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## **The evolutionary history of parasitic gastropods and their coral hosts in the Indo-Pacific**

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# 6

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# The wentletrap *Epitonium hartogi* spec. nov. (Gastropoda: Epitoniidae), associated with bubble coral species, *Plerogyra* spec. (Scleractinia: Euphyllidae), off Indonesia and Thailand

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Key words: parasitic snails; coral reefs; coral/mollusc associations; egg-capsules; veligers; Epitoniidae; *Epitonium*; larval development; radulae; jaws; Euphyllidae; *Plerogyra*; Indo-Pacific

## Abstract

This is the first record of an association between a wentletrap species (Gastropoda: Epitoniidae) and coral species of the Euphyllidae (Scleractinia), i.e. *Plerogyra simplex* and *P. diabolotus*. While describing *Epitonium hartogi* spec. nov., special attention is given to the ontogenetic development within the egg-capsules, the structure and microsculpture of the opercula, the radulae, and the microsculpture on the radular jaws. These characters proved to be at least partly diagnostic in the epitoniid species *Epitonium albidum*, *E. billeeanum*, *E. costulatum*, *E. hoeksemai*, *E. ingridae*, *E. lochi*, *E. millecostatum*, *E. pyramidalis*, *E. twilae*, *E. ulu* and *Nitidiscala tincta*. Spiculae-like crystals covering the epitoniid egg-capsules are described; such crystals are also present within the tentacles of the *Plerogyra* host.

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## Introduction

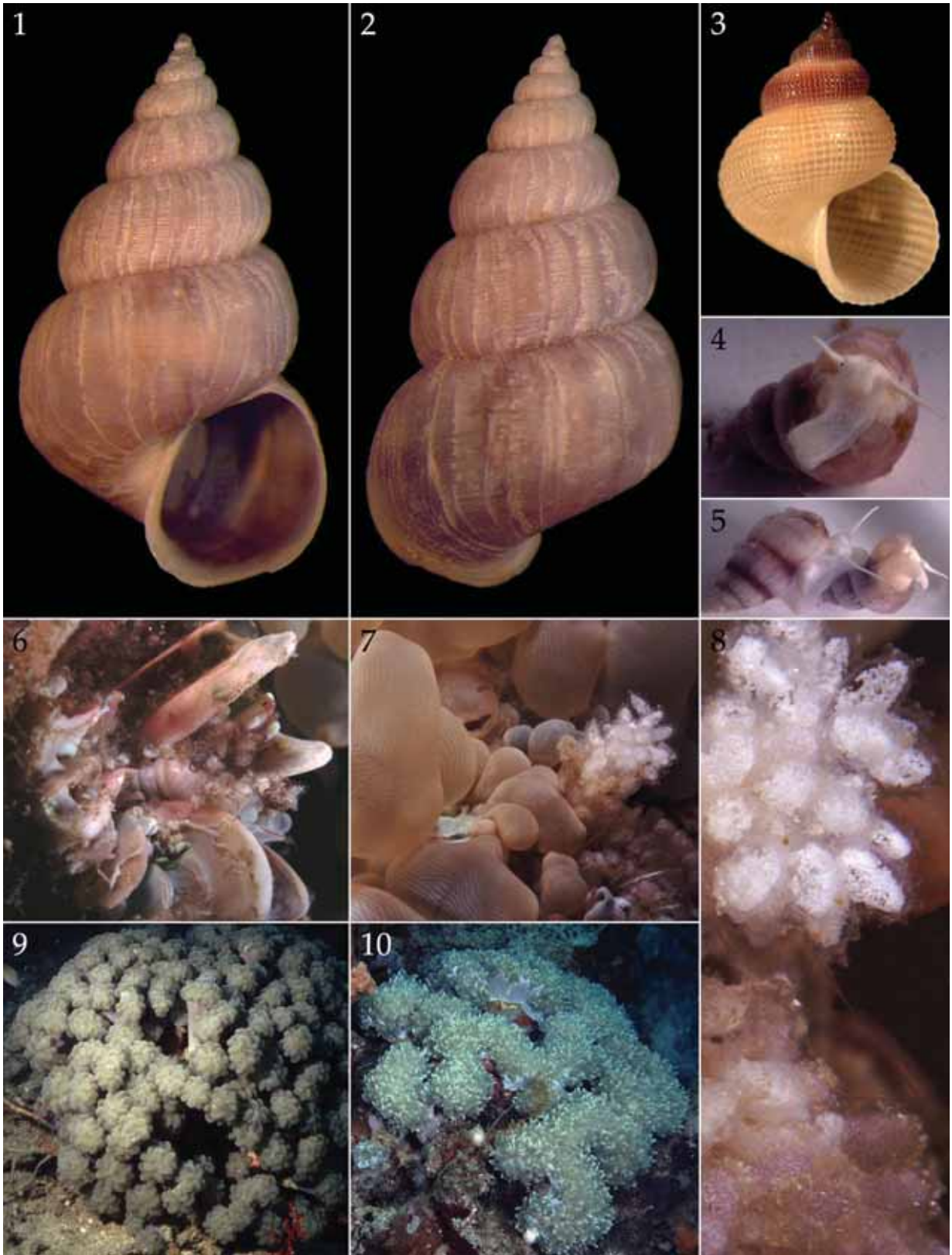
Most *Epitonium* species (>100) are found associated with sea anemones (Actiniaria). Less commonly, these snails are found with corals (Scleractinia). More specifically, seven epitoniid species are known to be hosted by coral species of the Fungiidae (Gittenberger et al., 2000; Bonfitto and Sabelli, 2000) and two by species of the Dendrophyllidae (Dushane and Bratcher, 1965; Bouchet and Warén, 1986).

The present article describes the first record of an epitoniid associated with corals of the Euphyllidae. A new *Epitonium* species was found associated with bubble corals of *Plerogyra simplex* Rehberg, 1892, and *P. diabolotus*, Ditlev, 2003. It is reported from off Makassar, Sulawesi, Indonesia and off Ko Phiphi Don island, Krabi, Thailand.

