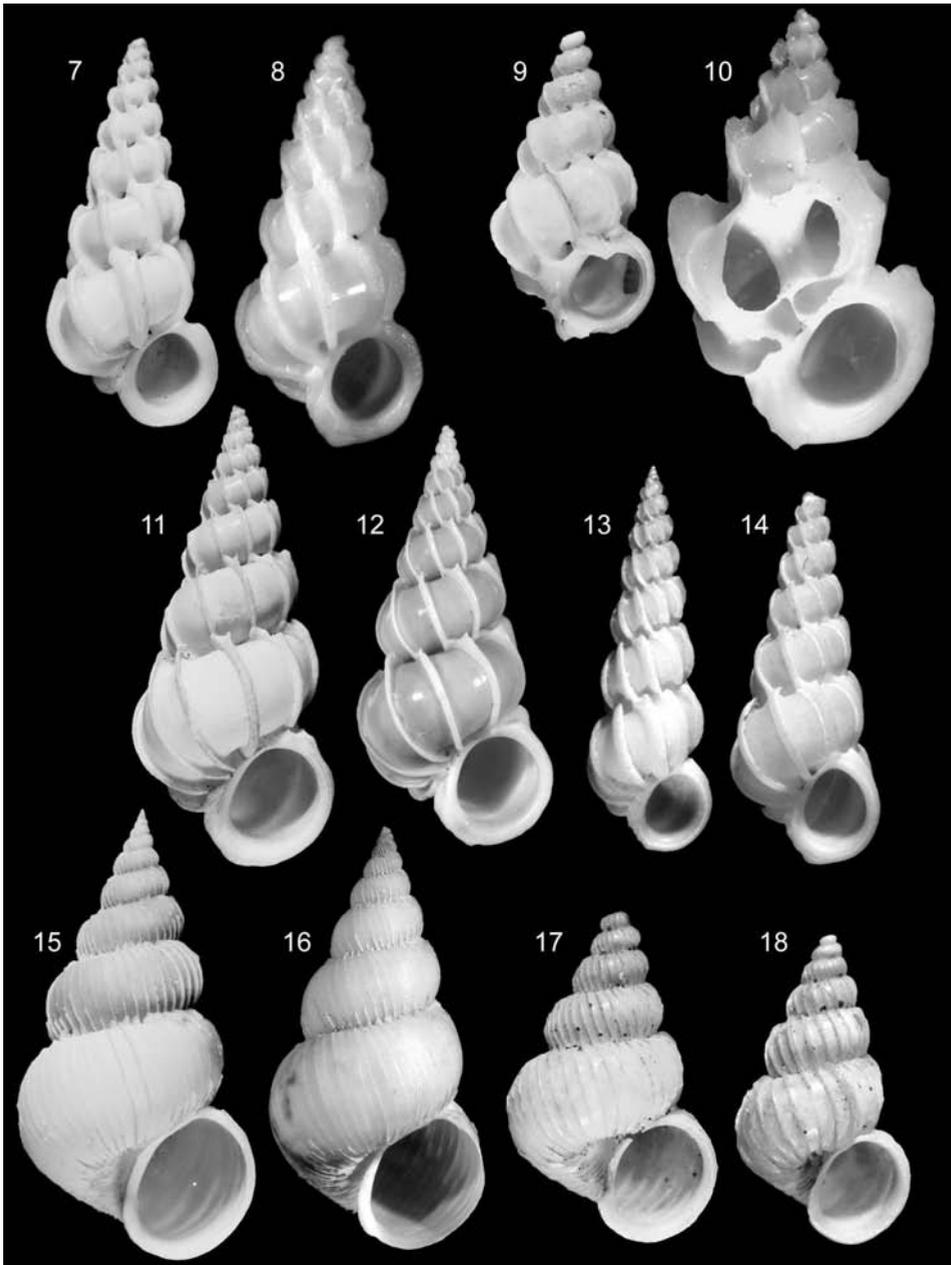
Description (n = 8). — Shell very similar to *C. multiperforata*, but reaching 54.8 [34.5] mm in height. Height/width ratio 2.9-3.3-3.9 [2.6]. Protoconchs all damaged or absent. Teleoconch whorls up to 11? (in a 54.8 mm high specimen). The number of costae remains constant over the whorls. Costae coronate, peaks often merged with costae on preceding whorl. Third teleoconch whorl with 16-19 costae; fifth one with 16-20 [18] costae. Apertural height/shell height 0.2-0.3.

Habitat. — The snails were found at 2-25 m on sand (3x), sand/rubble (4x) and coral/rubble (1x). They were collected from underneath the anemones *Stichodactyla haddoni* (1), *Actinodendron plumosum* (1), *Actinodendron arboreum* (1), *Heteractis crispa* (3), *Macroductyla doreensis* (1). One host species could not be identified.

Remark.— The lectotype in the Lamarck collection (Museum of Natural History, Geneva), selected by Mermod & Binder (1963: 163, fig. 228), clearly represents this species. It has to be considered a lectotype, since the number of shells on which the original description was based, is unknown.



Figs 2-6. *Cirsotrema* spec. 2-3, *Cirsotrema multiperforata* (Sowerby [II], 1874); 2, syntype (BMNH 198144), H=16.3 mm; 3, E. side of Samalona island (RMNH 87814), H=18.1 mm; 4-6, *C. varicosum* (Lamarck, 1822); 4, Indonesia, Bali, NE. side of Pulau Serangan island, 22 m depth, RMNH 91205, H=15.0 mm; 4a, H=26.6 mm; 5, W. side of Kudingareng Keke island (RMNH 87813), H=54.7 mm; 6, W. side of Kudingareng Keke island (RMNH 87771), H=47.1 mm).



Figs 7-18. *Epitonium* spec. 7-8, *E. moolenbeeki* Van Aartsen, 1996; 7, lectotype (BMNH 198134), H=16.3 mm; 8, E. side of Samalona island (RMNH 87801), H=6.8 mm. 9-10, *E. replicatum* (Sowerby [II], 1844); 9, lectotype (BMNH 1966409), H=13.7 mm; 10, NW. side of Lumulumu island (RMNH 88481), H=11.7 mm; 11-12, *E. pyramidale* (Sowerby [II], 1844). 11, lectotype (BMNH 198144), H=31.1 mm; 12, E. side of Samalona island (RMNH 87750), H=26.4 mm. 13-14, *E. cf. sandwichense* (Nyst, 1871); 13, W. side of Bona Baku reef (RMNH 87795), H=6.7 mm; 14, NW. side of Kudingareng Keke island (RMNH 87772), H=7.7 mm. 15-16, *E. ancillottoi* Cossignani & Cossignani, 1998; 15, holotype, Museo Malacologico Piceno, Cupra Marittima, Italy, H=30.2 mm; 16, W. side of Bona Baku reef (RMNH 87768), H=36.1 mm. 17-18, *E. irregulare* (Sowerby [II], 1844), syntypes (BMNH 1966402), resp. H=12.3 mm and H=9.5 mm.

Epitonium Röding, 1798.

Most species of *Epitonium* s.l. are represented by only one or very few specimens.

Epitonium moolenbeeki Van Aartsen, 1996 (figs 7, 8)

Scalaria aculeata Sowerby [II], 1844: 12 ("Hong Kong, China, et Macassar, Malacca, Amboyna; R.B. Hinds legit: ad Bais, ins. Negros, et ad Catanauan, ins. Luzon; H. Cuming legit. Some specimens were taken at Bais, isle of Negros, in coarse sand at six fathoms"); 1847: 86, pl. 32 figs 35-37. Syntypes: BMNH 198134/7 shells (fig. 7).

Epitonium moolenbeeki Van Aartsen, 1996: 3. Nomen novum for *Scalaria aculeata* Sowerby [II], 1844, not *Turbo aculeatus* Brown, in Allan, 1818 (see Van Aartsen, 1996).