## Material and methods

Wentletraps were collected in 2001 at the coral reefs surrounding the islets Samalona, Kudingareng Keke and Bone Tambung, off Makassar, SW Sulawesi, Indonesia. One specimen, with egg-capsules, was collected off Ko Phiphi Don island, Krabi, Thailand. The identifications of the coral hosts were made on the basis of photographs by Dr. H. Ditlev and Dr. B.W. Hoeksema. In total, off Makassar, 4 colonies of *P. simplex* Rehberg, 1892, 8 colonies of *P. diabolotus* Ditlev, 2003, and 40 colonies of *P. sinuosa* (Dana, 1846), were searched for snails. The snails were conserved in 96% alcohol. Some egg-capsules were kept in an aquarium. Each day some of those were cut open in a drop of sea-water on a glass-slide, in such a way that the embryos and/or veligers were alive during the observations. While doing so, the larval developmental stages were studied through a microscope and photographed with a digital camera (Fujifilm MX-2700).

The number of specimens is indicated after the slash following the collection number. Only shells with a height of more than 4 mm have been measured. The number of specimens used (n) is mentioned



between brackets behind the values. Means are indicated between the extremes (minimum-mean-maximum). The morphology of the operculae, radulae, jaws, protoconchs, costae, spiral ribs, egg-capsules and the mucus threads, was studied with a SEM. The SEM was also used to study the sharp spiculae-like crystals that were found on the egg-capsules.

In the present article some morphological characters of the new species which are rarely mentioned in the epitoniid literature are compared with those of *E. albidum* (Orbigny, 1842), *E. costulatum* (Kiener, 1838), *E. hoeksemai* Gittenberger and Goud, 2000, *E. ingridae* Gittenberger and Goud, 2000, *E. lochi* Gittenberger and Goud, 2000, *E. millecostatum* (Pease, 1860), *E. pyramidalis* (Sowerby, 1844), *E. twilae* Gittenberger and Goud, 2000, *E. ulu* Pilsbry, 1921, and *Nitidiscala tincta* (Carpenter, 1865). The conchologically similar “golden wentletrap”, i.e. *Epitonium billeeaanum* (Dushane and Bratcher, 1965) (fig. 3), which occurs associated with corals of the family Dendrophylliidae, is compared in more detail.

Abbreviations: RMNH, National Museum of Natural History, Leiden (formerly Rijksmuseum van Natuurlijke Historie).

## Systematics

Family Epitoniidae Berry, 1910

Genus *Epitonium* Röding, 1798

### *Epitonium hartogi* spec. nov.

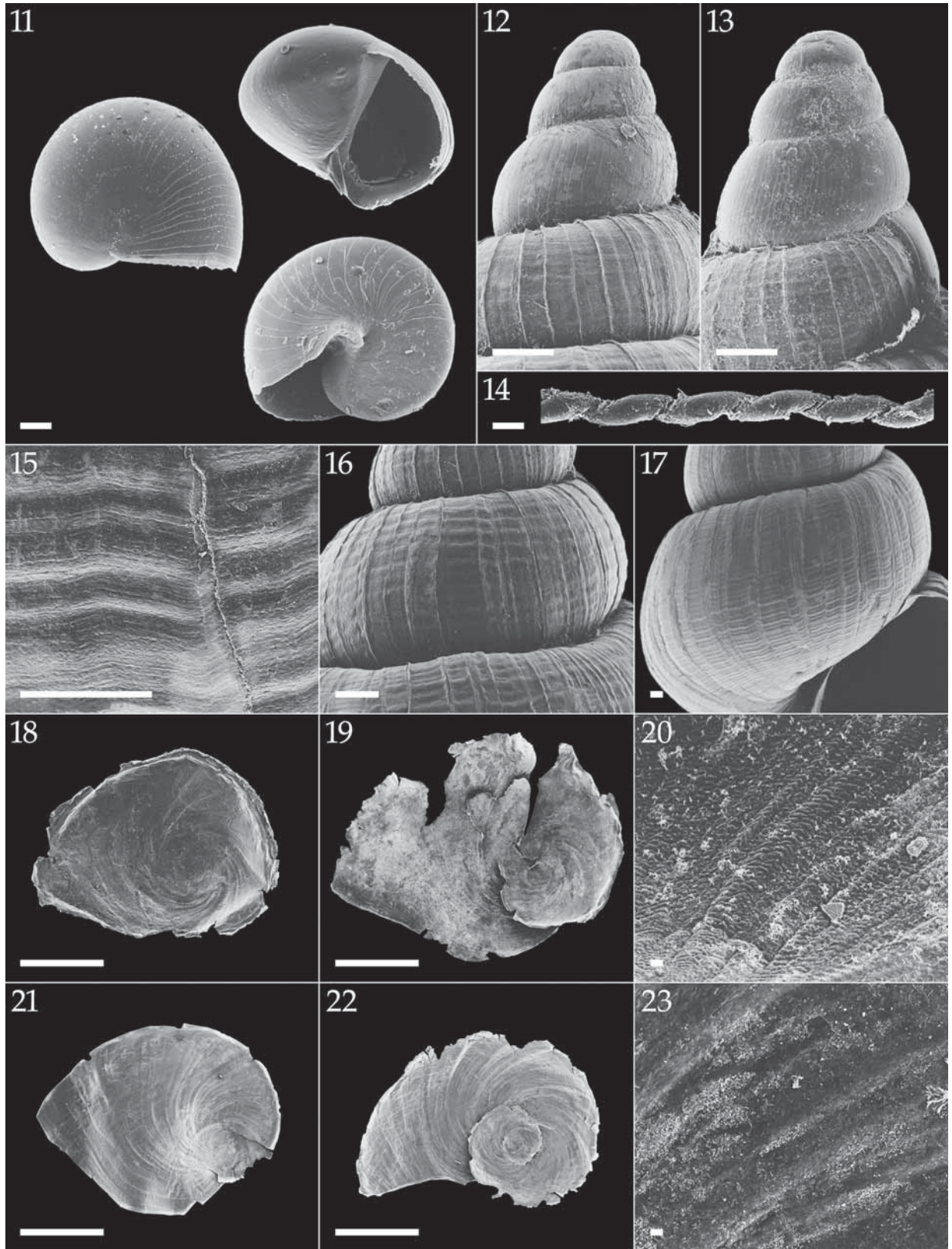
Material: Indonesia, Sulawesi, off Makassar. Holotype, snail (RMNH 94924) with egg-capsules (RMNH 94934): W Samalona Island (05°07'31"S/

119°20'31"E), hosted by *Plerogyra simplex*. Paratypes: type locality, with the holotype, snail (RMNH 94925/1); type locality, also hosted by *P. simplex*, 4 snails (RMNH 94926/1, RMNH 94927/3), snails with egg-capsules (RMNH 94928/3); type locality, hosted by *Plerogyra diabolotus*, 9 snails with egg-capsules (RMNH 94932/2, RMNH 94933/7); W Kudingareng Keke (05°06'09"S / 119°17'09"E), hosted by *P. diabolotus*, 4 snails with egg-capsules (RMNH 94930/1, RMNH 94931/3); W Bone Tambung Island (05°02'05"S / 119°16'16"E), 1 snail with egg-capsules (RMNH 94929/1).

Thailand, Krabi, NW Ko Phiphi Don, La Nah Bay (07°46'01"N/98°45'42"E), paratype, snail with egg-capsules (RMNH 95989/1), hosted by *P. diabolotus*.

Shell: Shell (figs 1, 2) very fragile, elongate-conical, whitish but coloured purple by the mucus (fig. 5) of its host coral (which can be removed). The inside of the shell, except for the apertural border in front of the operculum in situ, has an irregularly purplish colour (which cannot be removed), especially when wetted (figs 4-6). The holotype measures 7.0 x 4.1 mm. One damaged specimen reaches at least 8.2 mm in height. Height/width ratio 1.4-1.6-1.8 (n = 13). Apart from the smooth apical part, the protoconch is sculptured with evenly spaced, very fine, incised, radial lines, c. 14 per 0.2 mm on the third whorl (fig. 12). Protoconch as in *Epitonium costulatum*, *E. ingridae*, *E. lochi*, and *E. ulu* s. lat., all with c. 15 lines per 0.2 mm (Gittenberger et al., 2000); differing from *E. billeeaanum* with c. 21 lines per 0.2 mm (fig. 13). Protoconch 1 + 2 with 3½ whorls (fig. 12). Protoconch 1 consisting of c. ½ whorl (fig. 11). With up to at least 6 (damaged specimen) teleoconch whorls, separated by a deep suture. Teleoconch sculptured with orthocone, usually not continuous, lamellar, low costae without any particular notches or processes, barely touching the preceding whorl, and less prominent, low spiral ribs, covered by numerous very fine, incised spiral lines (fig. 15). One specimen showed continuous spiral ribs more prominent than the costae. Second teleoconch whorl (fig. 16) with 20-22.8-26 (n = 23) rather irregularly spaced costae, and 9-10.3-12 (n = 22) evenly spaced, mostly continuous, spiral ribs. Fifth teleoconch whorl (fig. 17) with 32-37.3-40 (n = 8) very unevenly spaced, irregular, and often split costae, and 29-34.3-40 (n = 12) somewhat unevenly spaced spiral ribs,

*Figs 1-10.* Material from off Makassar, SW Sulawesi, Indonesia. Figs 1, 2, 4, 5-8, *Epitonium hartogi* spec. nov. 1, 2, holotype (height 7.0 mm); 4, head with proboscis (shell height 6.9 mm); 5, crawling snails partly covered by purple mucus from the coral host (largest shell height 6.9 mm); 6, snail between retracted tentacles within polyp (shell height 6.9 mm); 7, egg-capsules on polyp (capsule length 1.6 mm); 8, egg-capsules with white undifferentiated eggs (upper) and ones with fully grown veligers (lower) appearing purple because of pigmented mantle organs (capsule length 1.6 mm). Fig. 3, *Epitonium billeeaanum* (height 6.0 mm). Fig. 9, *Plerogyra simplex* (colony diameter c. 35 cm). Fig. 10, *Plerogyra diabolotus* (colony diameter c. 30 cm). Photos: A. Gittenberger.



mostly not continuous, ending on top or in front of the costae. Apertural height/shell height ratio 0.34-0.38-0.43 (n = 10). Umbilicus narrow.

Operculum (n = 4): Operculum paucispiral. The coils either interconnected (two of four) to form the shield-like operculum most common in prosobranchs (fig. 18), or scalaroid (loosely) coiled (two of four) (fig. 19), as is also found in e.g. some hydrobiids (Solem, 1974: 129, 130). This dimorphism is also present in *E. billeanum* (figs 21, 22). On the outside there are numerous, very fine but prominent, wavy line segments, running at about 80° in between irregularly spaced growth-lines (fig. 20). Bonfitto and Sabelli (2000) illustrate a similar pattern in *Epitonium oliverioi*, where the growth-lines are regularly spaced. In *E. billeanum* (n = 4) such wavy lines are lacking (fig. 23). Although the microsculpture of the operculum can easily be studied by SEM photography, and seems at least to be specific for the species mentioned above, it is hardly ever described in the literature.

Anatomy: The soft parts of the animal are whitish, with small, dark eye-spots (figs 4, 5). There is a pattern of white, non-transparent dots on the transparent whitish proboscis (fig. 4). It was concluded that the adult snails have a pigmented mantle organ, because they released purplish dye when they were collected. Because the epitoniids were conserved in alcohol 96%, the tissue had hardened which hampered dissection.