Epitonium (Lamelliscala) aculeatum; Weil et al., 1999: 98, fig. 302.

Epitonium (Hirtoscala) aculeatum; Nakayama, 2003: 51, pl. 12 fig.13.

Epitonium aculeatum; Kaicher, 1981: Epitoniidae II: 3041.

Material studied. — E. side of Samalona Isl., 5°7'28"S / 119°20'38"E (RMNH 87801)

Habitat. — An empty shell was found underneath a *Ceriantharia* spec., on sand at a depth of 1 m.

Notes. — Since *Epitonium moolenbeeki* was introduced as a nomen novum for *Scalaria aculeata* Sowerby [II], 1844, its type series is identical to that of *S. aculeata*. These syntypes are of quite different origin and probably not conspecific. To stabilize the name of this species, in accordance with Weil et al. (1999) and Nakayama (2003), we here select from among the syntypes, the figured specimen (fig. 7), which is most similar to the shell figured by Sowerby [II] (1844: pl. 32 fig. 35) as lectotype (BMNH 198134). In that shell, the interspaces are smooth, as is the case in all but two of the syntypes. Those with sculptured interspaces probably belong to what we consider the *E. replicatum* species complex.

Epitonium replicatum (Sowerby [II], 1844) (figs 9, 10)

Scalaria replicata Sowerby [II], 1844: 11 ("Ins. "Lord Hood's.""); 1847: 84, pl. 32 figs 23-24. Type series: BMNH 1966409/lectotype (design. Dushane, 1974: 43)(fig. 9), 2 paralectotypes.

Epitonium (Epitonium) replicatum; Weil et al., 1999: 94, fig. 287.

Epitonium (Lamelliscala) replicatum; Nakayama, 2003: 47, pl. 11 figs 19-21.

Epitonium replicatum; Kaicher, 1980: Epitoniidae I: 2357.

Material studied. — NW. Lumulumu, 4°58'13"S / 119°12'35"E (RMNH 88481).

Habitat. — An empty, damaged shell was found at 30 m underneath an unknown host.

Remarks. — The single shell is very loosely coiled, with few, very prominent but relatively thin, moderately pointed, in-line costae, which are curved adapically; the interstices are glossy. It agrees very well with illustrations in the literature and the three specimens of the type series.

Epitonium pyramidale (Sowerby [II], 1844) (figs 11, 12)

Scalaria pyramidalis Sowerby [II], 1844: 12 ("Ins. Caminguing, Philippinarum"); 1847: 85, pl. 32 fig. 4. Syntypes: BMNH 198144/3 (fig. 11).

? *Epitonium* (*Epitonium*) *pyramidale*; Weil et al., 1999: 94, fig. 285.

Epitonium (*Hirtoscala*) *pyramidale*; Nakayama, 2003: 50, pl. 12 figs 7-9.

Epitonium pyramidale; Kaicher, 1981: Epitoniidae II: 3042.

Material studied. – E. side of Samalona Isl., 5°7'28"S / 119°20'38"E (1, RMNH 87750).

Habitat. – The snail, with egg capsules, was found at 3 m, on sand, underneath *Actinodendron plumosum*.

Notes. – It is unclear whether the rather contrasting figures in the literature (for example: Weil et al., 1999, fig. 285; Nakayama, 2003, pl. 12 figs 7-9) refer to the same species indeed. We could not determine with certainty the specimen that was figured by Sowerby [II] (1847: pl. 32 fig. 4. Here we select a similar syntype (fig. 11) as lectotype and illustrate the shell of a snail from the Spermonde archipelago, which we consider conspecific.

The loosely coiled shells are slender conical, with coronate, in-line costae, that are curved adapically over their entire length; the interstices are glossy.

Epitonium cf. *sandwichense* (Nyst, 1871) (figs 13, 14)

Scalaria decussata Pease, 1867: 289, pl. 24 fig. 10 ("Hawaii"). Not Lamarck, 1804.

Scalaria sandwichensis Nyst, 1871: 132. Nomen novum for *Scalaria decussata* Pease, 1867, not Lamarck, 1804.

Epitonium kanemoe Pilsbry, 1921: 375 ("Haena, Kauai" [Hawaii]).

Epitonium (*Laeviscala*) *sandwichense*; Weil et al., 1999: 98, fig. 300.

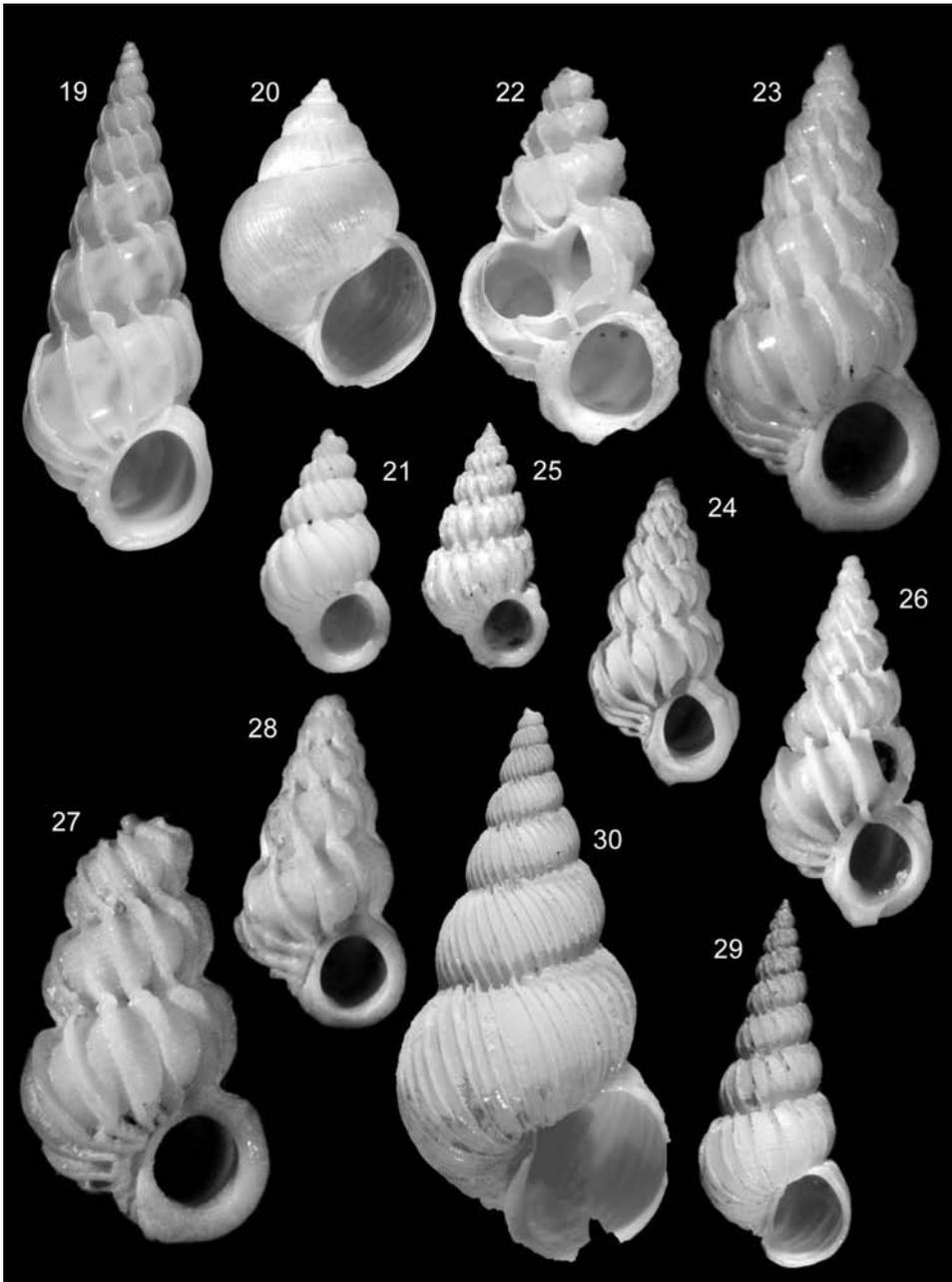
Material studied. – NW. side of Kudingareng Keke Isl., 5°6'8"S / 119°17'17"E (RMNH 87772); SW. side of Kudingareng Keke Isl., 5°6'21"S / 119°17'3"E (RMNH 87971); E. side of Samalona Isl., 5°7'28"S / 119°20'38"E (RMNH 87760); W. side of Bona Baku reef, 5°7'56.3"S / 119°21'38.9"E (RMNH 87795).

Description (n = 4). – Shell very slender conical, white; reaching 8.7 mm in height. Height/width ratio 3.4-3.6 (n = 2). With 3/4 glossy protoconch whorls and up to c. 7 teleoconch whorls, which are separated by a very deep suture, but not detached. Teleoconch with evenly spaced, moderately thick costae. The costae of adjoining whorls are in line, which is somewhat masked by the fact that their outer margins are strongly curved adapically over their entire length, especially so on the youngest whorls. Costae coronate, with peaks that are also strongly curved adapically.

A reticulate microsculpture of fine spiral and axial lines covers the interstices and is also present, though less prominently, on the costae. Fifth teleoconch whorl with 7-9 costae. Aperture subcircular, with a broad callus at its columellar side. Umbilicus absent.

Habitat. – All four specimens were empty shells, slightly to severely damaged. They were found at 12-18 m, underneath different hosts in sand (2x) or a mixture of coral-rubble and sand (1x). The hosts were *Macrodactyla doreensis*, *Heteractis crispa*, *Stichodactyla hadroni* and one unidentified host.

Notes. – We could not compare our specimens with shells from Hawaii and, there-



Figs 19-30. *Epitonium* and *Globiscala* spec. 19, *E. glabratum* (Hinds, 1844), E. side of Samalona island (RMNH 87797), H=10.9 mm; 20, *Globiscala arjani* Kokshoorn & Goud, 2007, NW. side Kudingareng Keke island (RMNH 91225), H=5.5 mm; 21-30, Unidentified *Epitonium* spec.; 21, *E.* spec. 1, SW. side Samalona island (RMNH 87805), H=5.1 mm; 22, *E.* spec. 2, W. side of Bona Baku reef (RMNH 87770), H=8.0 mm; 23-24, *E.* spec. 3, SW. side of Kudingareng Keke island (resp. RMNH 87776, H=5.7 mm and 87796, H=5.0 mm); 25, *E.* spec. 4, W. side of Bone Lola reef (RMNH 88482), H=5.1 mm; 26, *E.* spec. 5, E. side of Samalona island (RMNH 87763), H=6.1 mm; 27-28, *E.* spec. 6, SW. side of Kudingareng Keke island (resp. RMNH 87773, H=5.1 mm and 87777, H=5.4 mm); 29, *E.* spec. 7, W. side of Samalona island (RMNH 109038), H=8.0 mm; 30, *E.* spec. 8, W. side of Bona Baku reef (RMNH 87803), H=14.4 mm.



Figs 31-33. Unidentified *Epitonium* spec. 31, *E.* spec. 9, NW. side of Bone Tambung island (RMNH 87785), H=18.9 mm; 32-33, *E.* spec. 10; 32, W. side of Kapodasang reef (RMNH 88486), H=9.6 mm; 33, W. side of Samalona island (RMNH 109039), H=24.3 mm.

fore, are not convinced that this is indeed the species that was originally described from that archipelago as *Scalaria decussata* by Pease (1868) and *Epitonium kanemoe* by Pilsbry (1921).

Epitonium ancillottoi Cossignani & Cossignani, 1998 (figs 15, 16)

Epitonium (Limiscalca) ancillottoi Cossignani & Cossignani, 1998: 38 ("Australia, Filippine"), 2 figs. (holotype (fig. 15), paratype 1 in Museo Malacologico Piceno, Cupra Marittima (Italy); paratypes 2, 3, in colln Cossignani.

Material studied. — W. side of Samalona Isl., 5°7'31"S / 119°20'31"E (RMNH 88483, 88484); SW. side of Samalona Isl., 5°7'42"S / 119°20'31"E (RMNH 87810, 87811); E. side of Samalona Isl., 5°7'28"S / 119°20'38"E (RMNH 88487); NNW side of Samalona Isl. (RMNH 109037); W. side of Bona Baku reef, 5°7'56.3"S / 119°21'38.9"E (RMNH 87768, 87769, 87794, 87806, 87808); SW. side of Kudingareng Keke Isl., 5°6'21"S / 119°17'3"E (RMNH 87773).

Habitat. — All snails were found at 3-30 m, buried underneath their hosts in sand (3×) or rubble/sand (2×). The hosts were: *Heteractis crispa* (2), *Macroductyla doreensis* (5), *Stichodactyla haddoni* (1) and two unidentified hosts (2).

Notes. — The broadly conical, white shells are very fragile for their relatively large size, reaching nearly 4 cm in height (30.2 mm in the holotype). The teleoconch is ornamented with many, thin, low, not coronate costae (usually damaged), which are curved abaperturally over almost their entire height, but adaperturally where they are enlarged while contacting the previous whorl near the very deep suture.

In recent publications (Bosch et al., 1995; Springsteen & Leobrera, 1986; Weil et al., 1999 Weil et al.) this species is apparently referred to as *Epitonium irregulare* (Sowerby [II], 1844), which we consider specifically distinct, however. *Epitonium ancillottoi* differs from *E. irregulare* most clearly by the appearance of the interspaces, which are smooth in *E. irregulare* and provided with a dense spiral sculpture in *E. ancillottoi*. Carefull examination of the type specimens of *E. irregulare*, which are worn and damaged shells (figs 17, 18), did not reveal any spiral striation, not even near the suture, where wear and tear are much less than on the more exposed surfaces.

Epitonium glabratum (Hinds, 1844) (fig. 19)

Scalaria glabrata Hinds, 1844: 124 ("Amboina; Straits of Macassar; Straits of Malacca."). Sowerby [II], 1847: 88, pl. 34 fig. 101.

Epitonium (Hyaloscala) glabratum; Weil et al., 1999: 96. Nakayama, 2003: 53, pl. 12 figs 30-31. *Epitonium glabratum*; Kaicher, 1980: Epitoniidae I: 2323.

Material studied. — E. side of Samalona Isl., 5°7'28"S / 119°20'38"E (RMNH 87797).

Habitat. — An empty shell was found at 16 m, buried in sand underneath *Macroductyla doreensis*.

Notes. — Apparently there is consensus about the identity of this species in the literature. The loosely coiled, slender conical shells are whitish with some light brown blotch-

es; the costae are very strongly curved adapically, except for their enlarged, broadly raised, upper parts, which contact the relatively narrow lower parts of the costae on the preceding whorls. The interstices are glossy.

Globiscala De Boury, 1909

Type species: *Scalaria bullata* Sowerby [III], 1844.

Globiscala De Boury, 1909: 258.

Sagamiscala Masahito, Kuroda & Habe, in Kuroda, Habe & Oyama, 1971: 258. Type species: *Sagamiscala globosa* Masahito, Kuroda & Habe in Kuroda, Habe & Oyama, 1971: 258.

Shells more or less globular, radial costae partly or entirely reduced; in the latter case with only a microsculpture of growth lines and some vague spiral lines. Without a reflexed apertural lip.

Kilburn (1985: 276) referred to *Sagamiscala* as an “inadequately known genus”, which “may prove to be non-epitoniid”. Weil et al. (1999: 124) pointed out that *Sagamiscala* resembles *Globiscala* but lacks costae. We agree and, for the time being, regard the two nominal genera as synonyms, in particular also because the costae may even be obsolete in specimens of *G. bullata*.