Radulae: Epitoniids have a ptenoglossan radula without a rachidian (Graham, 1965; Boss, 1982; Bandel, 1984; Page and Willan, 1988). In *E. billeanum* the radula changes when a male grows and becomes a female (Page and Willan, 1988). It is un-

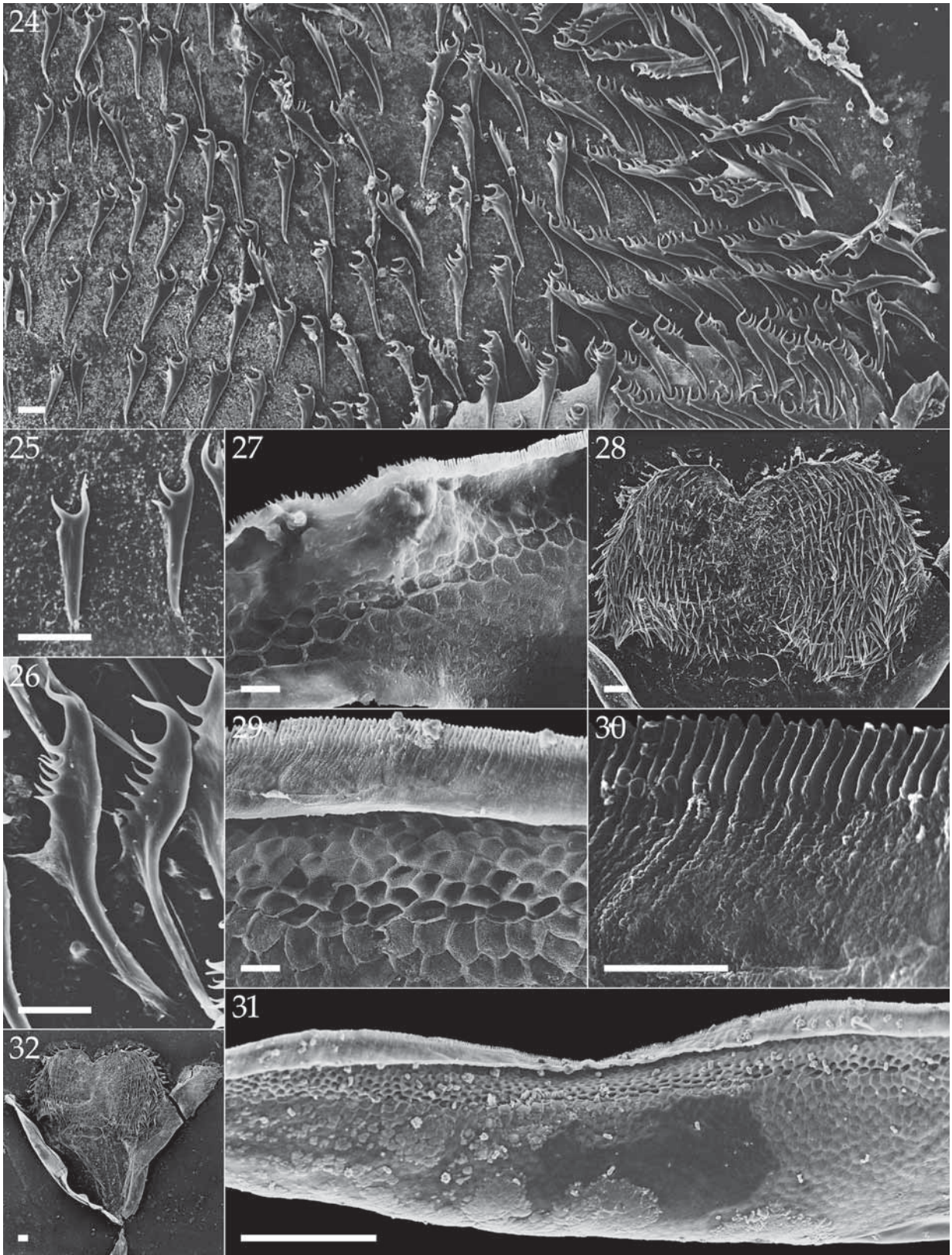
known whether this occurs more generally in epitoniids. The three radulae that were investigated are from relatively large specimens, with shell heights of 5.4, 6.9 and 7.4 mm, respectively. These snails were found within a cluster of egg-capsules, without any other large wentletraps nearby, suggesting that they are females. Two of the radulae were damaged while preparing them, making it impossible to accurately count the number of teeth in a row. The radula that was not damaged is described here. It belongs to the specimen with a shell height of 5.4 mm. In half a row (fig. 24) 25 teeth are present, which cannot be distinguished as laterals and marginals, because they change in size and number of cusps gradually, from the centre to the margin of the radula. The innermost teeth (fig. 25, left one) measure about 22 µm in length and the penultimate ones (fig. 26, right one) 50 µm. The most marginal teeth have a reduced length of c. 40 µm. The teeth have an acute primary cusp at the top and 1 to 6 equally sharp, shorter, secondary ones somewhat lower along the blade. In half a row the innermost tooth has one secondary cusp, followed by four teeth with two, seven with three, seven with four, four with five, one tooth with six and the ultimate tooth with two secondary cusps. The three radulae that were investigated resembled each other closely, although the numbers of teeth with a certain number of secondary cusps slightly varied (one more or less). As a malformation, some teeth are split, having a double number of cusps (fig. 26, left one). For nearly 2/3 of its length each tooth is attached to the radular plate, i.e. up to just before the lowest cusp (fig. 26).

In *E. billeanum* (figs 28, 32) the morphology of the radular teeth is quite different. Especially the size difference between the inner teeth (c. 30 µm long) and the penultimate teeth (about 150 µm long) is apparent. In general, there are fewer cusps on a tooth as well.

Jaws: Epitoniid snails have jaws, flanking the radula, as is shown in fig. 32 (*E. billeanum*). Because the jaws on the SEM photographs (figs 27, 29-32) are dried, their actual sizes in situ will be somewhat larger.