Nakayama (2003) studied the operculum and protoconch of ‘*Sagamiscala*’ *globosa* (Masahito, Kuroda & Habe in Kuroda, Habe & Oyama, 1971). Based on the paucispiral operculum and the glossy protoconch of this species he classified the genus *Sagamiscala* within the family Epitoniidae in concordance with Masahito et al. (1971). The species is recorded here associated with a sea anemone. This again strongly suggests that we deal with a true epitoniid.

Globiscala arjani Kokshoorn & Goud, 2007 (fig. 20)

Material studied. – NW. side of Kudingareng Keke Isl., 5°6'8"S / 119°17'17"E (RMNH 91225).

Habitat. – The specimen was found at 8 m, inside the gastral cavity of its host, *Phyllodiscus semoni*.

Remarks. – See Kokshoorn & Goud (2007) for further data on this species.

UNIDENTIFIED TAXA

Key to *Epitonium* spec. 1-10

- | | | |
|-----|--|----------|
| 1a. | Shells with many, thin, regularly curved (not pointed) costae and dense, irregular, spiral striae; suture very deep; similar to <i>Epitonium ancillottoi</i> but smaller | 6 |
| 1b. | Shells different, usually much smaller | 2 |
| 2a. | Whorls loosely coiled, contacting each other (mainly) by the costae | 3 |
| 2b. | Whorls separated by a deep suture; costae very prominent and solid, as broad as the interstices, which are spirally striate | spec. 1 |
| 3a. | Interstices glossy | 4 |
| 3b. | Interstices with a spiral sculpture | 5 |
| 4a. | Seven high, relatively thin costae; whorls far apart | spec. 2 |
| 4b. | Costae narrower than the interstices, with radial lines, vaguely pointed halfway between the periphery and the suture | spec. 3 |
| 4c. | Costae as broad as the interstices, sharply pointed above and finely sculptured with spiral line segments and radial lines | spec. 4 |
| 5a. | Costae prominent but thin, moderately prominently pointed above, curved adapically, most clearly on the youngest whorls | spec. 5 |
| 5b. | Like 5a but costae regularly rounded above | spec. 7 |
| 5c. | Costae radially sculptured, strongly curved adapically, in particular also their uppermost parts | spec. 6 |
| 6a. | Relatively small, densely sculptured, last whorl clearly higher than half the total shell height, 7.2 mm broad, with 41 costae | spec. 8 |
| 6b. | Resembling a small <i>E. ancillottoi</i> , last whorl clearly higher than half the total shellheight, with 36 costae | spec. 9 |
| 6c. | More slender conical, suture deeper, last whorl measuring about half the total shell height, with ca. 25 costae (10th teleoconch whorl) | spec. 10 |

Epitonium spec. 1-10

Shells that might belong to no less than ten additional epitoniid species could not be identified with certainty. They are listed below, with key-wise diagnoses, short notes, a reference to the anemone host species data, and a reference to a figured specimen.

Epitonium spec. 1 (fig. 21)

Material studied. — SW. side of Samalona Isl., 5°7'42"S / 119°20'31"E (RMNH 87805).

Diagnosis. — Whorls separated by a deep suture; costae very prominent and solid, as broad as the interstices, which are spirally striate.

Habitat. — The empty shell was found at 19 m in sand, underneath *Macroductyla doreensis*.

Epitonium spec. 2 (fig. 22)

Material studied. — W. side of Bona Baku reef, 5°7'56.3"S / 119°21'38.9"E (RMNH 87770).

Diagnosis. — Whorls loosely coiled, contacting each other (mainly) by the costae. Interstices glossy. Few (7 on a whorl), high, relatively thin costae; whorls far apart.

Habitat. — An empty shell was found at 6 m between coral/rubble underneath *Phyllo-discus semoni*.

Epitonium spec. 3 (figs 23, 24)

Material studied. — SW. side of Kudingareng Keke Isl., 5°6'21"S / 119°17'3"E (RMNH 87776, 87796).

Diagnosis. — Whorls loosely coiled, contacting each other (mainly) by the costae. Interstices glossy. Costae narrower than the interstices, with radial lines, vaguely pointed halfway between the periphery and the suture.

Habitat. — Both empty shells were found on sand/rubble underneath *Heteractis crispa* at 8 and 30 m, respectively.

Notes. — The specimens somewhat resemble *E. crassicostatum* Gittenberger & Gittenberger, 2005. They differ in the smooth interspaces between the costae, where there are up to 17 spiral striae in *E. crassicostatum*.

Epitonium spec. 4 (fig. 25)

Material studied. — W. side of Bone Lola reef, 05°03'07"S / 119°21'09" E (RMNH 88482).

Diagnosis. — Whorls loosely coiled, contacting each other (mainly) by the costae. Interstices glossy. Costae as broad as the interstices, sharply pointed above and finely sculptured with spiral line segments and radial lines.

Habitat. — The empty shell was found at 7 m on sand, underneath an unidentified host.

Epitonium spec. 5 (fig. 26)

Material studied. — E. side of Samalona Isl., 5°7'28"S / 119°20'38"E (RMNH 87763).

Diagnosis. — Whorls loosely coiled, contacting each other (mainly) by the costae. Interstices with a spiral sculpture. Costae prominent but thin, moderately prominently pointed above, curved adapically, most clearly on the youngest whorls.

Habitat. — This empty shell was found at 19 m in sand, underneath *Heteractis aurora*.

Epitonium spec. 6 (figs 27, 28)

Material studied. — SW. side of Kudingareng Keke Isl., 5°6'21"S / 119°17'3"E (RMNH 87773, 87777).

Diagnosis. — Whorls loosely coiled, contacting each other (mainly) by the costae. Interstices with a spiral sculpture. Costae radially sculptured, strongly curved adapically,

	<i>Actinodendron plumosum</i>	<i>Actinodendron arboreum</i>	<i>Heteractis magnifica</i>	<i>Heteractis aurora</i>	<i>Heteractis crispa</i>	<i>Macroactyla doreensis</i>	<i>Stichodactyla</i> sp.	<i>Stichodactyla haddoni</i>	<i>Stichodactyla gigantea</i>	<i>Entacmaea quadricolor</i>	<i>Cryptodendrum adhaesivum</i>	<i>Phyllodiscus semoni</i>	<i>Ceriantharia</i> sp.	<i>Amplexidiscus fenestrafer</i>	<i>Discosoma</i> sp.	Unknown	Total
<i>Cirsotrema</i>																	
<i>C. multiperforata</i>	5	2			1	1	1	3					3			6	22
<i>C. varicosum</i>	1	1			3	1		1								1	8
<i>Epitonium</i>																	
<i>E. moolenbeeki</i>													1				1
<i>E. replicatum</i>																1	1
<i>E. pyramidale</i>	1																1
<i>E. cf. sandwichense</i>					1	1		1								1	4
<i>E. ancillottoi</i>					2	5		1								2	10
<i>E. glabratum</i>						1											1
<i>E. spec. 1</i>						1											1
<i>E. spec. 2</i>												1					1
<i>E. spec. 3</i>					1												1
<i>E. spec. 4</i>																1	1
<i>E. spec. 5</i>				1													1
<i>E. spec. 6</i>					1												1
<i>E. spec. 7</i>								1								1	2
<i>E. spec. 8</i>					1												1
<i>E. spec. 9</i>																1	1
<i>E. spec. 10</i>					1	1		2								2	6
<i>Globiscala</i>																	
<i>G. arjani</i>												1					1
Total no. of associations	7	3	0	1	9	8	1	9	0	0	0	2	4	0	0	15	65
Total no. searched	14	3	19	7	46	29	17	15	4	17	1	3	12	3	2	30	228
Percentage parasitized	50	100	0	14.3	19.6	27.6	5.88	60	0	0	0	66.7	33.3	0	0	50	28.5

Table 2. Associations between specimens of the epitoniid species and their Anthozoan hosts found during this project. The association between *C. varicosum* and *H. crispa* has been published previously by Hori & Yanagi (2002).

in particular also their uppermost parts.