The dried jaw of *E. hartogi* measures about 525 x 115 µm. The edge of the side where the jaw is attached to the radular plate is relatively smooth. On the other side the edge is provided with about 13 per

*Figs 11-23. Material from off Makassar, SW Sulawesi, Indonesia. Figs 11, 12, 14-20, Epitonium hartogi. 11, protoconch 1, i.e. hatching veliger shell; 12, protoconch; 14, twisted mucus thread; 15, spiral ribs and lines; 16, second teleoconch whorl; 17, fifth teleoconch whorl; 18, operculum, interconnected coils; 19, operculum, scalaroid; 20, operculum, microsculpture. Figs 13, 21-23, Epitonium billeanum. 13, protoconch; 21, operculum, interconnected coils; 22, operculum, scalaroid; 23, operculum, microsculpture. Scale: 20, 23 = 10 µm; 12-13, 15-17 = 100 µm; 11, 14 = 20 µm; 18, 19, 21, 22 = 1 mm. SEM photos: J. Goud.*



10  $\mu\text{m}$ , 4  $\mu\text{m}$  long, sharp tooth-like processes (fig. 27). The jaw surface is smooth to slightly granulated on the inside, facing towards the radula. On the outside, three vaguely delimited zones parallel to the edge can be distinguished. The denticulated edge is followed by a zone, c. 20  $\mu\text{m}$  broad, with a smooth surface, a second zone, c. 10  $\mu\text{m}$  broad, with a pattern of erect edges forming about two rows of irregular penta- or hexagonals, and a third zone, where the irregular penta- or hexagonals gradually become obsolete towards the smooth edge. The third zone is characterized by the presence of small perforations.

In *E. billeeatum* the jaws look quite different. In that species, a jaw (figs 29-32) has about 8 per 10  $\mu\text{m}$ , 6  $\mu\text{m}$  long, lamellar sharp processes on a granulated edge, which is c. 19  $\mu\text{m}$  broad (fig. 30). There is an adjoining first zone with three to four rows of irregular penta- or hexagonals on a finely perforated surface, a second zone of 1 to 2 rows of irregular, deepened, penta- or hexagonals on a slightly granulated surface, and a third zone in which the penta- or hexagonals gradually become obsolete on a surface with perforations, slightly larger than the ones in the first zone (figs 29, 31). The structure of the jaws is described here in considerable detail. Since only a single jaw or pair of jaws could be studied for both species, the amount of intraspecific variation remains unknown. It may be hypothesized that the conspicuous differences in jaw structure observed here, refer at least partly to species level variation. This is also supported by the figure of the marginal processes on the jaw of the epitoniid *Nitidiscala tincta* in Collin (2000), which do not resemble those in *E. hartogi* and *E. billeeatum*.

In epitoniids, the jaws probably function as attachment surfaces for muscles, aiding in keeping the esophagus open for the reception of food. Therefore, Clench and Turner (1952: 353) argue that they should be referred to as “esophageal plates”.

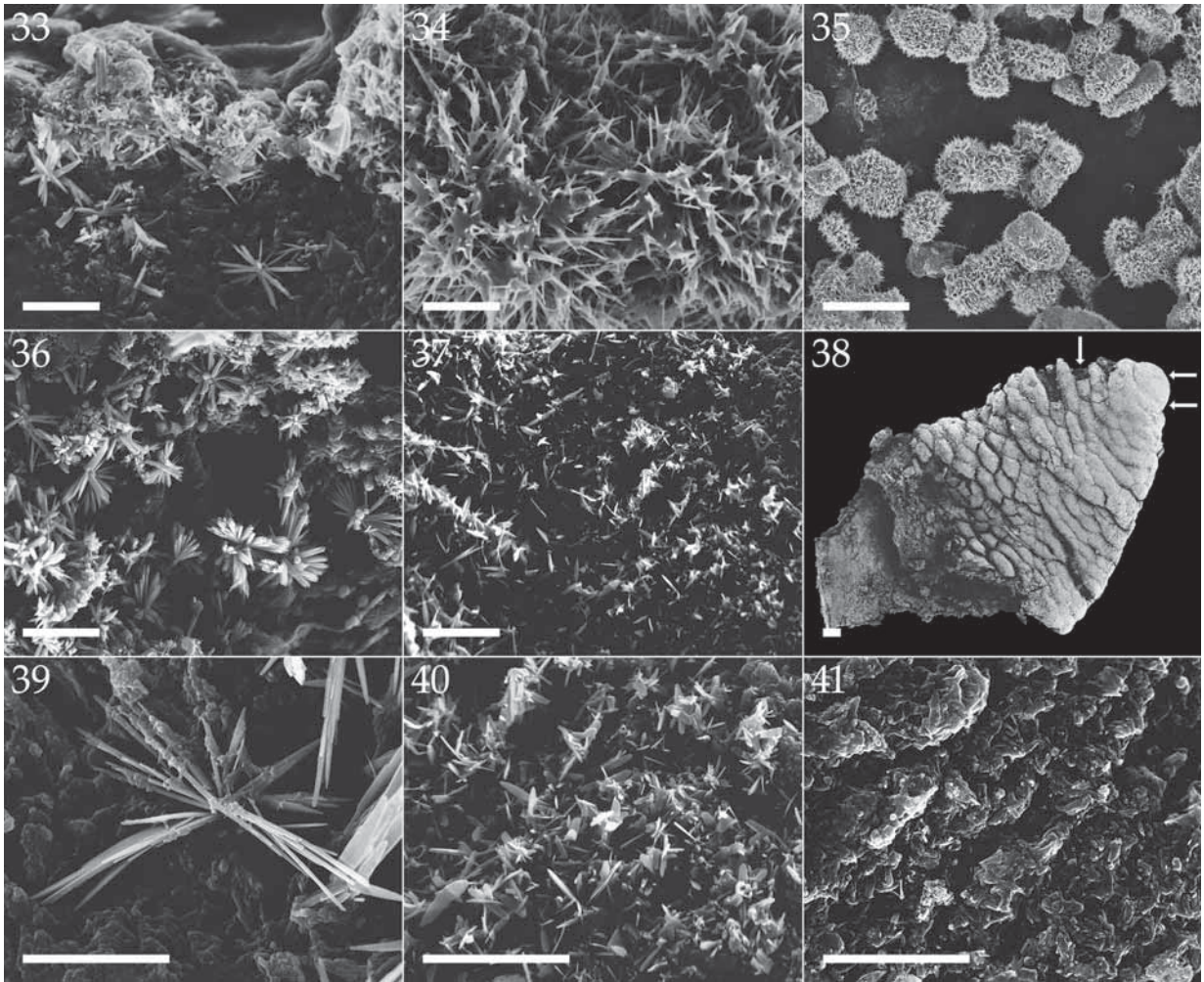
*Figs 24-32. Material from off Makassar, SW Sulawesi, Indonesia. Figs 24-27, Epitonium hartogi. 24, half a row of radular teeth; 25, inner tooth (left one); 26, penultimate tooth with six secondary cusps (right one), tooth with split cusps (left one); 27, detail outside jaw. Figs 28-32, Epitonium billeeatum. 28, rows of radular teeth; 29, detail outside jaw; 30, lamellar processes at edge of jaw; 31, overview outside jaw; 32, radular teeth and laws. Scale: 23-27, 29, 30 = 10  $\mu\text{m}$ ; 28, 31, 32 = 100  $\mu\text{m}$ . SEM photos: J. Goud.*