Habitat. — The empty shells were found on coral/sand/rubble at 4 m underneath *Heteractis crispa*.

Epitonium spec. 7 (fig. 29)

Material studied. — E. side of Samalona Isl., 5°7'28"S / 119°20'38"E (RMNH 87790); W. side of Samalona Isl., 5°7'31"S / 119°20'31"E (RMNH 109038).

Diagnosis. — Whorls loosely coiled, contacting each other (mainly) by the costae. Interstices with a spiral sculpture. Costae prominent but thin, regularly rounded above, curved adapically, most clearly on the youngest whorls.

Habitat. — One shell was found at 23 m near an unidentified host and the other one at 21 m, on sand, underneath *Stichodactyla haddoni*.

Epitonium spec. 8 (fig. 30)

Material studied. — W. side of Bona Baku reef, 5°7'56.3"S / 119°21'38.9"E (RMNH 87803).

Diagnosis. — Shells with many, thin, regularly curved (not pointed) costae and dense, irregular, spiral striae; suture very deep; similar to *Epitonium ancillottoi* but smaller. Last whorl clearly higher than half the total shell height, 7.2 mm broad, with 41 costae.

Habitat. — A single shell was found at 5 m, on sand, underneath *Heteractis crispa*.

Epitonium spec. 9 (fig. 31)

Material studied. — NW. side of Bone Tambung Isl., 5°2'5"S / 119°16'16"E (RMNH 87785).

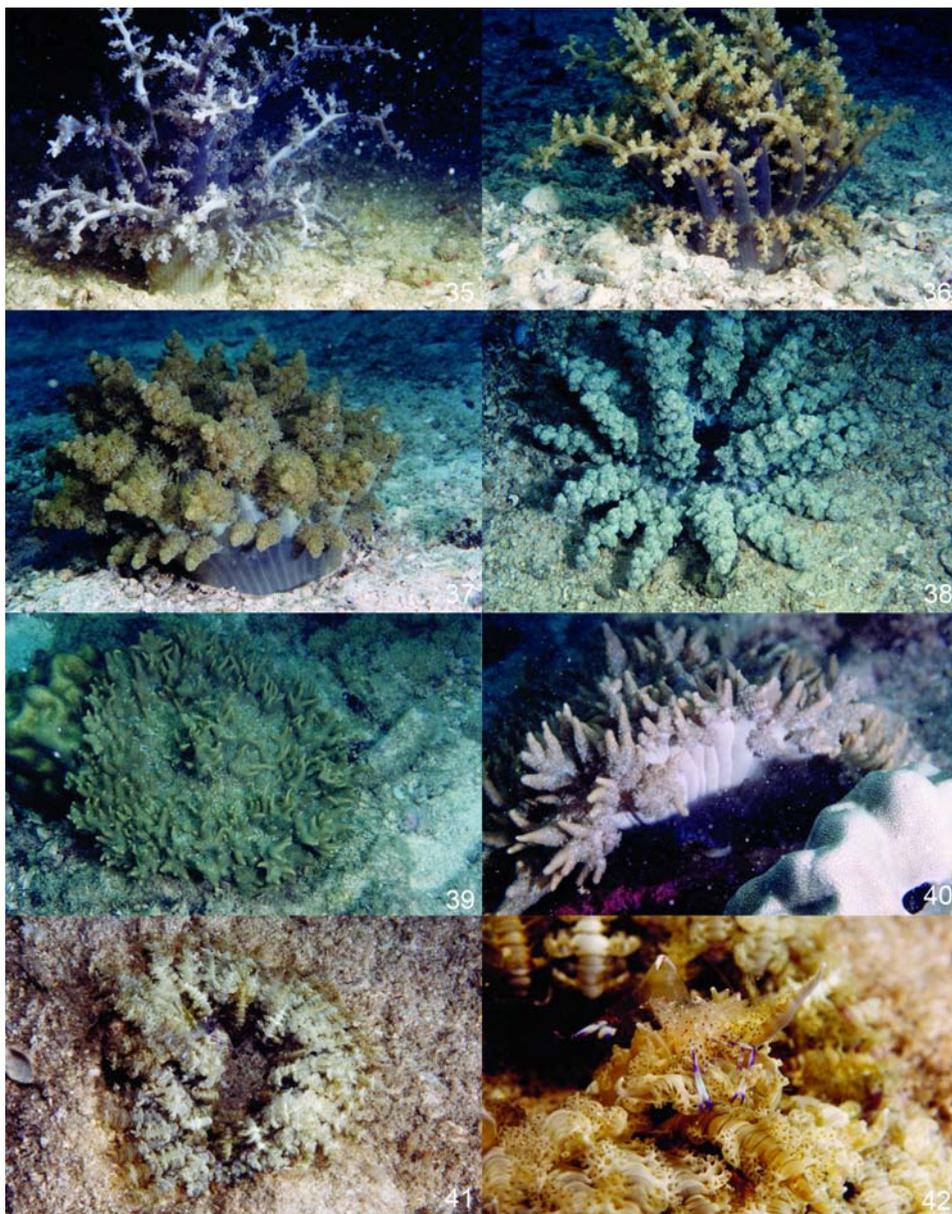
Diagnosis. — Shell with many, thin, regularly curved (not pointed) costae and dense, irregular, spiral striae; suture very deep; Resembling a small *E. ancillottoi*; last whorl clearly higher than half the total shell height, with 36 costae.

Habitat. — A single shell was found at 28 m, on sand, underneath an unidentified host.

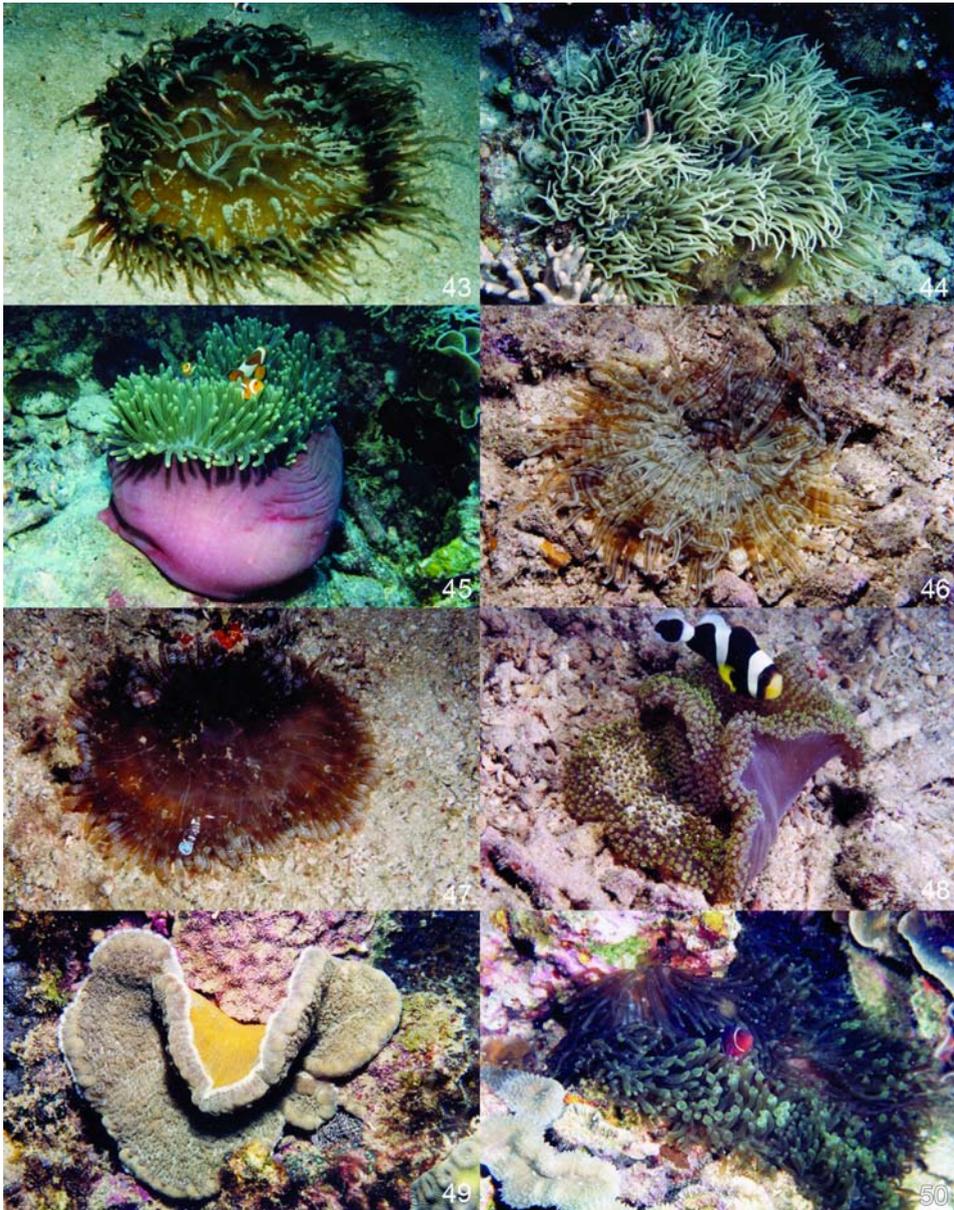
Epitonium spec. 10 (figs 32, 33)