**Egg-capsules:** The ovoid egg-capsules (figs 7, 8), with conspicuous protuberances, are 1.55-1.56-1.57 mm long and 1.12-1.19-1.25 mm broad ( $n = 4$ ). They are interconnected along a twisted mucus thread (fig. 14) and contain 230-328-415 ( $n = 6$ ) eggs each. The uncleaved eggs are 39-40-41  $\mu\text{m}$  in diameter ( $n = 20$ ).

The wall of an egg-capsule is covered with small spiculae-like crystals (fig. 33) and small grains (figs 34, 35), apparently consisting of a mixture of such crystals. When a tentacle (fig. 38) of the host coral was dried and its surface and inside (holes were made with a needle) studied with a SEM, very similar crystals were seen. On top of a tentacle (figs 37, 40) crystals are seen which are much smaller than the ones of the egg-capsules. Just underneath the top (fig. 41) no such crystals were observed on the outside. Inside the tentacle, in particular near the top, many crystals were present with the same size as the ones on the egg-capsules (figs 36, 39). How these crystals can be present both inside tentacles of the coral and on the outside of the egg-capsule of the snail is unclear. The fact that the wentletraps eat coral tissue is probably relevant here.

“The crystals appear to be aragonitic and extracellular. They seem to be the result of a physico-chemical process in which crystal deposition occurs spontaneously in an enriched calcium environment with sufficient carbonate ions available. Using a TEM, this process, which is not necessarily biologically-regulated, was also observed for other coral species” (Hayes, personal communication; see also Hayes and Goreau, 1977).

**Veliger growth within the egg-capsules:** In *Epitonium hartogi*, all larvae within a single egg-capsule develop more or less synchronously, as in other Epitoniidae studied (Collin, 2000; A. Gittenberger, unpublished data). By opening the egg-capsules along a mucus thread, the larvae were found ordered by developmental stage. The duration of each of these stages could not be studied, but it was observed that undifferentiated eggs develop into hatchlings in about 5 days, in a sea-water aquarium under laboratory conditions. In two cases, mucus threads were found with many egg-capsules, together showing the entire developmental trajectory, i.e. with undifferentiated eggs in capsules on one end, and empty capsules on the other end of the thread, where the veligers had



Figs 33-41. Material from off Makassar, SW Sulawesi, Indonesia. Fig. 33, egg-capsule wall, *Epitonium hartogi*. Figs 33, 34 grains consisting of crystals, from egg-capsule wall, *Epitonium hartogi*. 34, detail; 35, overview. Figs 36-41, *Pterogyra simplex*. 36, 39, crystals inside tentacle; 37, 40, crystals on surface tentacle top; 38, overview tentacle, arrows indicating location of detailed figs 36, 37, 39-41, vertical one: figs 36, 39, horizontal ones: figs 37, 40 (upper) and fig. 41 (lower); 41, surface just underneath tentacle top (without crystals). Scale: 33, 34, 36, 37, 39-41 = 10  $\mu$ m; 35, 38 = 100  $\mu$ m. SEM photos: A. Gittenberger and J. Goud.

apparently hatched already; see fig. 8 for one of these cases.

The early larval developmental stages resemble those described for the epitoniid species *Nitidiscala tincta* by Collin (2000) and *Epitonium albidum* by Robertson (1983, 1994). The descriptions in this paper are based on a total of 456 photographs of the larvae. Because most organs are minute and translucent at first, they can easily be overlooked and, therefore, their real order of development might slightly differ from what is described here. A zygote first goes through three synchronous cleavages (fig. 42a),

followed by many asynchronous ones, resulting in a round blastula that changes by epiboly into a gastrula that actively swims around, using minor cilia on an “early” velum (fig. 42b). After becoming slightly oval, the pigmented mantle organ begins to form, in order of recognizable development followed by, the foot, the shell (fig. 42c), the operculum, the visceral muscle, the digestive gland, the velar lobes, the statocysts, the eyes (fig. 42d), the larval heart, the columellar muscle, the stomach and finally the right cephalic tentacle with small sensory cilia on top (fig. 42e, h). Before the veliger hatches, the proto-