Material studied: W. side of Kapodasang reef, 5°5'35"S / 119°15'20"E (RMNH 88486); SW side of Samalona Isl., 5°7'42"S / 119°20'31"E (RMNH 87809); W. side of Samalona Isl., 5°7'31"S / 119°20'31"E (RMNH 109039); E. side of Samalona Isl., 5°7'28"S / 119°20'38"E (RMNH 87759, 87789); W. side of Kudingareng Keke Isl., 5°6'9"S / 119°17'9"E (RMNH 87766).

Habitat. — The specimens were found at 1-27 m, buried in sand underneath *Heteractis crispa* (1), *Stichodactyla haddoni* (2), *Macroductyla dorensis* (1), and two unidentified hosts.



Figs 35-42. Sea anemone species found at the Spermonde archipelago. 35-36, *Actinodendron plumosum* Haddon, 1898. 37, *Actinodendron arboreum* (Quoy & Gaimard, 1833), found associated with *Cirsotrema multiperforata* (RMNH 87791). 38, *Actinodendron arboreum*. 39-40, *Phyllodiscus semoni* Kwietniewski, 1897. 41-42, *Phymathus* cf. *laevis* Kwietniewski, 1898. Photographs: A. Gittenberger.



Figs 43-50. Sea anemone species found at the Spermonde archipelago (continued). 43, *Macrodactyla doreensis* (Quoy & Gaimard, 1833), found associated with *C. multiperforata* (RMNH 87758). 44, *Heteractis crispa* (Ehrenberg, 1834). 45, *Heteractis magnifica* (Quoy & Gaimard, 1833). 46, *Heteractis aurora* (Quoy & Gaimard, 1833), found associated with *Epitonium* spec. 5 (fig. 26). 47, *Heteractis* sp. 48, *Heteractis* sp. 49, *Cryptodendrum adhaesivum* Klunzinger, 1877. 50, *Entacmaea quadricolor* (Rüppell & Leuckart, 1828).

Photographs: A. Gittenberger

CONCLUSIONS

In 32 cases, the amount of sand collected near a potential sea anemone host was doubled, to see whether additional parasites might be found. This was not the case. None of the additional bags of sand that were collected contained wentletraps. Therefore, the collecting method is considered reliable in terms of finding the parasites when they are present.

During this project 228 individual anemones were investigated, 65 of which were found parasitised, 8 by more than 1 epitoniid species. The wentletraps belonged to 19 alleged species, whereas 15 species of anemones were identified (plus a number of non-identified *Actiniara* spec. and *Ceriantharia* spec.). A total of 41 associations between wentletrap and sea anemone species were found (table 2), all but one apparently not recorded previously (Hori & Yanagi, 2002). There appears to be little host specificity in the wentletrap species found. When more than a single individual of a species is available, in all cases more than one sea anemone species is involved. Assuming that the alleged species are true biological species and not cryptic radiations, this stands in sharp contrast with the species associated with *Scleractinia* (Gittenberger, 2006). Here there is strong host specificity, each wentletrap species is associated with a single host species.

There are six sea anemone species recorded without any associated wentletraps. Four of these (*Stichodactyla gigantea*, *Cryptodendrum adhaesivum*, *Amplexidiscus fenestrafer* and *Discosoma* sp.) were found in low numbers, but *Heteractis magnifica* and *Entacmaea quadricolor* (19 and 17 individuals resp.) are rather common on the reefs in the Spermonde. The absence of associates with these species might be correlated with the habitat preferences of these anemone species. Both occur only on strictly solid substratum, without possibilities for the wentletraps to bury themselves. The anemone associated wentletraps have a strong preference for loose substratum types (fig. 56). Overall, 28.5% (65 out of 228) of all sea anemones was found parasitized by wentletraps. When the species are left out that were never found parasitized, this increases to 35.7% (65 out of 182).

Obviously, more associations and many more species of epitoniids still await discovery.

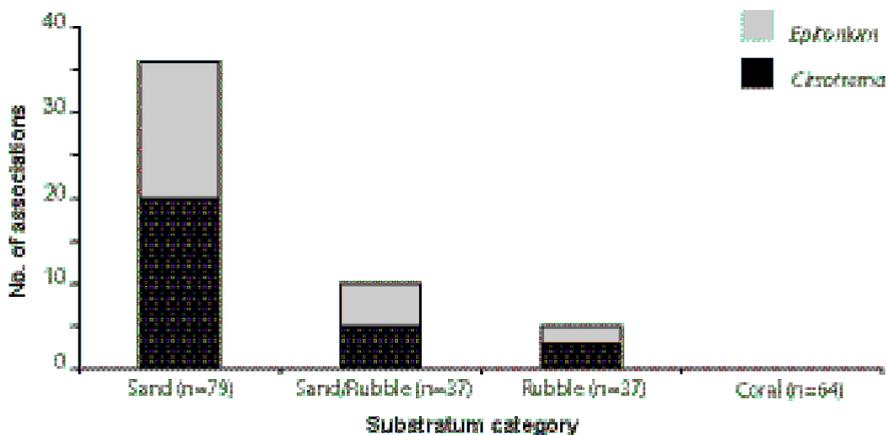


Figure 56. The number of wentletrap – sea anemone associations per substratum type. For seven associations the substratum type is unknown.