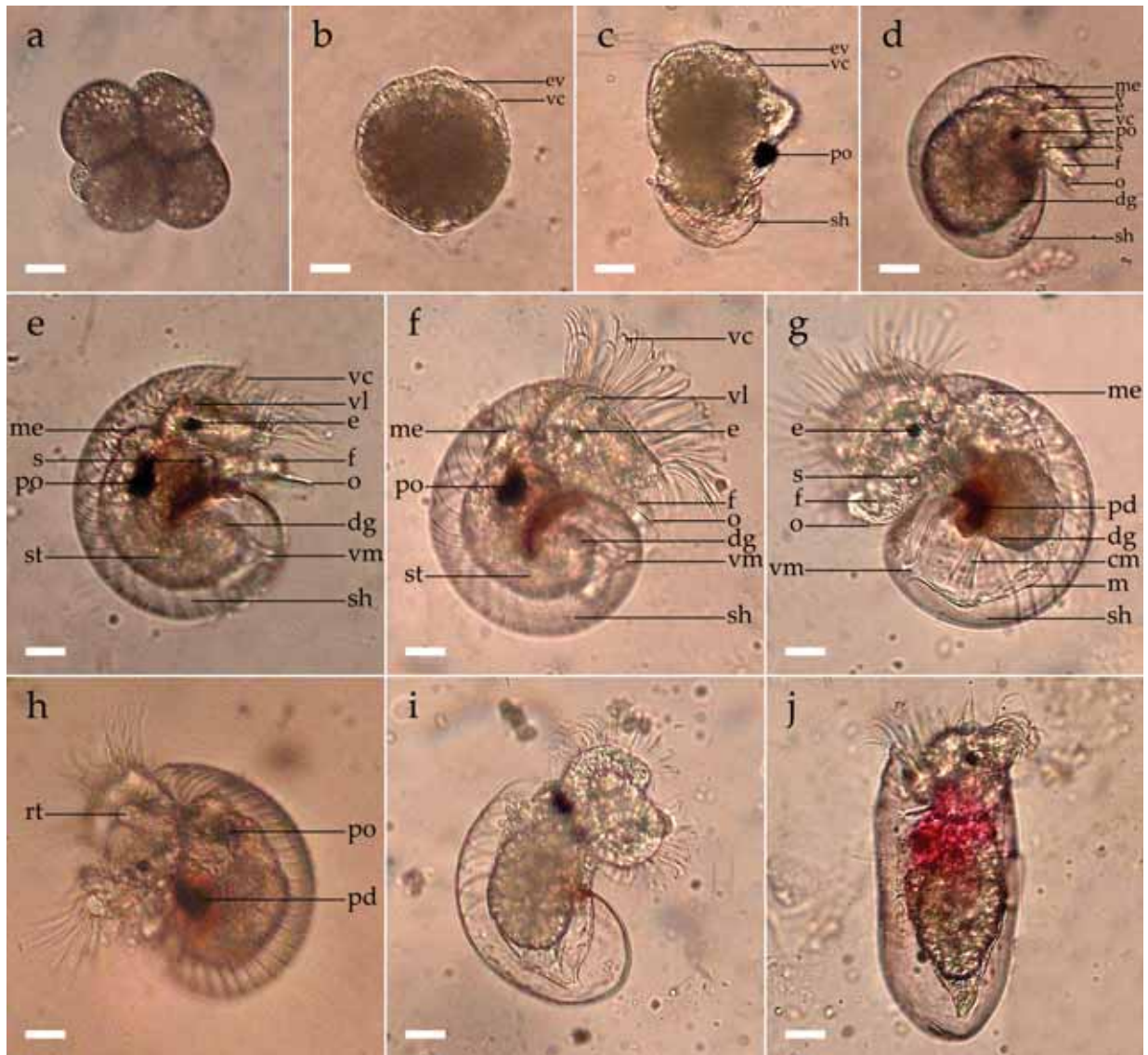


Fig. 42. Material from off Makassar, SW Sulawesi, Indonesia. Veliger development of *Epitonium hartogi* spec. nov. a, 3rd cleavage of cells; b, gastrula; c, first shell growth, black dot is purple dye excreted by the here invisible small pigmented mantle organ; d, early veliger, right lateral view; e, later veliger, right lateral view; f, hatched veliger, right lateral view; g, hatched veliger, left lateral view; h, hatched veliger with right tentacle, left lateral/dorsal view; i, malformed veliger, ventral view; j, malformed veliger, ventral view. Scale = 20  $\mu$ m. Abbreviations (mainly after Robertson, 1983): cm, columellar muscle; dg, digestive gland; e, eye; ev, early velum; f, foot; m, mantle; me, mantle edge; o, operculum; pd, cavity with purple dye; po, pigmented mantle organ; rt, right tentacle; sh, shell; s, statocyst; st, stomach; v, velar lobe; vc, velar cilia; vm, visceral muscle (?). Photos: A. Gittenberger.

conch shell, the velar lobes and cilia will grow little more (fig. 42f, g). Its left tentacle becomes visible c. one day after hatching. Asymmetric tentacle growth was also found for the “coral-associated” wentletraps *Epitonium billeeanum*, *E. costulatum*, *E. hoeksemai*, *E. ingridae*, *E. ulu* Pilsbry, 1921 (A. Gittenberger,

unpublished data) and *E. twilae* (fig. 43a), and for some wentletrap species associated with sea-anemones, i.e. *E. albidum* (see Robertson, 1983, 1994), *E. millecostatum* (see Robertson, 1980), *E. pyramidalis* (fig. 43b, c) and *Nitidiscala tincta* (see Collin, 2000). This asymmetric growth seems to be characteristic for