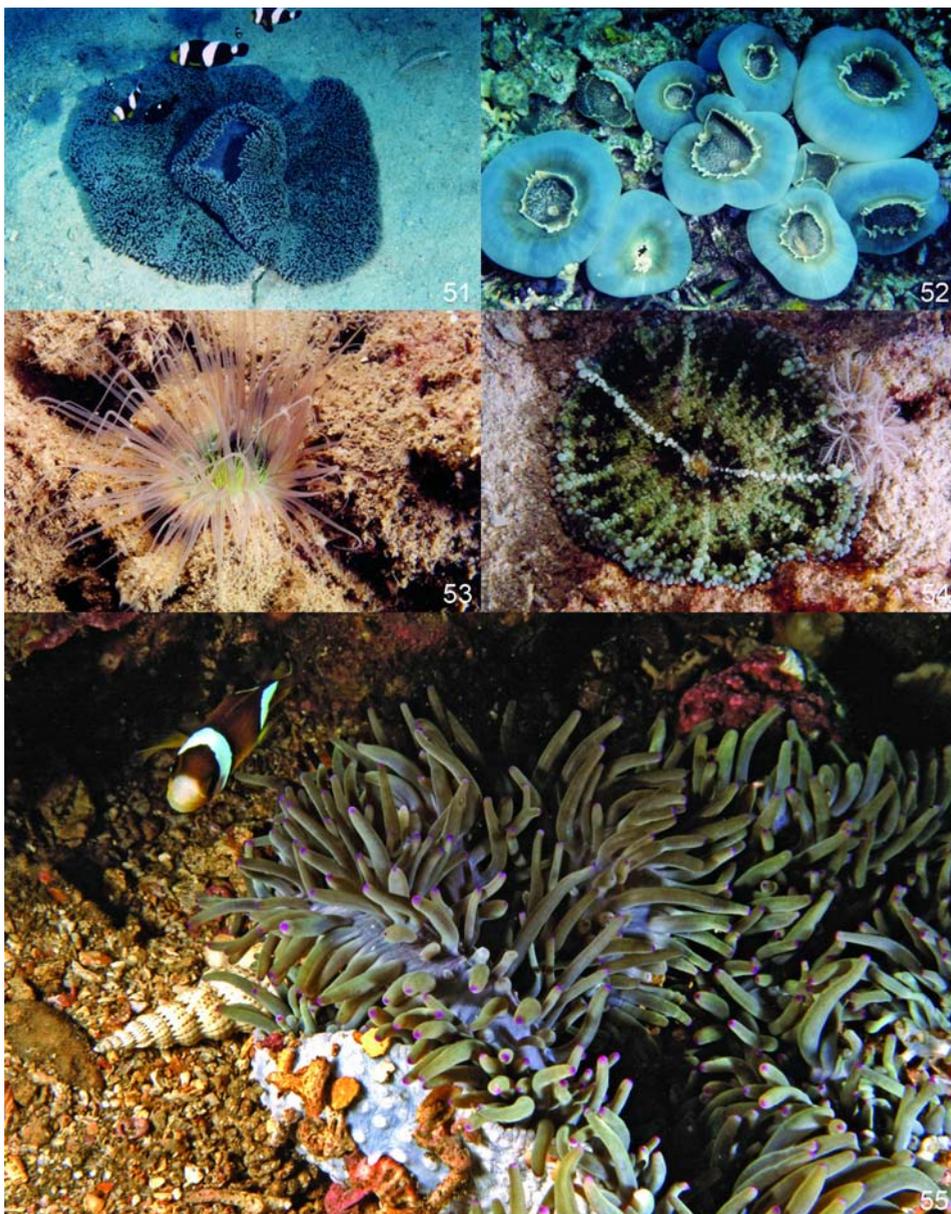
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REFERENCES

- AARTSEN, J.J. VAN, 1996. Nomenclatorial notes, 8. On *Turbo aculeatus* T. Brown, 1818 (Gastropoda, Prosobranchia, Epitoniidae). — *Basteria* 60: 3.
- ALBERGONI, A., FRANCHINI, S., FRANCHINI, D.A., & G. SARTORE, 1970. Note sul ritrovamento e sull'habitat di numerosi esemplari di *Opalia* (Dentiscala) *crenata* (Linneo), e di altre *Scalidae* nel mare di Almeria (Spagna). — *Conchiglie* 6(9-10): 119-127.
- ANKEL, W.E., 1937. Beobachtungen an Prosobranchiern der schwedischen westküste. — *Arkiv für zoologi* 30a(9): 1-28.
- ARNOLD, W.H., 1965. A glossary of a thousand-and-one terms used in conchology. — *The Veliger* 7(Supplement), 1-50.
- BELL, J.L., 1985. Larval growth and metamorphosis of a prosobranch gastropod associated with a solitary coral. — *Proceedings of the Fifth International Coral Reef Congress, Tahiti* 5: 159-164.
- BOSCH, H.F., 1965. A gastropod parasite of solitary corals in Hawaii. — *Pacific Science* 19: 267-268.
- BOURY, E.A. DE, 1909. Catalogue des sous-genres de *Scalidae*. — *Journal de Conchyliologie* 57: 255-258.
- BRATCHER, T., 1982. The *Fungia* coral: It's full of surprises. — *Hawaiian Shell News* 30(3): 3.
- BREYER, A., 1981. Observations on the reproduction, feeding and ecology of the wentletrap *Epitonium tinctum* (Gastropoda: Mesogastropoda). — Thesis, unpublished.
- COSSIGNANI, T. & V., 1998. Descrizione di una nuova specie di *Epitonium* Röding, 1798 (Gastropoda: Prosobranchia, Epitoniidae) dall'Australia. — *Malacologia Mostra Mondiale* 27: 38.
- DUNN, D.G. FAUTIN, 1981. The clownfish sea anemones: Stichodactylidae (Coelenterata: Actiniaria) and other sea anemones symbiotic with pomacentrid fishes. — *Transactions of the American Philosophical Society, New Series* 71(1): 3-115.
- DUSHANE, H., 1974. The Panamic-Galapagan Epitoniidae. — *The Veliger* 16, supplement: 1-84.
- DUSHANE, H., 1988a. Geographical distribution of some Epitoniidae (Mollusca: Gastropoda) associated with fungiid corals. — *The Nautilus* 102: 30-35.
- DUSHANE, H., 1988b. Hawaiian Epitoniidae. — *Hawaiian Shell News* 36(4): 6-7.
- DUSHANE, H., 1988c. Hawaiian Epitoniidae (continued). — *Hawaiian Shell News* 36(11): 7, 9.
- FAUTIN, D.G. & G.R. ALLEN, 1992. Field guide to the anemone fishes and their host sea anemones. — *Western Australian Museum*, 1-160.
- FRETTER, V., & A. GRAHAM, 1962. British prosobranch molluscs. — *The Ray Society, London, Great Britain*: 1-755.
- GITTENBERGER, A., GOUD, J., & E. GITTENBERGER, 2000. *Epitonium* (Gastropoda: Epitoniidae) associated with mushroom corals (Scleractinia: Fungiidae) from Sulawesi, Indonesia, with the description of four new species. — *The Nautilus* 114(1): 1-13.



Figs 51-55. Sea anemone species found at the Spermonde archipelago (continued). 51, *Stichodactyla haddoni* (Saville-Kent, 1893), found associated with *Epitonium* cf. *sandwichense* (RMNH 87760). 52, *Amplexidiscus fenestrafer* Dunn & Hamner, 1980. 53, *Cerianthus* sp. 54, *Discosoma* sp. 55, *Cirsotrema varicosum* (RMNH 87771, fig. 6) under *Heteractis crispa* including wentletrap egg capsules (lower left corner) and the clownfish *Amphiprion clarkii* (Bennett, 1830). Photographs: A. Gittenberger.