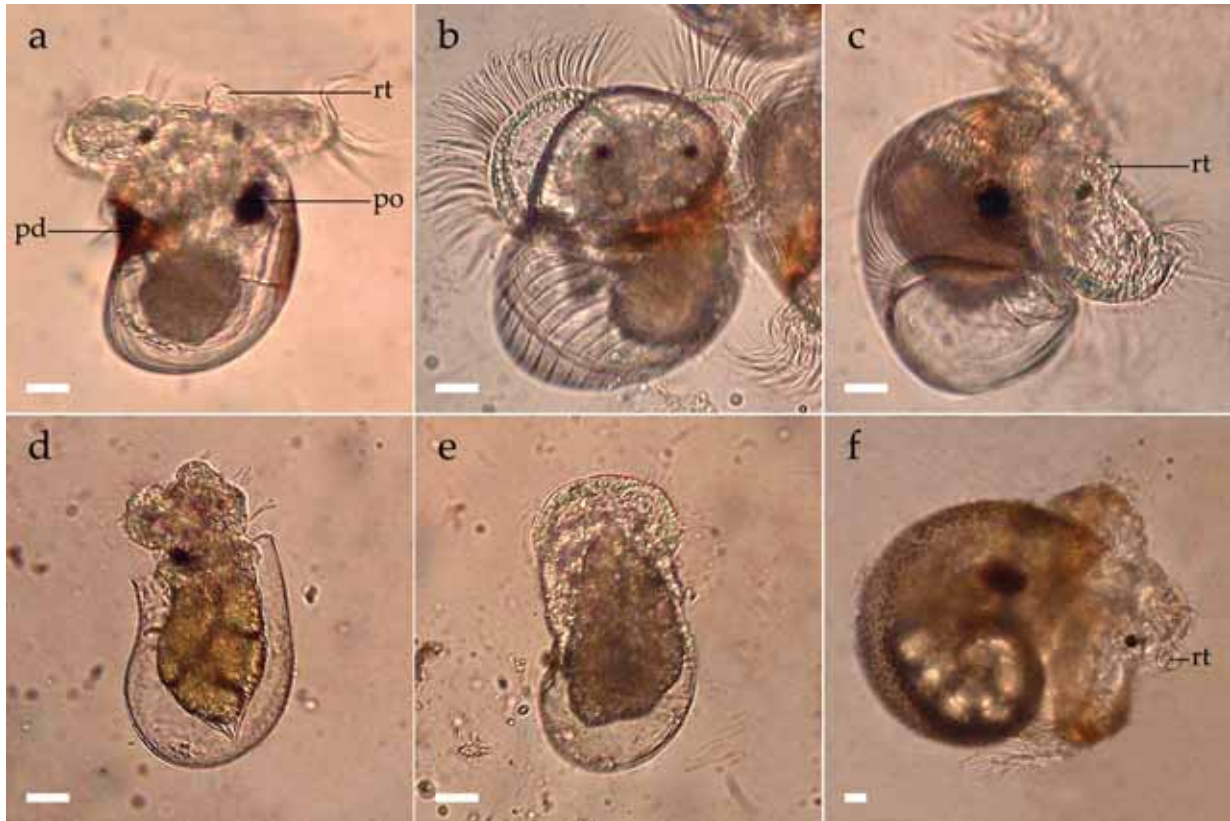


Figure 43. Material from off Makassar, SW Sulawesi, Indonesia. Prosobranch veligers. a, hatching veliger of *Epitonium twilae*, dorsal view; b, c, hatching veliger of *Epitonium pyramidalis*, ventral view (b), lateral/dorsal view (c); d, malformed veliger of *Epitonium billeeanum*, ventral view; e, malformed veliger of *Epitonium costulatum*, dorsal view; f, hatching veliger of *Leptoconchus exopolitus*, right lateral/dorsal view. Scale = 20  $\mu\text{m}$ . Abbreviations: pd, cavity with purple dye; po, pigmented mantle organ; rt, right tentacle. Photos: A. Gittenberger.

epitoniid veligers in general. It was also present in the larvae of a *Leptoconchus exopolitus* Shikama, 1963 (Coralliophilidae) specimen collected off Makassar, SW Sulawesi, Indonesia by the author (fig. 43f), and it was described for *Concholepas concholepas* (Bruguière, 1789)(Muricidae) by DiSalvo (1988), and for *Thais haemastoma* (Linnaeus, 1767) (Muricidae) by D'Asaro (1966). Asymmetric tentacle growth might even be a character common to prosobranch veligers in general, as was postulated by D'Asaro (1966).

The developmental stage, at which an epitoniid veliger hatches, can differ between species. The veligers of *E. pyramidalis*, another sea-anemone associate, hatch from their egg-capsules with 2 tentacles, the left one of which is the smallest, further developed organs and a protoconch consisting of

about 1 whorl (fig. 43b, c).

About one percent of the c. 1200 veligers of *Epitonium hartogi* studied has almost uncoiled shells ( $n = 12$ )(fig. 42i, j). Such specimens can survive at least until hatching. Similar malformations were found in *E. billeeanum* (fig. 43d) and *E. costulatum* (fig. 43e), collected off SW Sulawesi.

Habitat: *Epitonium hartogi* was recorded at 9-18 m depth, associated with bubble corals (*Plerogyra* spp.). The specimen from Thailand was found on *P. diabolotus*. Off Makassar, the wentletraps were found on all four colonies of *P. simplex* (fig. 9) that were investigated and five of eight colonies of *P. diabolotus* (fig. 10). None of the 40 colonies of *P. sinuosa*, by far the most common *Plerogyra* species present off Makassar, was found with epitoniid parasites. Most of the

wentletraps were completely submerged within the mouth cavity or in between the septae of a polyp (fig. 6). Their presence is indicated by egg-capsules laid on the coral polyp or by some “bubble-tentacles” that can be recognised as damaged (fig. 7). However, it is not unlikely that many specimens also remain within completely healthy looking polyps. After poking the bubbles until they retracted or by breaking away a bit of coral skeleton, the snails were discovered. Only the first specimen ever recorded was not hidden, but crawled over the coral stem of a *P. simplex* colony.

Etymology: This species is named after Jacobus Cornelis den Hartog, former curator of Coelenterata et al., National Museum of Natural History, who died in October 2000.

### Acknowledgements

I am grateful to Dr. H. Ditlev (Aarhus, Denmark) and Dr. B.W. Hoeksema (Leiden, The Netherlands) for checking the identification of the host coral *Plerogyra* species and to Dr. R.L. Hayes (Washington, USA) for his information about the crystals. Dr. Claude Massin (Brussels, Belgium) is thanked for his help identifying *Leptoconchus exopolitus*. I would also like to thank Dr. E. Gittenberger (Leiden, The Netherlands) for critically discussing the manuscript, Dr. R. Robertson (Philadelphia, USA), for reviewing it, J. Goud (Leiden, The Netherlands), for making SEM photographs, and Dr. Lisa-Ann Gershwin (Berkeley, USA) for her advice on photographing with a microscope and digital camera. Dr. A. Noor (Makassar, Indonesia) is thanked for his help concerning the permits and facilities enabling the research off Makassar, Indonesia. This study was supported by WOTRO (grant nr. W 82-249).

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