- GITTENBERGER, A., 2006. The evolutionary history of parasitic gastropods and their coral hosts in the Indo-Pacific. — PhD Thesis, Leiden University, The Netherlands.
- HABE, T., 1943. Observations on *Habea inazawai*, with special reference to its development. — *Venus* 13(1-4): 65-67.
- HADFIELD, M.G., 1976. Molluscs associated with living tropical corals. — *Micronesica* 12(1): 133-148.
- HARTOG, J.C. DEN, 1987. Observations on the wentletrap *Epitonium clathratulum* (Kanmacher, 1797) (Prosobranchia, Epitoniidae) and the sea anemone *Bunodosoma biscayensis* (Fischer, 1874) (Actinaria, Actiniidae). — *Basteria* 51(4-6): 95-108.
- HARTOG, J.C. DEN, OFWEGEN, L.P. VAN, & S. VAN DER SPOEL, 1997. Gastropods carrying actinians. — Proceedings of the Sixth International Conference on Coelenterate Biology. National Museum of Natural History, Leiden, The Netherlands I-XVIII, 1-542.
- HINDS, R.B., 1844. Descriptions of new species of *Scalaria* and *Murex*, from the collection of Sir Edward Belcher, C.B. — Proceedings of the Zoological Society 11: 124-129.
- HOCHBERG, F.G., 1971. Functional morphology and ultrastructure of the proboscis complex of *Epitonium tinctum* (Gastropoda: Ptenoglossa). — *Echo* (Western society of malacologists) 4: 22-23.
- HOEKSEMA, B.W., 1988. Mobility of free-living fungiid corals (Scleractinia), a dispersion mechanism and survival strategy in dynamic reef habitats. — Proceedings of the Sixth International Coral Reef Symposium, Townsville, Australia: 715-720.
- HOEKSEMA, B.W., 1989. Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). — *Zoologische Verhandelingen* 254: 1-295.
- HORI, S., & K. YANAGI, 2002. Sull'associazione tra *Cirsotrema varicosa* (Lamarck, 1822) (Gastropoda: Epitoniidae) e l'anemone *Radianthus crispus* (Ehrenberg, 1834) (Cnidaria: Anthozoa: Actiniaria). — *La Conchiglia* 303: 13-14.
- KAICHER, S.D., 1980. Card Catalogue of World-wide Shells: Epitoniidae I. - Pack 23.
- KAICHER, S.D., 1981. Card Catalogue of World-wide Shells: Epitoniidae II. - Pack 30.
- KAY, E.A., 1979. Hawaiian marine shells. Reef and shore fauna of Hawaii. Section 4: Mollusca. — Special publication 64(4). Bernice P. Bishop Museum, Honolulu, Hawaii: 1-653.
- KILBURN, R.N., & E. RIPPEY, 1982. Sea shells of Southern Africa. Johannesburg, South Africa: 1-249.
- KILBURN, R.N., 1985. The family Epitoniidae (Mollusca: Gastropoda) in southern Africa and Mozambique. — *Annals of the Natal Museum* 27: 239-337.
- KILBURN, R.N., 1994. Description of a remarkable new species of *Opalia* (Gastropoda: Epitoniidae) from the Philippines. — *Basteria* 58(1-2): 49-51.
- KOKSHOORN, B. & GOUD, J., 2007. One more poorly known *Globiscala* species. — *Basteria* 71(1-3): 75-76.
- KURODA, T., T. HABE & K. OYAMA, 1971. The sea shells of Sagami Bay. Collected by his Majesty the Emperor of Japan: i-xix, 1-741, pls 1-121, 1-489, 1-51. Tokyo.
- LAMARCK, [J.B.P.A. DE MONET DE], 1822. Histoire naturelle des animaux sans vertèbres, 6 (2): 1-232. Paris.
- LOCH, I., 1982. Queensland epitoniids. — *Australian Shell News* 39: 3-6.
- LOO, G.K.M., & L.M. CHOU, 1988. Corals of the genus *Fungia*. — *Nature Malaysiana* 13: 26-29.
- MASAHITO Y., KURODA, T., & T. HABE, 1971. in: KURODA, T., T. HABE & K. OYAMA, 1971. The sea shells of Sagami Bay. Collected by his Majesty the Emperor of Japan: 258. Tokyo.
- MERMOD, G., & E. BINDER, 1963. Les types de la collection Lamarck au muséum de Genève. Mollusques vivants V. — *Revue Suisse de Zoologie* 70: 127-172.
- MIENIS, H.K., 1994. *Calliactis polypus*: a new host of *Epitonium bullatum*. — *Epinet* 3(2): 5-6.
- NAKAYAMA, T., 1991. A new epitoniid species from the pacific coast of the Kii peninsula, Japan. — *The veliger* 34 (1): 88-90.
- NAKAYAMA, T., 2003. A review of Northwest Pacific epitoniids (Gastropoda: Epitoniidae). — *Monographs of Marine Mollusca* 6: 1-143.
- NYST, H., 1871. Tableau synoptique et synonymique des espèces vivantes et fossiles du genre *Scalaria* ..

- Annales de la Société Malacologique de Belgique 6: 77-147.
- OLIVERIO, M., 1986. Brief notes on the ecology of *Cirsotrema pumiceum* (Brocchi, 1814). — *La Conchiglia* 18(204-205): 3.
- OLIVERIO, M., TAVIANI, M., & R. CHEMELLO, 1997. A coral-associated epitoniid, new to the red sea (Prosobranchia, Ptenoglossa). — *Argonauta* 9(10-12): 3-10.
- OKUTANI, T. (ed.), 2000. Marine molluscs in Japan: . — Tokai University Press, Tokyo, Japan.
- PAGE, A.J. & R.C. WILLAN, 1988. Ontogenetic change in the radula of the gastropod *Epitonium billeana* (Prosobranchia: Epitoniidae). — *The Veliger* 30(3): 222-229.
- PEASE, W.H., 1867. Descriptions of sixty-five new species of marine Gastropoda, inhabiting Polynesia. — *American Journal of Conchology* 3: 271-297.
- PERRON, F., 1978. The habitat and feeding behaviour of the wentletrap *Epitonium greenlandicum*. — *Malacologia* 17(1): 63-72.
- PETERSON, C.H., & R. BLACK, 1986. Abundance patterns of infaunal sea anemones and their potential benthic prey in and outside seagrass patches on a western australian sand shelf. — *Bulletin of Marine Science* 38(3): 498-511.
- PILSBRY, H.A., 1921. Marine mollusks of Hawaii. xiv, xv. — *Proceedings of the Academy of Natural Sciences of Philadelphia* 72 (1921): 360-382.
- ROBERTSON, R., 1963. Wentletraps (Epitoniidae) feeding on sea anemones and corals. — *Proceedings of the Malacological Society, London* 35: 51-63.
- ROBERTSON, R., 1970. Review of the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods. — *Pacific Science* 24: 43-54.
- ROBERTSON, R., 1981. Protandry with only one sex change in an *Epitonium* (Ptenoglossa). — *The Nautilus* 95(4): 184-186.
- ROBERTSON, R., 1983a. Observations on the life history of the wentletrap *Epitonium echinaticostum* in the bahamas. — *The Nautilus* 97(3): 98-103.
- ROBERTSON, R., 1983b. Observations on the life history of the wentletrap *Epitonium albidum* in the west indies. — *American Malacological Bulletin* 1: 1-12.
- ROBERTSON, R., 1993. Two new tropical western atlantic species of *Epitonium*, with notes on similar global species and natural history. — *The Nautilus* 107(3): 81-93.
- SABELLI, B., & M. TAVIANI, 1984. Red sea record of a *Fungia*-associated Epitoniid. — *Bolletino Malacologico* 20(1-4): 91-94.
- SALO, S., 1977. Observations on feeding, chemoreception and toxins in two species of Epitonium. — *The Veliger* 20(2): 168-172.
- SHIMEK, R.L., 1986. A diet that stings; sea anemones as food for snails. — *Shells and Sea Life* 18(11): 173-175.
- SOWERBY, G.B. (II), 1844. Descriptions of new species of *Scalaria*, collected by Mr. H. Cuming, to be figured in the fourth part of *Thesaurus Conchyliorum*. — *Proceedings of the Zoological Society of London* 12: 10-31.
- SOWERBY, G.B. (II), 1847. Monograph of the genus *Scalaria*. — *Thesaurus conchyliorum or monographs of genera of shells* 1: 83-108.
- THORSON, G., 1957. Parasitism in the marine gastropod-family *Scalidae*. — *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening, København* 119: 55-58.
- WEIL, A., BROWN, L., & B. NEVILLE, 1999. The wentletrap book. Guide to the recent Epitoniidae of the world. Rome, Italy: 1-246.
- WOODWARD, A.J., 1987. On the rak. — *Shells and sealife* 19(9): 3-4.
- YAMASHIRO, H., 1990. A wentletrap *Epitonium bullatum* associated with a coral *Sandalolitha robusta*. — *Venus the Japanese Journal of Malacology* 49(4): 299-305.